PROCEEDINGS, XIII INTERNATIONAL ORNITHOLOGICAL CONGRESS

Ithaca 17-24 June 1962

VOLUME II

Published by
THE AMERICAN ORNITHOLOGISTS' UNION
ROBERT J. NEWMAN, Treasurer
Museum of Zoology, Louisiana State University
Baton Rouge, Louisiana
1963
The Nesting Times of Finnish Birds

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In 1954, the present author started to collect statistical data about the nesting habits of Finnish birds. The study has been sponsored by the Finnish Society of Sciences. In the present paper, the nesting times of passerine birds are dealt with. Three sources of information have been used:

1) Nest cards, similar to the English ones (see Campbell, 1960). The total number of nest cards concerning passerine birds that I examined was 13,970. Of course, not all cards are as complete as one would wish. If one knows the incubation and nestling times of a species, however, the start of egg laying can often be calculated with some accuracy, even from cards that do not contain any observations during the laying period. As a rule, I have only made use of cards in which the date of the first egg can be calculated with a probable error of less than 5 days. This means that the cards have to contain observations on the status of the nest on at least two different occasions.

2) Simple cards for recording data from the bird-ringers' lists which are dispatched to the Zoological Museum of the University, Helsinki. The ringers are requested to mark, in the lists, the young belonging to the same brood. Thus, one gets information on brood size at the date of ringing but not on the age of the young birds at this time. The number of ringing cards reviewed in this study was 33,559.

3) Cards for recording data from published or other public sources. The Finnish ornithological literature (including the more important scientific journals and single papers, but not the data scattered in the nonscientific literature), the archives of Palmén at the Zoological Museum, Helsinki, and the egg collection of that museum were used as sources. In all, 11,676 “literature cards” were obtained. The value of a great many data in the literature is lessened by the fact that the authors did not give any clue as to the status of the clutch, whether incubated or not, and even whether complete or not.

The famous American author Samuel Clemens, better known as Mark Twain, used to say that there are three grades of lie: lie, damned lie, and statistics. One may raise the question of where these cards fit. In Finland, schools do not close until the last day of May, and the universities only a little earlier. It may, therefore, be suspected that clutches from June-July are overrepresented in the material. The English ornithologists, on the contrary, seem to be afraid that late broods are neglected, because they are scarce, and bird enthusiasts may have therefore lost their interest in searching for them.

The best way to verify the reliability of the cards is to determine whether

or not the different methods give consistent results. One may choose one of the commonest birds, the Great Tit (*Parus major*), and compare the yearly variations of its egg laying as calculated from the nest cards and from ringing cards. As a final test, one may use the data I have obtained from a population study at Lemsjöholm in southwestern Finland. The Great Tit population there has varied between 10 and 24 pairs, and the nest boxes have been checked both before and during the egg-laying period, correct data being thus obtained for the laying of the first egg in each clutch. Fig. 1 shows that the results obtained with the three methods coincide fairly well. Early years appear as early, and late years as late, irrespective of whether one uses the ringing cards, the nest cards, or the data from my population study. The fact that the nest cards from southern Finland indicate a somewhat delayed egg laying, as compared with the data from Lemsjöholm, may be interpreted either as a slight error of the former, or as a real difference. I am rather inclined to believe that there is a difference, as the Great Tits not infrequently started to lay in April at Lemsjöholm, which is obviously very unusual in other parts of southern Finland.

This and other similar tests entitle us to maintain that the statistical data on the nesting times of Finnish birds are, considered carefully, reliable. Although perhaps not perfect, they are certainly better than statistics *sensu Twaini*.
YEARLY VARIATIONS IN EGG-LAYING TIME

The yearly variation of the egg-laying time of the Great Tit can be shown to be closely correlated with the April temperature. Instead of analyzing any single species, I will try to treat a number of species synphenologically. I will choose only the years 1959 and 1960, as the spring temperature varied in quite an interesting way in these years. Fig. 2 shows that 1959 was warmer than 1960 until the middle of May, and thereafter colder. The species laying mainly before the turning point were earlier in 1959 than in 1960, whereas the species laying mainly thereafter were later in 1959. Between these groups were a couple of "undecided" species (Motacilla alba, Oe. oenanthe) in which egg laying falls around the middle of May and which nested at about the same time in both years. Even before seeing any temperature data and without remembering any details, I was able, on the basis of the egg-laying times, roughly to reconstruct in my mind the temperature conditions during the springs in question.

Even the very late species seem to be influenced by the temperature, at
least to some extent. Obviously none of the species studied is an “instinct” bird in which egg laying is related precisely, without any influence of the momentary temperature conditions. Migratory and nonmigratory species seem to be about equally influenced by the temperature conditions. Winter temperature obviously does not play any decisive role with respect to the nonmigratory birds, judging from the fact that the uniquely mild and snowless winter of 1960–61 was not followed by any record early egg laying in the Crested (Parus cristatus) and Great tits.

**Egg-Laying Time and Latitude**

Because of Finland’s great extent in the south–north direction, one may expect considerable differences in egg-laying times between southern Finland and Lapland. The distance from the southernmost to the northernmost point
of the country is somewhat more than 10°, i.e. as much as from southern England to southern Finland. Foreigners do not always realize this when they compare the nesting times of "Finnish" or even "Scandinavian" birds with those of some restricted areas in central or western Europe.

In order to investigate the relation between nesting time and latitude, Finland was divided into five zones, as in Fig. 3. The nesting times of a number of species are shown in Fig. 4 and 5. The former is based on data on bird ringing, the latter on data from the literature. Neither of the figures should be trusted in detail. Unfortunately, the number of data from northern Finland and Lapland is much smaller than from the southern parts of the country. This shows conspicuously in the odd zigzagging of the histograms in northern Finland.

At any rate, some general conclusions seem safe enough. As is to be expected, the farther northward we go, the later the birds start to lay. The difference, however, is much more striking with respect to the early-laying
species than to the later ones. This convergence of egg-laying times is confined both by the ringing data and the literature data. (The number of nest cards from northern Finland is too small to permit any conclusions.)

At first sight, it seems plausible to assume that the convergence of nesting times is due to the summer coming more rapidly in the North, or, in other words, that the rise in temperature in spring takes place more rapidly in the North so that the thermic threshold values for egg development are reached within a shorter time by the different species. The temperature data available do not, however, support this explanation.

Fig. 6 shows the average temperature for the months of March–July at five meteorological stations, each representing one of the zones between 60° and 70° N. The temperature curves converge to some extent, but obviously not as much as the egg-laying times. It is provisionally possible to calculate the thermic threshold values for egg laying in various species at various latitudes. The Starling (*Sturnus vulgaris*) and the Spotted Flycatcher (*Muscicapa striata*) may be used as examples representing an extremely early and a late species.

As indicated in Table 1, an early-nesting species starts its reproduction
Table 1.—Environmental Temperatures and Estimated Dates of the Start of the Rapid Growth of the Ovocytes in Southern and Northern Finland

<table>
<thead>
<tr>
<th></th>
<th>60°-62°</th>
<th>66°-68°</th>
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</thead>
<tbody>
<tr>
<td><strong>Starling</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average ringing date</td>
<td>1 June</td>
<td>19 June</td>
</tr>
<tr>
<td>Average day of laying</td>
<td>8 May</td>
<td>—</td>
</tr>
<tr>
<td>Start of rapid growth of ovocytes</td>
<td>3 May^a</td>
<td>21 May^b</td>
</tr>
<tr>
<td>Approximate mean temperature^®</td>
<td>6.8°</td>
<td>6.2°</td>
</tr>
<tr>
<td><strong>Spotted Flycatcher</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start of rapid growth of ovocytes^d</td>
<td>5 June</td>
<td>10 June</td>
</tr>
<tr>
<td>Approximate mean temperature^®</td>
<td>12.5°</td>
<td>10.2°</td>
</tr>
</tbody>
</table>

^a Estimated at 5 days earlier than laying date; from data on the Pied Flycatcher (*Ficedula hypoleuca*) as reported by v. Haartman (1951, 1956).

^b Estimated (in accordance with the left column) at 29 days prior to the average ringing date.

^c At Helsinki in the southern zone and Sodankylä in the northern zone.

^d Method of estimation: as for the Starling.

at a relatively constant temperature, despite the latitude, and a late-nesting species starts at a markedly lower temperature in the North.

This is not the place to discuss the physiological and evolutionary implications of this finding. I only wish to mention one problem of the utmost importance: Does the insect fauna (i.e. the food of the young birds of most
species) show the same trend as the nesting times? Future studies must reveal whether it does so. For the present, however, I wish to point out that there is a certain convergence toward the North among the phenological plant phenomena (Fig. 7). Whether this convergence is of the same magnitude as the convergence of the nesting times is, taking all sources of error into consideration, somewhat difficult to decide, but it hardly seems to be so.

**Fig. 7.** The leafing time (*Betula, Populus*) and start of flowering (*Prunus, Ledum*) at different latitudes in Finland. Data 1920–50 from Reuter (1927–52).

**SUMMARY**

Nest-record cards, bird-ringers’ lists, and other sources of data show a well-correlated annual variation in the nesting phenology of Finnish birds, egg laying being influenced by temperatures. In 1960, early nesters were 1–8 days ahead of their dates in 1959, while late nesters were 1–5 days later. Latitudinal differences were much more striking among early-laying species (due to their reproducing at a relatively constant temperature), whereas late-laying species start at markedly lower temperatures in the North.
LITERATURE CITED


Reuter (Pipping), M. 1927–52. Pflanzenphänologische Beobachtungen in Finnland. Bidr. känned. Finl. natur och folk 80:7–9; 83:3; 87:4; 89:1; 92:1, 3.
Rainy Season Nesting in Arizona

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What determines the time of breeding in desert birds? Four years' nesting records of the Abert's Towhee (Pipilo aberti) at Tucson, Arizona, appear in Fig. 1. Almost the entire range of this large sparrow is contained within southern Arizona, a region on the boundary between winter rainy seasons to the north and summer rains to the south. Annual rainfall at Tucson is about 30 cm, divided equally into two periods: winter-spring storms which cover wide areas, and very local summer thundershowers concentrated in the months of July, August, and September. These rains are indicated by dark bars (Fig. 1). June is the driest month. I want to show you that the Abert's Towhee nests principally after rains in both of these periods, with scattered nestings between, thereby increasing its chances for successful reproduction.

These nest records come from birds banded on a 50-acre area of closed mesquite woodland (Prosopis juliflora) in a river bottom 10 miles south of Tucson. Water is available to the birds at all seasons, and there is shade, so that the environment is neither extreme nor harsh, though temperatures in summer exceed 40° C. Insects, which abound in the verdure brought by summer rains, are necessary for feeding the young towhees.

The mesquite trees, naked in winter, leaf regularly in the latter half of April (as shown by the letters M in Fig. 1), which may or may not be ahead of nest building. However, the birds are adept at concealing themselves and their nests, even in bare mesquites.

Each square on the graph, entered in 5-day intervals, represents the time when incubation starts for one nesting attempt, as deduced or guessed from the state of affairs after discovery. You can see that many pairs nest simultaneously about 10–15 days after the principal or only rain of spring, and that this inception of general nesting varies from year to year by as much as a whole month. Thus, the synchronous first nesting of the population is “timed” by the environment. Subsequent nestings fall out of step owing to the varying fortunes of the eggs and nestlings; their span of survival determines how soon the parents will try again to rear young in the face of devastating predation by mice (Peromyscus sp.) in these arboreal nests, and interference by parasitic cowbirds (Molothrus ater). The numerical order of a nest, where known, is indicated by a number. Look at the interval 21–25 August 1959, and you will see a fifth nesting by a certain banded pair. The four previous had been destroyed at the egg or nestling stage, but the fifth proved successful, and the young were accompanying their still unmolted parents in October!

Following the July rains of 1959, there was a great resurgence of nesting
by the whole population. That year was “normal” in that the mesquites were still in good leaf, and I conclude that ordinarily the Abert’s Towhee population, capable of breeding as early as February, has a long nesting season begun in early spring after a rainstorm and culminating in a second peak in late summer in response to rains. At that time the vegetation becomes greenest, the insects are most abundant, and the cowbirds have departed for the stockyards.

Lest I sound overconfident in these conclusions, let me add that in 1958, with apparently the same rains, an Abert’s Towhee population 20 miles from that dealt with above began nesting in the last 10 days of February, a month ahead of those south of Tucson. In 1962, nesting did not follow a medium-sized rain of early March.

Since 1959 the mesquite trees have been dying or wilting due to a progressive drought, broken in 1960 by July rains at night, which failed to stimulate nesting, and broken in 1961 by August floods that came too late. Hence the lack of agreement in late-summer nestings during these years.

Among other birds at Tucson, the Brown Towhee (*Pipilo fuscus mesoleucus*) is similarly ambivalent as to nesting season; these two members of the genus have here as long a nesting season as do the doves. Nests have been recorded in every month from February through September. They benefit from whatever are the advantages of a “northern” spring nesting season.
(shared by their close relative, \textit{Pipilo fuscus crissalis}, and other races on the California Coast) and the more obvious rewards of a “tropical” or “rainy season” nesting (shared by their relatives \textit{P. f. fuscus}, \textit{P. f. albigula}, and \textit{P. albicollis} to the south). Most of the other desert birds at Tucson nest in late winter and spring, but a few, such as the Yellow-billed Cuckoo (\textit{Coccyzus americanus}) and Blue Grosbeak (\textit{Guiraca caerulea}), nest in late summer. Our most tropical bird, the Rufous-winged Sparrow (\textit{Aimophila carpalis}), nests only after the summer rains.

I gratefully acknowledge the expert assistance of R. S. Crossin in discovering these nests, and I thank the National Science Foundation for financial support. I am grateful to P. J. Gould and D. Dietrich for tracing the banded birds in the summer of 1960.

\textbf{SUMMARY}

The synchronous start of nesting by an Arizona population of Abert’s Towhees (\textit{Pipilo aberti}) follows by 10 days to 2 weeks a heavy daytime rain in March or April. There is scattered nesting through the summer until September. But in some years a second peak of general reproduction follows the major rains of July.
The Breeding Seasons of Birds in the Rhodesias and Nyasaland

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Moreau (1950) discussed the breeding seasons of birds in the Ethiopian region as a whole, and inevitably could only do so along the broadest lines. The present paper deals with a relatively small part of the region, for which a large body of data is now available. Records from Northern and Southern Rhodesia and Nyasaland are justifiably treated together as, with the exception of *Eremopterix* and *Fringillaria* spp. discussed below, they agree well by months for individual species. Nevertheless, as suggested by Winterbottom (1963), comparison of closely adjoining areas, contrasting strongly in intensity of rainfall, is certainly desirable, but beyond the scope of this paper. So, too, is possible variation in breeding seasons from year to year, influenced, for example, by lateness or earliness of the rains.

I have been able to use a total of some 22,600 breeding records, only about half of which were available when the respective territorial check lists were compiled by Smithers et al. (1957), Benson and White (1957), and Benson (1953). Information from these authors on other points, especially ecological, is often used without quotation. Further records from Southern Rhodesia, from the nest-record cards of the Rhodesian Ornithological Society, have been available up to 30 June 1960, with the inclusion of some to 31 December 1961. Some of the information in Benson and White is indeterminate, such as records merely of "breeding," and has not been used. The further records from this territory are from nest-record cards (largely supplied by the South African Ornithological Society) filed at the headquarters of the Department of Game and Fisheries, Chilanga, up to 31 December 1961. Details from some of these cards have already been published, the latest installment being by Benson and Pitman (1961). The further records for Nyasaland are all from Long (1960–61).

The data are summarized by months in tables, each record being assigned to the month in which it is calculated that egg laying started (e.g. Benson, 1953:2), the term "breeding" wherever used being restricted accordingly. Thus, in Table 2 there are 94 records of egg laying by *Podiceps ruficollis*, 6 months being represented, with the records arranged proportionately in percentages by months. Percentages are rounded to the next whole number (28.1 is thus shown as 29), and any resultant figure less than 5 is omitted, the significantly favored months thus at once catching the eye. Most of the data have been calculated from records of eggs, although some cases involve young under parental care. Female specimens that contained enlarged, yolk-ing oocytes have also been used, but not males with enlarged testes. Data for more than one species are only grouped together when there is no reason
to suppose from those of the individual species that there is any marked
difference. Species for which there are very few records are usually omitted,
as are all parasitic groups (Cuculidae, Indicatoridae, etc.). Some records of
colonial breeders are treated collectively, as explained in footnotes to the
tables. Records of other species with a tendency to colonialism are shown
individually, for example the Aegypiidae and *Rhynchops flavirostris*. The
nomenclature followed is that in Smithers et al. (1957) and Benson and
White (1957), practically identical down to specific level.

**THE PHYSICAL BACKGROUND**

The following brief outline is derived largely from the description of the
climate by Peake (in Brelsford, 1960:11–29) and from Moreau (1950:244),
whose account for Northern Rhodesia applies to the greater part of the area
now considered. The season of the rains is from November to March or
April, while the hottest months are September and October, the coldest June
and July. Toward the end of August, “spring” begins. Humidity is still
low, but there is a sharp rise in temperature. September and October become
progressively hotter, and humidity increases. Flowering and development of
foliage of trees becomes general in September, especially of *Brachystegia*
and *Julbernardia* spp., which dominate large areas. By October, fruits of such
trees as *Uapaca*, *Syzygium*, and *Ficus* spp. are abundant. With the increase
of temperature, insects become more plentiful and abound throughout the
rainy season. Although there is some sprouting after the passage of fire, it
is not until the start of the rains that there is any heavy flush of grass, which
in more open treeless areas may attain a height of 6 ft or more. After the
rains, by June the grass is dry enough for burning to start. As the dry sea¬
son advances, fires become progressively fiercer and more extensive, and
grassy cover correspondingly reduced. Fires are almost invariably started
by human agency. In times before human settlement they may not have
been of regular annual occurrence, but may have been started occasionally
toward the end of the dry season by lightning.

**THE RECORDS BY TABLES**

The same six groupings as used by Moreau (1950:224) are followed and
are reflected in the tables. There are some borderline cases for which alloca¬
tion is inevitably somewhat arbitrary. A seventh (miscellaneous) group has
been added for a few families and species which it has been impossible to
assign elsewhere.

*Evergreen-forest Birds* (Table 1).—Data are much less numerous than for
species of the same groups inhabiting open woodlands (Table 6, to be pre¬
sent later), but are adequate in some cases for comparative purposes. It
might be thought that in this habitat, with more uniform conditions through¬
out the year (fire in particular being excluded except on the edges), breeding
seasons would be more diverse and less sharply defined. There is no evi-
dence that this is so, the more numerous data, for the Pycnonotidae, Musci-
capidae, Turdidae, and Sylviidae, agreeing quite well with those for these
families in Table 6. The Nectariniidae (N. olivacea, N. verticalis, N. mediocris, Anthreptes collaris) show a diversity comparable to some other
species in the family, although N. olivacea, with 18 records, all for Sep-
tember-January, may be strictly seasonal.

Table 1.—Evergreen-forest Birds

<table>
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<th>Family or Subfamily</th>
<th>Number of Species</th>
<th>Number of Records</th>
<th>J</th>
<th>F</th>
<th>M</th>
<th>A</th>
<th>M</th>
<th>J</th>
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* Ploceus bicolor.

Water and Swamp Birds (Table 2).—Some species show much diversity,
although with a tendency to a peak during the rains and early dry season
when water levels are high and suitable habitat most extensive, and little
breeding toward the end of the dry season when levels are low and habitat
at a minimum. This is well shown by the Phalacrocoracidae and Anhingidae,
and to some extent by the Ardeidae. Excluded from the latter are the few
records for Ardea melanocephala and Ardeola ibis, which are associated with
a drier habitat than other species in this family. This leaves in these three
families species subsisting largely on fish. It is possible to find as many as
five species, representative of all three, breeding together at the same season
in the same colony. Breeding may in some cases be purely correlated with an
abundance of fish. Thus, in one mixed colony on the Zambezi above the
Victoria Falls during 1956–59, egg laying always started in June, and all
young were fledged by the end of August (Benson, 1960b).

The Anatidae, already discussed by Benson (1963), show a similar di-
versity. Data for the first four species of Rallidae, associated with permanent
water, are also diverse, but they likewise do little breeding in the last 4
months of the year. The remainder, associated rather with areas liable to
temporary flooding, show a well-marked season. Among them, Crex egregia
and Porzana marginalis may even be migratory, see especially Benson (1957),
while Sarothrura boehmi and Gallinula angulata extend during the rains into
areas where they could not exist in the dry season (Benson, 1959).

Podiceps ruficollis also shows some diversity, but has a marked breeding
peak in January and February, for which no reason can be suggested. The best example of diversity, however, is *Actophilornis africanus*, for which there are a few records for every month. *Scopus umbretta* shows a peak in August and September, when pools are low and frogs can most easily be caught. The difference between the two cranes *Balearica pavonina* and *Grus carunculatus* is remarkable, but no explanation can be offered. Both are common on parts of the Kafue Flats in Northern Rhodesia, and reflect this

<table>
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<th>Family, Genus, or Species</th>
<th>No. of Sp.</th>
<th>Number of Records</th>
<th>PERCENTAGES OF RECORDS BY MONTHS</th>
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<td><em>Alopecoen egyptiacus</em></td>
<td>1</td>
<td>51</td>
<td>J 6 J 32 A 16 S 26 O 10</td>
</tr>
<tr>
<td>Other spp.</td>
<td>12</td>
<td>295</td>
<td>J 11 J 30 A 19 S 8 J 9 J 7</td>
</tr>
<tr>
<td>Rallidae</td>
<td>1</td>
<td>19</td>
<td>J 6 J 26 A 11 S 11 J 6</td>
</tr>
<tr>
<td><em>Limnocorax flavirostris</em></td>
<td>1</td>
<td>23</td>
<td>J 9 J 13 A 5 S 9 J 35 A 18 S 5 A 5 S 5</td>
</tr>
<tr>
<td><em>Porphyrio</em></td>
<td>1</td>
<td>46</td>
<td>J 5 J 5 A 33 S 16 J 22 A 13</td>
</tr>
<tr>
<td><em>Gallinula chloropus</em></td>
<td>1</td>
<td>46</td>
<td>J 5 J 7 A 22 S 33 A 20 J 9</td>
</tr>
<tr>
<td><em>Fulica cristata</em></td>
<td>1</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>Other spp.</td>
<td>9</td>
<td>169</td>
<td>J 37 J 42 A 16 S 6</td>
</tr>
<tr>
<td><em>Actophilornis africanus</em></td>
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<td>89</td>
<td>J 6 J 13 A 14 S 16 J 16 A 5 S 8 A 11</td>
</tr>
<tr>
<td><em>Balearica pavonina</em></td>
<td>1</td>
<td>26</td>
<td>J 47 J 8 A 12 S 27</td>
</tr>
<tr>
<td><em>Grus carunculatus</em></td>
<td>1</td>
<td>55</td>
<td>J 6 J 22 A 19 S 28 A 11 S 6 A 8</td>
</tr>
<tr>
<td><em>Himantopus himantopus</em></td>
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<td>17</td>
<td>J 12 J 53 S 36</td>
</tr>
<tr>
<td><em>Rhynchops flavirostris</em></td>
<td>1</td>
<td>35</td>
<td>J 15 J 15 A 20 S 32 A 20</td>
</tr>
<tr>
<td><em>Ceryle rudis</em></td>
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<td>38</td>
<td>J 6 J 8 A 11 S 11 A 29 A 24</td>
</tr>
<tr>
<td><em>Alcedo cristata</em></td>
<td>1</td>
<td>30</td>
<td>J 7 J 17 A 14 S 14 A 17 A 14</td>
</tr>
<tr>
<td><em>Sylviidae</em></td>
<td>7</td>
<td>104</td>
<td>J 19 J 22 A 9 S 7 J 6</td>
</tr>
</tbody>
</table>

* Normally colonial breeders. A record of a species so breeding is shown as a single entry, but records for more than 1 month from the same colony, whether in the same or different years, are shown separately.
C. W. Benson: Breeding Seasons in the Rhodesias and Nyasaland

typical of the Sylviidae in Table 5, but in 17 records for *C. galactotes* every month is represented except May and October, and in 22 for *Acrocephalus gracilirostris* every month except October.

Two cases of breeding in an unstable environment may be mentioned. *Pelecanus onocrotalus* has only been found breeding on Mweru Wantipa, a shallow lake without drainage outlet in Northern Rhodesia, in an exceptionally dry year (1954), when the water level was very low and fish easily obtainable (Benson, 1956). Due to a lack of the rain normally to be expected in this area, in November–December 1954 and January 1955, there was in February 1955 attempted breeding of flamingos (*Phoenicopterus minor*), the only record from the Rhodesias and Nyasaland. This was a failure, however, due to a subsequent rise in the water level, when the rains did eventually break (Brown, 1957). By contrast *P. onocrotalus* may breed regularly in small numbers in March and April in the more stable conditions of the Kafue Flats (Benson, 1960a), and *P. rufescens* definitely does so, in February and March, in trees at Port Herald (Long, 1960–61).

**Raptors and Scavengers** (Table 3).—Brown (1955:209–217) has discussed breeding seasons of the larger eagles, with particular reference to the Embu District of Kenya. He suggests that the time of greatest stress is when the young are probably eating as much as the attendant female, about the age of 3–4 weeks. It is obviously less for the smaller species in the table, such as the smaller *Accipiter* spp. *Aquila* spp. (except *wahlbergi*) show a peak of laying in May and June, and the young would make their greatest demand in July and August. Certainly by August, fires are rampant and grass cover reduced, so that prey is more easily visible. *Polemaëtus* and the scavenging Aegypiidae and *Leptoptilos* show a rather similar season to these *Aquila* spp., when (applicable to the scavengers) mortality among the larger ungulates is liable to be high from a lack of grazing and water.

On the other hand, there are many species with a breeding peak in September or even October. The contrast between *Aquila wahlbergi* and the other larger *Aquila* spp. is particularly noteworthy. *A. wahlbergi* must prey on rodents rather than larger mammals. The case of *Milvus migrans*, largely a scavenger around villages, where conditions do not vary much through the year, is especially puzzling but, as this is a species given to spectacular migrations, its feeding ecology is clearly much more exigent than might be supposed. For the smaller *Accipiter* and *Falco* spp., an important factor may be an increase in insects with the warmer weather and of smaller passerines generally (see especially Table 6). By October the *Brachystegia* woodlands are already in heavy leaf, so that visibility from above is poor. But the smaller *Accipiter* spp. hunt under the canopy, so that visibility of prey is unaffected (there is no flush of concealing grass until the rains). *Polyboroides radiatus* is largely dependent on nestling weavers for food, and its season seems well adapted to this (see Table 5) but is more concentrated.

According to D. Vesey-FitzGerald (pers. comm.), on the plains of the
Rukwa Valley in southwestern Tanganyika, *Elanus caeruleus*, showing no marked season, feeds largely on *Arvicanthis* and other diurnal rodents that presumably are easily caught at any season. *Circus aeruginosus* is remarkable for showing a breeding peak during the rainy period. This is the season when, in a similar marshy habitat, young Anatidae and Rallidae (Table 2), *Macronyx* (Table 4), and *Centropus* (Table 5) would be available. *Circaetus* spp. and *Terathopius ecaudatus*, preying largely on snakes, show no very marked season (as also found by Brown, 1955). Practically all the data

### Table 3.—Raptors and Scavengers

<table>
<thead>
<tr>
<th>Family, Genus, or Species</th>
<th>No. of Sp.</th>
<th>Number of Records</th>
<th>Percentages of Records by Months</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>J F M A M J J A S O N D</td>
</tr>
<tr>
<td><strong>EARLY DRY-SEASON BREEDERS</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aegypiidae</td>
<td>4</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td><em>Polemaetus bellicosus</em></td>
<td>1</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td><em>Aquila</em> (except <em>wahlbergi</em>)</td>
<td>4</td>
<td>108</td>
<td></td>
</tr>
<tr>
<td><em>Haliaeetus vocifer</em></td>
<td>1</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td><em>Bubo lacteus</em></td>
<td>1</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td><em>Scotopelia peli</em></td>
<td>1</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td><strong>LATE DRY-SEASON BREEDERS</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leptoptilos crumeniferus</em></td>
<td>1</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td><em>Sagittarius serpentarius</em></td>
<td>1</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td><em>Mileus migrans</em></td>
<td>1</td>
<td>134</td>
<td></td>
</tr>
<tr>
<td><em>Accipiter, Melierax</em></td>
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<td></td>
</tr>
<tr>
<td>Larger spp.</td>
<td>3</td>
<td>106</td>
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<tr>
<td>Smaller spp.</td>
<td>5</td>
<td>235</td>
<td></td>
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<tr>
<td><em>Kapilfalcio monogrammicus</em></td>
<td>1</td>
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<td></td>
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<tr>
<td><em>Buteo rufocanescens</em></td>
<td>1</td>
<td>38</td>
<td></td>
</tr>
<tr>
<td><em>Lophaetus occipitalis</em></td>
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<td>8</td>
<td></td>
</tr>
<tr>
<td><em>Aquila wahlbergi</em></td>
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<td>241</td>
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<tr>
<td><em>Polyboroides radiatus</em></td>
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<td>44</td>
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</tr>
<tr>
<td><em>Falco</em></td>
<td>8</td>
<td>66</td>
<td></td>
</tr>
<tr>
<td><em>Ciccaba woodfordii</em></td>
<td>1</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td><em>Otus scopis</em></td>
<td>1</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td><em>Otus leucotis</em></td>
<td>1</td>
<td>48</td>
<td></td>
</tr>
<tr>
<td><em>Glaucidium</em></td>
<td>2</td>
<td>21</td>
<td></td>
</tr>
<tr>
<td><em>Bubo africanus</em></td>
<td>1</td>
<td>121</td>
<td></td>
</tr>
<tr>
<td><strong>RAINY-SEASON BREEDERS</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Circus aeruginosus</em></td>
<td>1</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td><em>Asio capensis</em></td>
<td>1</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td><strong>NO DEFINITE SEASON</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Elanus caeruleus</em></td>
<td>1</td>
<td>35</td>
<td></td>
</tr>
<tr>
<td><em>Stephanoaetus coronatus</em></td>
<td>1</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td><em>Terathopius ecaudatus</em></td>
<td>1</td>
<td>58</td>
<td></td>
</tr>
<tr>
<td><em>Circaetus</em></td>
<td>3</td>
<td>38</td>
<td></td>
</tr>
<tr>
<td><em>Tyto alba</em></td>
<td>1</td>
<td>71</td>
<td></td>
</tr>
<tr>
<td><em>Tyto capensis</em></td>
<td>1</td>
<td>11</td>
<td></td>
</tr>
</tbody>
</table>

* Colonial; see note in Table 2.
indicate a period of stress (young aged 3 or 4 weeks) for *Haliaeetus vocifer* in the dry season. This might be related to water being clear and fish therefore easier to catch, although Brown (1960:295) suggests that the real reason may be more obscure. But another point is that, in the latter part of the dry season, fish could easily be caught at drying pools. G. Bell-Cross (pers. comm.) has witnessed congregations of herons, marabous, and fish-eagles at such pools in the upper Kafue and upper Zambezi basins.

Among the owls, the breeding data for *Tyto alba* might indicate a seasonal abundance of rodents, but there is no evidence that this is actually so. Data for the marsh-dwelling *Asio capensis* are rather similar to those for *Circus aeruginosus*, but there is no evidence of any connection. The fish-eating *Sco*topelia *peli* seems to have a season like that for *Haliaeetus*. The data for *Bubo lacteus*, which is capable of taking large prey, are rather like those for the larger *Aquila* spp. Disregarding the scanty data for the marsh-dwelling *Tyto capensis*, the remaining species of owls show a peak mainly in September. They are largely insectivorous, and this rather surprisingly applies even to the relatively large *Bubo africanus*.

**Ground Birds** (Table 4).—The Charadriidae, Glareolidae, and Burhinidae all show a peak in September or October, when conditions are favorable for species frequenting bare, open ground. By this season the grass is likely to have been burned or trampled down. This might also apply to *Struthio camelus*. Several species must avoid the rains because they nest in sites that will be inundated—*Glareola pratincola* on dried mud flats, *Charadrius alex-

### Table 4.—Ground Birds

<table>
<thead>
<tr>
<th>Family, Genus, or Species</th>
<th>Number of Species</th>
<th>Number of Records</th>
<th>PERCENTAGES OF RECORDS BY MONTHS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>J</td>
</tr>
<tr>
<td><em>Struthio camelus</em></td>
<td>1</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>Phasianidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Francolinus coqui</em></td>
<td>1</td>
<td>71</td>
<td>27</td>
</tr>
<tr>
<td><em>F. afer</em> and <em>F. swainsoni</em></td>
<td>2</td>
<td>174</td>
<td>7</td>
</tr>
<tr>
<td><em>Coturnix delegorguei</em></td>
<td>1</td>
<td>31</td>
<td>30</td>
</tr>
<tr>
<td><em>Numida meleagris</em></td>
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<td>95</td>
<td>19</td>
</tr>
<tr>
<td>Otididae</td>
<td>5</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td>Charadriidae</td>
<td>9</td>
<td>484</td>
<td>8</td>
</tr>
<tr>
<td>Glareolidae</td>
<td>5</td>
<td>179</td>
<td>8</td>
</tr>
<tr>
<td>Burhinidae</td>
<td>2</td>
<td>94</td>
<td>14</td>
</tr>
<tr>
<td>Pteroclitidae</td>
<td>2</td>
<td>39</td>
<td>6</td>
</tr>
<tr>
<td><em>Turnix sylvatica</em></td>
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<td>93</td>
<td>7</td>
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<tr>
<td>Caprimulgidae</td>
<td>7</td>
<td>301</td>
<td>20</td>
</tr>
<tr>
<td>Alaudidae</td>
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<td></td>
<td></td>
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<tr>
<td><em>Mirafra</em></td>
<td>7</td>
<td>224</td>
<td>17</td>
</tr>
<tr>
<td><em>Eremopterix</em></td>
<td>2</td>
<td>24</td>
<td>5</td>
</tr>
<tr>
<td><em>Calandrella cinerea</em></td>
<td>1</td>
<td>31</td>
<td>7</td>
</tr>
<tr>
<td>Anthus</td>
<td>5</td>
<td>154</td>
<td>6</td>
</tr>
<tr>
<td>Macronyx</td>
<td>4</td>
<td>60</td>
<td>32</td>
</tr>
</tbody>
</table>
**ECOLOGY: BREEDING SEASONS AND ADAPTATIONS**

andrinus, Lobivanellus albiceps, and often Burhinus vermiculatus on sandy beaches, and Glareola nuchalis on rocks in perennial rivers.

The Caprimulgidae and Anthus spp. must avail themselves of the pre-rain flush of insects, but there is again the advantage of bare, open conditions. On the other hand, cover must be important for the grass-dwelling, mainly skulking Macronyx spp., breeding mostly during the rains. Among the Alaudidae, this applies to some extent to *Mirafra* spp. But Calandrella cinerea avoids the rains, and is largely migratory (White, 1959). Unlike *Mirafra africana* and *M. rufocinnamomea*, whose nests are concealed, it frequents and nests on bare, open ground, often where fires have recently passed. Of the 24 records of Eremopterix spp., of similar habitat to Calandrella, 13 are from Northern Rhodesia and Nyasaland and are all for April–September. The Southern Rhodesian records are all from Matabeleland, where conditions are drier (see below under *Fringillaria* spp.), and breeding during the rains is possible to some extent.

For game birds, information can be summarized from Benson (1963). Some Francolinus spp. show no marked season, but *F. afer* and *F. swainsonii*, associated with rank grass, show a peak in the late rains and early dry season, and breeding in July–December is almost completely avoided. Their season seems to be correlated with an abundance of cover and seed for food. Cover may also be important to *F. coqui*, frequenting short grass in Brachystegia woodlands, and breeding mainly in the rains. The largely migratory *Colurnix delegorguei* breeds from October to May, when there is at first an abundance of insects and later of grass, providing cover and seed for food. The same considerations may apply to *Numida meleagris*, and even to the Otididae, and to *Turnix sylvatica*, although data for the latter are scattered. The Pteroclitidae, which prefer open ground, resemble Calandrella in their breeding season. During the rains *Pterocles gutturalis* is absent, at least from most of its range in Northern Rhodesia.

Grass Birds (Table 5).—The birds in this table breed mostly during the rainy period, when there is an abundance of suitable nesting material, cover, and food. Centropus spp. are typical, building large bulky nests of grass and feeding mainly on insects. The Sylviidae contain all *Cisticola* spp. (except galactotes, pipiens, and tinniens, see Table 2), *Prinia subflava* and *P. flavicans*, *Chloropeta natalensis*, *Schoenicola*, *Sphenoeacus*, *Melocichla*, and *Heliolais*. The total is heavily weighted by 502 records for *Prinia subflava* and 700 for *Cisticola* spp. The peak of the breeding season is 3 months later than that of the Sylviidae in Table 6. The grass species must wait for the rains, to provide material and cover for their nests, if not also food.

Although they show a peak therein, *Passer* and *Ploceus* spp. start breeding before the rains, perhaps being able to take advantage, like many of the assemblage in Table 6, of the pre-rain flush of insects for the feeding of their young. Nesting sites would not be a material factor, *Passer* nesting in holes...
in trees or in the eaves of buildings, *Ploceus* largely in trees. On the other hand, *Amblyospiza* and *Euplectes* spp. must wait for the rains in order to have grass or reeds to which to attach their nests. *E. hartlaubi* and *E. psammochromius* seem to start breeding earlier than other species (Benson and White, 1957), perhaps because in their marshy habitat grass or reeds would be more readily available.

*Quelea* spp. have a season like *Amblyospiza* and *Euplectes*. *Q. erythrops* nests in reeds, but *Q. quelea* evidently more usually in the Rhodesias in trees (Stewart, 1959), and might therefore be expected to start before the rains, like *Ploceus* spp. But it may be that suitable material for the building of nests is not available until the rains, and Marshall (1959:468) quotes evidence that first-year *Q. quelea* are influenced by the green grass following rainfall.

Although the breeding season of *Sporopipes squamifrons* appears to be ill defined, it does have two peaks, in February–March and September–October. The data may be rather misleading, however, since most of them are from the Khami Dam near Bulawayo or from near human dwellings, where conditions would be more equable than elsewhere, water (and perhaps also seeds) always being obtainable. The Estrildinae, without any specific exceptions, show a peak during the rainy season, probably correlated with an abundance of grass for nest building and (as seeds) for food. *Ortygospiza atricollis* and *O. locustella*, inhabiting treeless grasslands, are especially seasonal. Of 88 records, all for December–June, 79 are for January–April. Breeding in such a habitat, after it has been burned and cover is lacking, would be disadvantageous. On the other hand, *Lagonosticta senega* has been found breeding in all months except November. It is associated with human dwellings, and the same considerations may apply as in the case of *Sporopipes*.

### Table 5.—Grass Birds

<table>
<thead>
<tr>
<th>Family, Subfamily, or Genus</th>
<th>Number of Species</th>
<th>Number of Records</th>
<th>PERCENTAGES OF RECORDS BY MONTHS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>J  F  M  A  M  J  J  A  S  O  N  D</td>
</tr>
<tr>
<td><em>Centropus</em></td>
<td>4</td>
<td>24</td>
<td>161 22 28 10 5 9 17</td>
</tr>
<tr>
<td><em>Sylviidae</em></td>
<td>24</td>
<td>1,264</td>
<td>155 28 24 13 9 22</td>
</tr>
<tr>
<td><em>Ploceidae</em></td>
<td>2</td>
<td>77</td>
<td>25 24 15 8 10 7 11</td>
</tr>
<tr>
<td><em>Passer</em></td>
<td>1</td>
<td>12</td>
<td>136 12 21 12 9 5 11 17 6 5</td>
</tr>
<tr>
<td><em>Sporopipes</em></td>
<td>1</td>
<td>1,445</td>
<td>11 15 14 30 39 10 23</td>
</tr>
<tr>
<td><em>Ploceus</em></td>
<td>1</td>
<td>44</td>
<td>11 15 14 30 39 10 23</td>
</tr>
<tr>
<td><em>Amblyospiza</em></td>
<td>3</td>
<td>1,037</td>
<td>10 15 20 28 15 8</td>
</tr>
<tr>
<td><em>Quelea</em></td>
<td>10</td>
<td>2,521</td>
<td>0 14</td>
</tr>
<tr>
<td><em>Estrildinae</em></td>
<td>21</td>
<td>1,037</td>
<td>10 14</td>
</tr>
</tbody>
</table>

a Some species breed colonially, the footnote in Table 2 being applicable; but some Southern Rhodesian records may refer to the same colony in the same month and year. There is no indication as to which they may be, so it is impracticable to lump them.
b Q. *quelea* breeds in enormous colonies during Jan.–Mar.; Q. *erythrops* breeds in colonies of 150–250 nests in the same period; one record for Q. *cardinalis*, single nest with eggs in Feb.
Mainly Insect- and Fruit-eating Birds (Table 6).—This large miscellany, nearly all with a peak in October, are mostly insect eaters, although some, such as the Coliidae, Capitonidae, and Pycnonotidae, are largely fruit eaters, while the Corvidae are scavengers, and Bucorvus leadbeateri will eat almost anything, animal or vegetable. Ample insect food is available at the start of the rains, especially termites, cockchafers, etc., on their nuptial flight, but thereafter until early January it is more sparse. In some groups (e.g. Picidae) breeding extends very little into the rainy season, even if they nest in holes affording protection from rain. In the case of this particular group,

<table>
<thead>
<tr>
<th>Family, Subfamily, Genus, etc.</th>
<th>No. of Sp.</th>
<th>Number of Records</th>
<th>PERCENTAGES OF RECORDS BY MONTHS</th>
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</thead>
<tbody>
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<td>J F M A M J A S O N D</td>
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<tr>
<td>Coraciidae</td>
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<td>148</td>
<td>17 52 28</td>
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<td>Ceyx picta</td>
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<td>10 20 55 10</td>
</tr>
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<td>Halcyon</td>
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<td>Meropidae</td>
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<td>8 55 25 6</td>
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<td>10 25 29 15 8</td>
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<td>540</td>
<td>6 28 36 14 5</td>
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<td>19 38 23 5</td>
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<tr>
<td>Petronia</td>
<td>1</td>
<td>68</td>
<td>11 31 40 12</td>
</tr>
<tr>
<td>Anaplectes</td>
<td>1</td>
<td>123</td>
<td>6 26 47 16</td>
</tr>
</tbody>
</table>

* M. nubicus (59 records) and M. bullocki (65) breed colonially, the footnote in Table 2 being applicable; but some Southern Rhodesian records may refer to the same colony in the same month and year. There is no indication as to which they may be, and so it is impracticable to lump them.
the explanation might be that the insect population of standing timber is highest in the dry season. Some groups (e.g. Laniidae), however, do show some extension into the rainy season. *Turdoïdes jardinei* has been found breeding in every month of the year (as explained above, percentages less than 5 are omitted), but does show a peak in October. The reason for this diversity is not clear. *Motacilla aguimp* has been found breeding in every month except January. Nearly all the records are from buildings, near where water would always be available. At Luanshya during 1946–48 a pair, of which one bird was certainly the same throughout, had eggs in December, March, July, November, February, and June (Haydock, 1949).

The Sylviidae placed in the present group are various species inhabiting *Brachystegia* and other woodlands. The total of 276 records includes 154 for *Sylvietta rufescens*, which is typical, showing a peak in October (69 records), and, respectively, 5, 1, and 1 records for January, February, and April. Of the 540 records for the Nectariniidae, 450 are for *N. talatala*, *N. chalybea*, *N. amethystina*, and *N. senegalensis*. While all four species show a peak in September–October, there is some diversity, not significant enough to be reflected in the table. There is at least one record for *N. chalybea* for every month. Records for *N. venusta* show no peak in September–October, being as follows: March, 8; April, 3; May, 3; June, 2; July, 1; August, 7; September, 2; October, 2; December, 1. The season for *N. famosa* may vary locally, even within northern Nyasaland (Benson, 1952), possibly related to the flowering of particular plants. Chapin (1959) has shown that in the eastern Congo *N. purpureiventris* is entirely dependent on the flowers of *Symphonia globulifera*.

The data for the Plocepasserinae, *Petronia*, and *Anaplectes* contrast with those for the Ploceidae as a whole (Table 5). This may be related to a difference in the food on which the young are fed, those of the species in this table perhaps being fed on insects of a kind not so readily available during the rainy season. Data for *Petronia* in Benson and White (1957), suggesting breeding in March and perhaps later, may require corroboration.

There are a few cases of species showing a recrudescence of breeding at the end of the rainy period; these are otherwise practically confined to the pre-rains. Thus, 187 records for *Melaenornis pammelaina* (Muscicapidae) are all for August–January (only 3 for January), except for a record for a fledged juvenile on 16 May (Benson, 1940;597), indicating laying in April, while 126 records of *Prinops plumatus* (Prionopidae) are all for September–December, except for one in March (Neave, 1907;71) and one from Southern Rhodesia in April. Such instances seem to suggest that the regeneration phase of spring-breeding birds is carried a stage farther than in the autumn in temperate regions (Marshall, 1959).

**Miscellaneous Groups** (Table 7).—Among the Columbidae, the fruit-eating, arboreal *Treron australis* (= *T. calva* and *T. delalandii* in Smithers et
Table 7.—Miscellaneous Groups

<table>
<thead>
<tr>
<th>Family, Genus, or Species</th>
<th>No. of Sp. Records</th>
<th>Percentages of records by months</th>
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<tr>
<td></td>
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<td>J</td>
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<td>Columbidae</td>
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<tr>
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<td>72</td>
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<td>403</td>
</tr>
<tr>
<td>Oena capensis</td>
<td>1</td>
<td>82</td>
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<td>Turtur chalcospilos and T. afer</td>
<td>2</td>
<td>58</td>
</tr>
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<td>Musophagidae</td>
<td></td>
<td></td>
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<tr>
<td>Tauraco corythaix and M. rossae</td>
<td>2</td>
<td>25</td>
</tr>
<tr>
<td>T. porphyreolophus</td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>Crinifer concolor</td>
<td>1</td>
<td>150</td>
</tr>
<tr>
<td>Poicephalus</td>
<td>3</td>
<td>31</td>
</tr>
<tr>
<td>Apodidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apus affinis and A. caffer</td>
<td>2</td>
<td>70</td>
</tr>
<tr>
<td>A. horus</td>
<td>1</td>
<td>24</td>
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<tr>
<td>Cypsiurus parvus</td>
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<tr>
<td>Hirundinidae</td>
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</tr>
<tr>
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<tr>
<td>H. abyssinica</td>
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<td>180</td>
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<tr>
<td>H. griseopyga</td>
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</tr>
<tr>
<td>H. other spp.</td>
<td>11</td>
<td>285</td>
</tr>
<tr>
<td>Riparia cincta</td>
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</tr>
<tr>
<td>R. paludicola</td>
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<td>9</td>
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<td>14</td>
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<tr>
<td>Fringillidae</td>
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<td></td>
</tr>
<tr>
<td>Serinus mozambicus</td>
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<td>105</td>
</tr>
<tr>
<td>S. sulphuratus</td>
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<td>S. mennelli</td>
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<td>11</td>
</tr>
<tr>
<td>S. atrogularis</td>
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<td>36</td>
</tr>
<tr>
<td>Emberiza</td>
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<td>261</td>
</tr>
<tr>
<td>Fringillaria tahapisi</td>
<td>1</td>
<td>126</td>
</tr>
<tr>
<td>F. capensis</td>
<td>1</td>
<td>14</td>
</tr>
</tbody>
</table>

al., 1957) has a peak in September and October. The Streptopelia and Turtur spp. and Oena capensis, all ground feeders (S. capicola and S. senegalensis often associated with cultivation), have no sharply defined breeding season, but a third of all the records for S. capicola and S. senegalensis are for September–October, and nearly another third for March–May. The reason is not at all clear but is perhaps related to an abundance of some kind of seed.

Among the Musophagidae, Tauraco corythaix and M. rossae, mainly evergreen-forest dwellers, breed chiefly in October–December. T. porphyreolophus, preferring deciduous thickets, apparently breeds rather later. The
data for *Crinijer concolor*, living in an open habitat, are quite different. The hole-nesting *Poicephalus* spp. are unique in breeding throughout the dry season. The controlling factor, presumably food, is unknown in all of these cases.

The Apodidae are, of course, insectivorous but, whereas *Cypsiurus parvus* is not markedly seasonal, *Apus affinis* and *A. caffer* avoid the cold, dry months and start in August; this is the case with many species in Table 6, although there is an unusually marked carry-over into the rainy season. It is not clear why *A. horus*, nesting in holes in riverbanks, should breed mainly during the rainy period, with a concentration later than any other swift, when there must be danger from flooding of holes. Records for the migratory *Pitta angolensis* are scanty but interesting. The birds do not arrive until the start of the rains when the deciduous thickets which they occupy are coming into leaf, providing conditions almost like the evergreen forest, and only then affording them and their bulky nests effective hiding.

The Hirundinidae breed both during the hot pre-rains and during the rains, in both of which periods insects are plentiful. *H. smithii* shows very little gap in the dry season, and there are a few records for May and June. Even in the case of *H. abyssinica* the only month for which records are completely lacking is June. Both are more markedly associated than any other species with human dwellings, where mud for nest building would always be available. *H. griseopyga* is an interesting peculiarity. Mud is not a requisite for its nests, and the disused rodent-burrows which it uses would be flooded out in the rains. *Riparia paludicola* is also odd. It nests in banks along perennial rivers, apparently in the dry season for the most part, when there would be no danger of flooding, but in perplexing contrast to *Apus horus*.

Virtually nothing is known locally about the diet on which nestling Fringillidae are fed, although according to Skead (1960:12–14) seeds predominate. He also states that *Serinus sulphuratus* (at any age) is more prone to a fruit diet than any other species, and likewise suggests that buntings are partial to insects. The data presented here are especially puzzling. Those for *Serinus* spp. as a whole indicate breeding both during the hot pre-rains and during the rains, a circumstance possibly related to the young being fed on insects. *S. mozambicus* breeds hardly at all during the pre-rains, while *S. sulphuratus* has a peak at this season. The fact that *Emberiza* spp. breed mostly during the early rains may be related to an insect diet. *Fringillaria* spp. show results quite like the Estrildinae (Table 5), perhaps related to a seed diet. Actually, all 88 records of *F. tahapisi* for January–March are from Southern Rhodesia, and according to C. J. Vernon (pers. comm.) at least 53 of them are from Matabeleland, where the annual rainfall averages less than 24 inches. Of 37 records for April–July, 30 are from parts of Northern Rhodesia and Nyasaland with a rainfall of over 40 inches. Vernon finds that at Bulawayo singing starts in January, but according to Belcher (1930) and Benson (1941:51) in Nyasaland not until March. The situation may
be the same with *F. capensis* as, except for one April record from Nyasaland, all are from Matabeleland.

**CONCLUSIONS**

The data summarized here enable monthly percentages to be calculated, whereas the records available to Moreau (1950) did not. However, the forest birds in my Table 1 show mostly the same peak in October and November as he deduced. His comment that the water birds’ breeding period is not sharply defined, and that they avoid the period of October–December is largely justified, but the new data show no difference in the breeding season between Northern Rhodesia and Nyasaland, as he suggests. The varied raptor and scavenger data are given in my Table 3 in some detail, and any comparison with Moreau’s generalized data is therefore impossible. His ground-bird data indicate a peak in the latter part of the dry season, which is in general agreement with the data in my Table 4, although some species breed when there is a plentiful grassy cover. The grass-birds’ data agree fairly well, except that my Table 5 shows that *Ploceus* spp. start breeding well before the rains. Data for insect and fruit eaters (Moreau’s “others”) also agree well.

We are still generally very ignorant about the factors regulating seasons. Many of the suggestions made are little more than guesses. Both Moreau (1950) and Marshall (1959) have emphasized the basic importance of a supply of suitable food, and this is especially well shown by the breeding data for the pre-rains insectivorous groups in Table 6. The contrast between the season of the Sylviidae in this table and of those in Table 5 (grass species) is striking. The latter must wait for the rains, apparently not so much because of a lack of food before the rains as of a lack of nesting material and protective cover for nests. In *Hirundo griseopyga*, which nests when most other *Hirundo* spp. do not, the importance of food is evidently outweighed by the necessity for security against the flooding of nesting holes. Security against flooding may also help to explain the season of *Rhynchos flavirostris* (Table 2), and of some Charadriidae, Glareolidae, and Burhinidae (Table 4). Other species in these three families, associated with a drier habitat, may wait until there is security from fire. The game birds in Table 4, however, breed mostly during the rainy season, when not only are insects and seeds for food plentiful, but also grassy cover for protection.

Some species associated with human dwellings tend to breed all the year round under relatively equable conditions, water in particular always being available. Examples are *Motacilla aguimp*, *Hirundo smithii*, and *H. abyssinica* (water needed for mudding of nests), and *Sporopipes squamifrons* and *Lagonosticta senegalata* (availability of seeds perhaps also important). Equability may also explain the diversity in some water and swamp birds, the extreme example being *Actophilornis africanus*. Attention may also be drawn to Belcher (1930:x) regarding out-of-season breeding of *Cisticola* and *Prinia*
in flooded banana gardens. Some Rallidae are markedly seasonal, however, and in some localities occupy during the breeding season temporarily flooded areas where they could not survive at all during the dry season. The evergreen-forest birds, living in apparently the most equable environment of any, are as seasonal as relatives living in more open habitats, a point which also puzzled Moreau. The seasons of the raptors and scavengers vary considerably, even within a genus (see *Aquila* and *Bubo*), and may be related to availability of prey, in terms of both abundance and visibility.

**ACKNOWLEDGMENTS**

I am especially grateful to R. K. Brooke and C. J. Vernon for generously making available the data for Southern Rhodesia, and for answering many questions. While the records for Northern Rhodesia and Nyasaland, totaling about 7,000, are plentiful by general African standards, those for Southern Rhodesia, totaling over 15,000, are outstanding. Both Brooke and Vernon, their predecessor in charge of the records, H. M. Miles, and their collaborators in the field are to be warmly congratulated. I must also thank various field collaborators in Northern Rhodesia, most of them my colleagues in the Department of Game and Fisheries.

I am also most grateful to R. E. Moreau for his advice during the preparation of this paper, and to my wife for much assistance. I must also thank Mrs. B. P. Hall, Captain C. R. S. Pitman, the Rev. Dr. W. Serle, Dr. J. M. Winterbottom, W. F. H. Ansell, D. Goodwin, C. J. O. Harrison, C. W. Mackworth-Praed, and D. Vesey-FitzGerald for advice or assistance.

**SUMMARY**

Moreau (1950) discussed breeding seasons of birds in the Ethiopian region as a whole. A much larger body of data has since been accumulated for the Rhodesias and Nyasaland, the particular area now treated, the number of records exceeding 22,000. The three territories are considered together, as data by months agree well for individual species.

The season of the rains is from November to March or April. The hottest months are September and October, the coldest June and July. Flowering and development of foliage of trees becomes general in September, especially of *Brachystegia* and *Julbernardia* spp., which dominate large areas, and by October various fruits are abundant. With a progressive increase of temperature and humidity in these two months insects become more plentiful, and abound throughout the rains. There is no heavy flush of grass until the start of the rains. After the end of the rains, as the dry season advances, fires become progressively more extensive, and cover correspondingly reduced.

The breeding records are classified into seven groups, reflected in tables, as follows:
1) Evergreen-forest species (Table 1) show no difference in season from related species inhabiting open woodlands (Table 6).

2) Water and swamp birds show much diversity, but with a tendency in some species to a peak in the rains and early dry season, when suitable habitat is most extensive.

3) Practically all raptors and scavengers breed in the dry season, when visibility is easiest, due to lack of cover.

4) Some ground birds breed when there is a minimum of cover, in September and October, others when it is thickest, in the rains.

5) Grass birds breed mostly in the rains, when there is an abundance of nesting material, cover, and food.

6) A large miscellany, mostly insect eaters, but containing some fruit eaters, show a peak of breeding in October.

7) Another miscellany, showing no general trend, is treated in Table 7.

LITERATURE CITED


Haydock, E. L. 1949. Field notes on Northern Rhodesian birds. Ibis 91:656-659.


Avian Breeding Seasons in Southern Africa

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When Moreau (1950) discussed the breeding seasons of African birds, he had no data worth consideration about the northern Cape Province and, indeed, implied that most of the Cape Province, except that part dominated by winter rains, falls into the "transition" area between winter and summer rains. This is true enough as far as the area from which Moreau had data is concerned—"an area about 120 miles ( Humansdorp to Grahamstown) by 100 (inland)"—but the two parts with which Moreau deals include only a fraction of the Cape Province, which, it is easy to forget, has an area greater than that of the rest of political South Africa put together. Reference to the map in Wellington (1955) shows that much of this area falls into the summer rainfall zone; and that some of it falls into Moreau's "semi-arid" category, with "rainfall not exceeding about 20 inches, with a severe dry season of at least six months." On this area, Moreau had no data at all worth discussion and his consideration of the "semi-arid" country in the south is confined to the much more severe environments of South-West Africa, for many of which the term "semi-arid" is, perhaps, an understatement (all western and southern South-West Africa is in Thornthwaite's "arid warm zone" and Köppen's "desert zone"—Schulze, 1947); and even for them, he did not use tabular treatment for his data.

Recently, I have had access to the manuscript notes of the late S. F. Townsend and his son-in-law, the late S. Tapscott (and I am deeply indebted to their daughters, Mrs. Chamberlain and Mrs. Moore, respectively, for putting these at my disposal). A good many of the former's and all of the latter's records refer to the neighborhood of Kimberley (average rainfall, 18.26 inches), chiefly to Riverton-on-Vaal. The total number of nesting records available from these two sources relating to this area is 268, for 84 species. Moreau is compelled, by the nature of his data, "to derive an annual curve of breeding activity ... from the number of species recorded as breeding in each month. ... The tendency of this method is to blur breeding seasons." Fortunately, there now exist adequate data for certain regions of Africa (particularly the admirable series of records compiled by H. M. Miles referred to below and for the Southwest Cape), which enable the breeding activity to be shown by totals of nests recorded. This method is not wholly free from objection, since the total tends to be weighted in favor of those species whose nests are easily found; and in one or two cases, where the data are not particularly full, grotesque results could be obtained, e.g. with colonially nesting birds. Consequently, both methods are

used in the present paper. Tables 1 and 2 present in summary form the data to be discussed below.

**GRIQUALAND WEST**

For Griqualand West, the most striking result emerging from the figures is the extraordinarily well-marked peak in October. In that month, 51 percent of the 84 species have been found breeding; and no less than 42 percent of all the nests recorded were found. An inconsistency between the two sets of figures is that, while slightly fewer nests were found in November (14 percent) than in either September or December (15 percent), a larger percentage of the species (31 percent) was breeding then than in either of the other 2 months.

If we consider the figures in relation to the other peak months as well, however, we find that the extreme concentration during October may be misleading. There is a period of 4 months (September–December) during each of which 14 percent or more of the nests were recorded and 20 percent or more of the species were breeding.

### Table 1.—Percentage of Nests Recorded in Each Month

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<td>6</td>
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<td>1¼</td>
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<td>2</td>
<td>15</td>
<td>42</td>
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<tr>
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</table>

### Table 2.—Percentage of Species Recorded Breeding in Each Month

<table>
<thead>
<tr>
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Unfortunately, no adequate data exist for compiling similar tables for the adjoining, and even more arid, areas of South-West Africa and the Bechuanaland Protectorate. Moreau rightly made no attempt to do so, and there have been few additional data made available since he wrote. However, for the arid area to the south and southwest of Griqualand West, the western karoo ("arid warm" of Thornthwaite, "desert" of Köppen), I have been able to assemble data on 434 nests of 115 species. These have come from a wide variety of sources, including the South African Ornithological Society's collection of nest-record cards, the notes of the late S. F. Townsend again, and records kindly sent me by W. F. Quinton. Although no single month approaches the dominance of October in Griqualand West, the main breeding season seems to be just as concentrated as farther north; the period during which 14 percent or more of the nests were recorded and 20 percent or more of the species were coincidentally breeding covers 3 months only, August, September, and October, as against 4 months in Griqualand West—but 12 percent of the nests were recorded in November, when 34 percent of the species were breeding, so that the difference is small.

A second feature of the karoo figures is the suggestion of some recrudescence of breeding in March. The firm establishment of such an hypothesis must await further data, but I am inclined to think that the phenomenon is true in respect to years in which the normal summer rains of much of the area are delayed until autumn. Townsend (ms.) notes examples of this; others have been mentioned to me by my friend W. F. Quinton; and further examples are quoted by Rowan (1953) and Winterbottom and Rowan (1962). Keast and Marshall (1954) produce strong evidence that Australian desert birds "can respond quickly to rainfall, or its effects, so that nidification may begin within a few days of heavy precipitation," even in winter. Data on this point are meager for South Africa, but Moreau remarks that "apparently most species breed in South-West Africa when and where it rains." It is hoped that one of my staff will be able to start a full-scale investigation on the karoo in the near future.

SOUTHERN RHODESIA

An extensive series of data, published since Moreau's paper, is Miles's contribution in Smithers et al. (1957) for Southern Rhodesia. This massive set of facts relates to 6,976 nests of 387 species in an area of summer rainfall where the precipitation is mostly heavier than the 20-inch maximum suggested by Moreau as the limit for a "semi-arid" region (only the west and south fall into Thornthwaite's "semi-arid" climate, the rest being "sub-humid"). The peak period of breeding is somewhat less than that for Griqualand West, since only 3 months (September–November) show 14 percent or more of the nests recorded; but the much less drastic restriction of the Southern Rhodesian breeding season in general than in either of the
other areas considered so far is shown by the fact that the period when 20 percent or more of the species are breeding covers 8 months (August–March). The maximum of 58 percent is higher even than in Griqualand West, and the minimum also is generally higher than in the other areas considered so far. Moreau separates the water birds and the grassland birds from the rest in his consideration of breeding seasons. This has not been done in Tables 1 and 2, where only gross figures are given; but the figures are given in Table 3, with those for the Southwest Cape similarly divided. The division of the Southern Rhodesian figures in this way makes it clear that the long breeding season (Tables 1 and 2) is partly due to the “lumping” of the three categories together, and that the situation in respect to breeding seasons there is quite different from that in the Cape. Although there are minor

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falls off drastically in November and December. On the karoo, the rainfall pattern is similar, except that the bulk of the rain falls in February and March; the breeding season is about a month later than in Griqualand West, with a drastic fall-off in December from its September–October peak. These areas perhaps fall between the state of affairs in Natal and that farther north; but the relationship between breeding season and rainfall is the same in both and shows no shift in relation to peak rainfall. The Southern Rhodesia pattern is that which has been described by Moreau for regions north of Natal.

**Fig. 1. Relation of nesting season to rainfall in Griqualand West.**

**SOUTHWEST CAPE**

Another set of figures that has become available since Moreau’s paper involves the Cape Bird Club collection of nest-record cards up to December 1960, which are housed in the Percy FitzPatrick Institute. They relate solely to the winter-rainfall area of the Southwest Cape and comprise records of 7,509 nests and 200 species. Moreau and all previous and subsequent authors have treated this area as a unit for the purposes of calculating breeding seasons. With the much more extensive data now available, however, it is possible in some cases to test this hypothesis, with unexpected results. Of the total of 7,509 records, 3,905 relate to the Cape Peninsula (the magisterial districts of Cape Town, Wynberg, and Simonstown) and a further 1,328 to
Hottentots' Holland (the magisterial districts of Somerset West and Stellenbosch). Analysis of these records by months reveals distinct differences. Thus, in Hottentots' Holland, there is a distinct secondary peak in April not shown at all in the Peninsula; and the prominent September peak in Hottentots' Holland is prolonged into October in the Peninsula. Analysis of the breeding seasons of individual species shows similar discrepancies. That for the Cape Sugarbird has already been recorded (Winterbottom, 1962); other species that show significant differences between the two areas, which are only some 30 miles apart, are the Orange-breasted and Malachite sunbirds

(Nectarinia violacea and N. famosa), Cape Turtle Dove (Streptopelia capicola), Cape Wagtail (Motacilla capensis), Fiscal (Lanius collaris), and Bokmakierie (Malaconotus zeylonus). In all of these, as with the sugarbird, the breeding peak is later in the Peninsula than in Hottentots' Holland, but in the Karoo Prinia (Prinia maculosa), the breeding peak is earlier (M. K. Rowan, pers. comm.). The other feature shown by the sugarbird, more concentrated breeding season in Hottentots' Holland, is shown also by the wagtail, Fiscal, and prinia cited above; but the reverse is true of the dove, the Bokmakierie, and the Malachite Sunbird. Correlation with the flowering seasons of Proteaceae and slight correlation with rainfall has been shown for the sugarbird. The Orange-breasted Sunbird was discussed in a paper pre-

\begin{center}
\includegraphics[width=\textwidth]{fig2.png}
\end{center}

Fig. 2. Relation of nesting season to rainfall on the karoo.
presented to this Congress by G. J. Broekhuysen. The temperature patterns of the two areas are similar.

Schulze's map (1947) of the climates according to Thornthwaite's classification shows a complicated picture in the Southwest Cape, but is on too small a scale to make detailed classification of the nest-record cards practicable.

It had been hoped to analyze the records for farther east—the Bredasdorp and Swellendam districts—to see what effect might be induced by the more even distribution of rainfall in these areas. Although over 400 records were available, analysis of their monthly distribution suggested rather strongly that they were biased toward school holidays—an unfortunate result of there being no resident ornithologists—and they could not be used for this purpose. Subjective impressions of several reliable observers are, however, that breeding is later in this area.

If we apply the double criterion used for the other areas to determine the main breeding season, we find that for Hottentots' Holland the period during which 14 percent or more of the nests were found and 20 percent or more of the species were coincidentally breeding occupies the 3 months of August, September, and October. This is a month shorter and a month earlier, respectively, than in Griqualand West and a month earlier than in Southern Rhodesia; but 20 percent or more of the species were recorded breeding

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**Fig. 3. Relation of nesting season to rainfall in Southern Rhodesia.**

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over a period of 5 months, as against 4 for Griqualand West and the karoo
and 8 for Southern Rhodesia.

The Cape Peninsula shows 4 peak months, the “14–20 percent” period
being prolonged into November; and the period during which 20 percent or
more of the species were breeding extends over 7 months (July–January),
only a month less than in Southern Rhodesia. In both Southwest Cape areas,
the peak month for species breeding shows a higher maximum percentage
(77 percent for the Peninsula, 64 percent for Hottentots’ Holland) than in
any of the other areas discussed. The Cape Peninsula also shows a slightly
higher minimum. Two species in the Peninsula, the White-fronted Plover
(Charadrius marginatus) and the Olive Thrush (Turdus olivaceus), have
been recorded with eggs in every month of the year and the Cape Sparrow
(Passer melanurus) in every month except June.

**DISCUSSION**

Following Moreau, it has been assumed here that most of the phenomena
discussed can be related to rainfall; and Ennion and Ennion (1962) have
adopted a similar view for Tenerife. We must, however, exercise some cau-
tion. On the “20 percent breeding” criterion, the area with the longest
breeding season is Southern Rhodesia; this is also the area with the most
extreme differences between wet and dry seasons (78 percent of the total
rain falls in the 4 wettest months and only 1 percent in the 4 driest months).
Next in length of breeding season comes the Cape Peninsula, where only 57
percent of the total rain falls during the 4 wettest months and as much as
15 percent during the 4 driest. The karoo and Griqualand West show a
marked similarity in breeding seasons, yet precipitation percentages of the
4 wettest months are 51 and 66 percent, respectively, and of the 4 driest
months, 12 and 15 percent. It was thought that reliability of rainfall or some
extreme factor, such as minimum precipitation (lowest rainfall as a per-
centage of the normal), might offer a solution, but inspection of the relevant
maps (Weather Bureau, 1957) did not confirm this. It is, however, possible
that the apparently very long breeding season in Southern Rhodesia is partly
due to combining the records for the whole territory in which rainfall aver-
ages vary from over 70 inches on the eastern border to less than 16 inches
in the Limpopo valley, and which both Thornthwaite and Köppen divide
between three different major climatic zones (although their boundaries do
not agree with one another); and that, by breaking the records down into
more homogeneous areas, considerable differences between various parts of
the country might be revealed, as has been shown here to exist within the
much more limited and homogeneous area of the Southwest Cape.

Finally, acceptance of the view that breeding seasons are geared to rainfall
does not necessarily invalidate the view, based on birds of the North Tem-
perate Zone, that the major regulating factor of the breeding cycle is light.
But for regions of irregular rainfall, like the karoo, I think that some factor
connected with rainfall must be an important proximal cause of breeding and may well completely override the normal cycle if abnormal rains fall. Disney and Marshall (1956) have shown the unlikelihood of light having any influence on the breeding of the Red-billed Quelea (*Quelea quelea*) in Tanganyika, and the whole problem needs full-scale investigation in Africa.

ACKNOWLEDGMENTS

I must thank my colleague, Mrs. M. K. Rowan, for reading this paper in draft, making helpful suggestions, and drawing my attention to certain references; G. Maclean for help in tabulating records and for drawing the graphs; and W. F. Quinton for unpublished records from the karoo.

SUMMARY

The peak of the breeding season in Griqualand West is in October; on the karoo in September and October; in Southern Rhodesia in October and November; and in the Southwest Cape in September. In Southern Rhodesia, birds dependent on grass show a breeding peak in January and water birds in September; but this is not the case in the Southwest Cape, where the peak breeding for these birds is the same as that for others. The main breeding season for all areas except the Southwest Cape is before the peak rainfall; in the Southwest Cape, it is after this peak. Analysis of figures for the Cape Peninsula and Hottentots’ Holland, areas of the Southwest Cape some 30 miles apart, shows that there are interesting differences between the two, both in general and in respect to certain individual species. The possibility of direct response to out-of-season rains on the karoo is suggested.

LITERATURE CITED


Drought Adaptations in Australian Desert Birds

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It has been known for a long time that most birds in northern and central Australia breed according to rainfall. The “ultimate factors” through which the breeding seasons have developed phylogenetically are food, nesting site, and nest-building material. For most species, they are at their best during, or shortly after, the wet season.

There is, however, a difference between northern and central Australia. In the North, there is a fairly regular wet season caused by monsoonal rains from about December to April (Fig. 1). Consequently, the birds of northern Australia have a fairly fixed breeding season. They start to breed in a definite sequence according to their special requirements. In general, the first to breed are insectivorous birds, followed by nectar feeders, frugivorous species, and, finally, by seed-eating birds (cf. Frith and Davies, 1961). Central Australia, on the other hand, is situated between the summer rains of the North and the winter rains of the South. Occasionally, a single cyclone from either region may reach the center of the continent. Theoretically, there may be rain in any month of the year, but rain may be lacking for many months or even for years (Fig. 1). Therefore, in central Australia birds may breed at any time of the year according to rainfall (cf. Keast and Marshall, 1954). Although the ultimate factors for the breeding seasons have to be the same in both regions, differences in the “proximate factors,” which actually influence gonadal development and breeding behavior, are to be expected. The proximate factors for the breeding seasons in northern Australia will be discussed elsewhere (Immelmann, 1963). They are similar to those in the equatorial regions of other parts of the world. The present paper is concerned with the proximate factors for central Australian birds, and with the special adaptations of these birds to their irregular breeding season.

In 1959 and 1960, I spent 8 months in northwestern (Kimberley Research Station), northern (Katherine), and central Australia (Alice Springs). In the North, I have seen the end of the dry season and the entire wet season. In the center of the continent, I was fortunate enough to see heavy rains after several months of dry weather.

PROXIMATE FACTORS FOR THE BREEDING SEASONS

Many authors have discussed the proximate factors for the breeding seasons of birds in lower latitudes (for literature, see Marshall, 1959). In contrast to the temperate zones, there is no all-important single factor, but a combination of many factors, most of them associated with rainfall, such as sudden changes in food supply (proteins, vitamins), humidity, cloud cover,

changes in the general appearance of the environment (growing of green grass), availability of soft nesting material, etc. In central Australia, however, the picture is quite different. Rain is completely irregular, and food supply depends entirely on rainfall. After a rainfall, insect life becomes abundant and fresh vegetation appears. But the time of food abundance, in general, lasts only for a few weeks. Therefore, the birds have to start breeding as soon as possible in order to complete at least one breeding cycle

![Figure 1. Monthly distribution of rainfall (30-year averages).](image)

before the food supply becomes scarce again. Consequently, most of the proximate factors mentioned above are just too late for the climatic conditions in central Australia. All factors connected with the astronomical year (e.g. light, temperature) are to be excluded as a whole since the birds may breed at any time of the year. Furthermore, even many factors causally connected with the rains can be ruled out. Food supply, the supply of nesting material, and the general appearance of the environment may still be unchanged, yet many birds start to breed before the effects of rains have caused any perceptible alteration. It is to be concluded, therefore, that rain itself must have a stimulating effect on gonadal development. Rain itself is the earliest possible timegiver for a breeding season causally connected with the influence of rain on food supply.
This hypothesis has been proved by several observations, concerned pri-
marily with the Zebra Finch (*Taeniopygia castanotis*) and the Black-faced
Wood-Swallow (*Artamus melanops*). In early May 1960, heavy rain fell
near Alice Springs, bringing a dry period of several months to its close. In
both species, a real outburst of courtship and nest-building activity was then
observed. In several pairs of the Wood-Swallow, courtship started several
minutes after the beginning of the rain. The first copulation occurred about
2 hours later. The Zebra Finches, too, started to copulate before the end of
the heavy downpour, which lasted for about 4 hours. A similar outburst of
courtship activity was seen in other passerines shortly after the rains had
ceased. Several species of parrots, the first being the Budgerigar (*Melopsit-
tactus undulatus*), suddenly began frequent mutual courtship feeding.
Furthermore, the Zebra Finch and Wood-Swallow began to pick up rootlets and
twigs while it was still raining. The next day both species were engaged in
nest-building activities. White (1950) observed swallows (*Hylochelidon
nigricans*) carrying nesting material a few hours after a heavy rain.

From these observations, it seems quite obvious that rain itself has an
important function as a *Zeitgeber*. The next question is concerned with the
way in which the rain acts upon the birds. It might be the sight, sound, or
smell of the rain, the low pressure, the high humidity, or the drenching of
the birds’ plumage. No decision is possible yet. Maybe the rain acts through
several receptors simultaneously. There are several indications, however,
that it might be the *sight of the falling rain* which acts as the actual Zeit-
geber. In the Kimberleys, one thunderstorm without any rain and one heavy
downpour of rain at night did not effect stimulation. Niethammer (pers.
comm.) made similar observations in Bolivia. Serventy (1946) was the first
to assume that “it might be the sight of the drenching rain itself” which
actually stimulates breeding activities. This hypothesis is supported by the
fact that other proximate factors known to bring birds into breeding condi-
tion are also acting through the eye (Farner, 1959: light; Matthews, 1939,
and Lehrman, 1958: presence of a mate, etc.).

As a result of the stimulating effect of the rainfall, the first three Wood-
Swallow nests were completed 6, 7, and 9 days after the beginning of the
rains. One Zebra Finch nest was ready for eggs 7 days after the rains had
begun. Similar observations were made in Western Australia where there
was an exceptional summer rain on 30 and 31 December 1959. On the 12th
and 13th of January, Dr. Serventy and I found in three breeding colonies 6
fresh clutches, 1 newly built nest, and 22 old nests reroofed, relined, and
ready for eggs. The first eggs must have been laid on 9 January, i.e. on the
11th day after the rains had begun. In Alice Springs, the first Wood-Swal-
lows laid eggs 12 days and the first Zebra Finches 13 days after the first
rains. McGilp (1919) observed in the interior of South Australia that the
Desert Chat (*Ashbyia lovensis*) ovulated 11 days after the beginning of a
2-day downpour which broke a prolonged drought.
SPECIAL ADAPTATIONS IN AUSTRALIAN DESERT BIRDS

In many birds of central Australia, peculiarities in behavior and in physiology have been observed that might help to speed up the response to rainfall and thus support the effect of the proximate factors. These peculiarities are clearly understood to be adaptations facilitating the quick start of breeding required after rain has fallen.

Pituitary Activity

In the Zebra Finch, Farner and Serventy (1960) noted a tonic gonadotropic activity of the hypothalamo–hypophysial axis unless inhibited by certain external factors (such as low temperatures, scarcity of water, etc.). Farner (pers. comm.) has never found any Zebra Finches with gonads completely inactive. This constant gonadotropic activity of the pituitary gland expresses itself through a certain amount of courtship activity that can be observed the year round. Both may considerably help to shorten the time between the first rain and ovulation.

Breeding Potential

Extended droughts may enormously reduce the populations of central Australian birds (cf. Finlayson, 1932; Keast, 1959). The short periods of favorable living conditions, therefore, have to be utilized for reproduction as profitably as possible. This is achieved by an increase in the number of broods and by an increased clutch size in a good year (for detailed discussion, cf. Keast, 1959). Furthermore, two special adaptations have been observed that might help to enlarge the number of breeding pairs:

a) Breeding Age.—Young birds are able to start breeding very early. Vaugien (1952, 1953) found spermatozoa in young Budgerigars 52 days after they had left the nest. Zebra Finches that were still in juvenal plumage at the beginning of the experiment developed spermatozoa within 60 days (Marshall and Serventy, 1958). In one bird, the testis was even seen to be undergoing postnuptial steatogenesis. A color-banded female in Australia laid her first egg on her 86th day of life. Other females started breeding at 13 and 14 weeks of age. Further data are available for captive Zebra Finches in Australia. Two pairs whose parents were captured in the interior of northwestern Australia started their first clutch at 11, and their second clutch at 16–17 weeks of age. One female laid her first egg on her 44th day of life (Serventy, pers. comm.). The Gouldian Finch (Chloebia gouldiae) may even start to breed in juvenal plumage, if conditions are favorable. I have seen young birds courting and copulating while still being fed by their parents. I have seen other families with both parents and young in juvenal plumage. These observations indicate that the species mentioned do not seem to have any juvenal refractory period. Miller (1959) reports the same for the South American Zonotrichia capensis.

b) Adaptation to Molt.—Even molting birds have been observed to start
breeding shortly after rain. The Ground Cuckoo-shrike (*Pteropodocys maxima*) has been found in full molt while sitting on eggs (Soderberg, 1918), and Apostle-birds (*Struthidea cinerea*) have been found to start nest building after an overnight rain (Keast, 1959). Although the latter birds were in full molt, the testes of the males were proliferating sperm and the ovaries of the females appeared to be equally ready. Such birds continue molting while they are breeding, but it is unknown whether the molt is slowed down. I have observed simultaneous molting and breeding in the Budgerigar, the Zebra Finch, and the Black-faced Wood-Swallow.

**Nomadism**

Many species of central Australian birds are distinctly nomadic (cf. Keast, 1960). Their migrations are primarily forced by the lack of food or water. In most species, these movements seem to be completely irregular. Robinson (1949), however, has suggested that certain species, such as the Masked Wood-Swallow (*Artamus personatus*), may follow a low-pressure gradient to reach localities where there has recently been rain. This might be the case in some wild ducks of central Australia. According to Frith (1957), newly flooded areas are almost immediately colonized by large numbers of Grey Teal (*Anas gibberijrons*).

**Nest-building Behavior**

A very interesting adaptation in nest-building behavior has been observed in the Zebra Finch. In this species, as in most members of the grass-finches (*Spermes tidae*), the male transports pieces of grass while the female sits in the growing nest and works them in. Much time is wasted as the female sits drowsily until the male brings a new piece of grass. In central Australia, however, both sexes participate in carrying the material to the nest. In this way, the time required for completion of the nest may be shortened considerably. In New South Wales, about 13 days are needed (Frith and Tilt, 1959), while in central Australia, nests have been completed within 7–11 days.

**Other Behavioral Adaptations**

Finally, several behavioral adaptations must be mentioned that seem to promote mutual stimulation and synchronization of a pair, or of a group.

a) **Pair Bond.**—The majority of Australian birds seem to pair for life. At least pair formation takes place long before the onset of the breeding season. After pair formation, several behavior patterns may serve to cement the pair bond:

α. Both sexes may sing in duets simultaneously or alternately. I have heard duet singing in 15 species (Table 1), and in the literature there are records for at least 10 more species (for literature and further discussion, see Immelmann, 1961).

β. In many grass-finches, special bowing ceremonies have been developed between the partners of a pair (Immelmann, 1962). In the parrots, frequent mutual feeding takes place between male and female.
Table 1.—Species Observed Duet Singing and Group Singing in Northern and Central Australia

<table>
<thead>
<tr>
<th>Species</th>
<th>Duet Singing</th>
<th>Group Singing</th>
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<tbody>
<tr>
<td>Grus rubicunda</td>
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<tr>
<td>Centropus phasianinus</td>
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<td>Daceo leachi</td>
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<td>Pomatostomus temporalis</td>
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<tr>
<td>Pachycephala rufiventris</td>
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<td>Melithreptus laetior</td>
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<tr>
<td>Myzomela pectoralis</td>
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<tr>
<td>Conopophila rufogularis</td>
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<tr>
<td>Meliphaga flavescens</td>
<td>X</td>
<td>—</td>
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<tr>
<td>Stomiopera unicolor</td>
<td>X</td>
<td>—</td>
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<tr>
<td>Acanthagenys rufogularis</td>
<td>X</td>
<td>—</td>
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<tr>
<td>Philemon argenteceps</td>
<td>X</td>
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<tr>
<td>Gymnorhina tibicen</td>
<td>X</td>
<td>X</td>
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<tr>
<td>Crearticus torquatus</td>
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<td>X</td>
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<tr>
<td>Grallina cyanoleuca</td>
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</table>

γ. Several insectivorous birds maintain a territory all the year round. It is defended jointly by male and female (cf. Robinson, 1949).

δ. In the Grey-crowned Babbler (Pomatostomus temporalis), most of the grass-finches, and a number of honeyeaters (Meliphagidae), a strong nest-building drive is maintained throughout the year, or at least long before the onset of the breeding season. The birds construct many nests until they finally start to lay.

b) Group Formation.—During the nonbreeding season, scarcity of food and water will force many birds of northern and central Australia to congregate in flocks. Several species, however, maintain the group formation even during the breeding season when there is no actual need for doing so. All northern and central Australian grass-finches breed in loose colonies. Once or twice a day the members of one or several colonies come together for social meetings during which they feed together, bathe together, preen each other, etc. (Immelmann, 1962). In colonies of wood-swallows, up to six adult birds have been observed to feed the young in one nest. In the Grey-crowned Babbler, the whole colony participates in constructing the nests and in feeding the young. Furthermore, birds that defend fairly large territories in coastal areas tend to breed in colonies in central Australia. This has been observed by White (1949, 1952) for Ephthianura tricolor and Lalage seuerii. In southwestern Australia, the breeding colonies of the Zebra Finch usually contained only one nest per tree. In central Australia, I found up to nine nests per tree, even when there were equivalent trees in the neighborhood. Near Oodnadatta, McGilp (1944) found 21 occupied nests in a single tree. The colonies of Artamus melanops, too, are more compact in central Australia. As in pair formation, several behavior patterns may serve to hold the group together:

a. In several species, two or more pairs may join to sing in choruses. This group singing, which probably originated in duet singing, has been observed in five species (Table 1).
β. Several species have developed greeting ceremonies between the members of a group or a breeding colony. In the wood-swallows, these ceremonies originated in juvenile food-begging. In the grass-finches and in the Grey-crowned Babbler, on the other hand, they have been derived from courtship activities which have become independent of gonadal development and probably have been coordinated with an independent social drive (for discussion, see Immelmann, 1962). *Poëphila personata* possesses a special call that is used only in group encounters. In several other species of grass-finches one bird may sing while other members of the colony are listening (“peering”) (cf. Moynihan and Hall, 1954; Morris, 1958; Immelmann, 1962).

γ. Finally, various joint activities may help to hold the group together. In the wood-swallows a predator is attacked by the whole colony. In the Grey-crowned Babbler the nests are built by the whole group. In the Magpie Lark (*Grallina cyanoleuca*), the flock may engage in joint flight displays (Robinson, 1946–47).

c) Conclusions on Other Adaptations.—In doves, it has been shown experimentally that ovulation in the female may be promoted by the courtship of a male, by the mere presence of a male, and by joint activities of the pair (Craig, 1911; Matthews, 1939; Lehrman, 1958, 1959). It has also been suggested that mutual stimulation in breeding colonies may help to synchronize the group and to accelerate ovulation (Darling, 1938; Johnson, 1941; F. H. A. Marshall, 1936; A. J. Marshall, 1960; White, 1952; and others). It therefore seems almost certain that the above-mentioned special behavior patterns and joint activities, or at least part of them, may serve the same purpose. Together with the constant activity of the gonads, the lack of a juvenile refractory period, the nomadism, etc., they contribute to achieving a quick response to the Zeitgeber for breeding. In this respect, they have to be regarded as being adaptations to the irregular breeding season in central Australia.

**SUMMARY**

Most of the birds of central Australia breed at any time of the year according to rainfall, this being a consequence of the irregular distribution of rain in this area. After rainfall there is a short period of abundant food supply. In order to use this period for reproduction as profitably as possible, birds have to start breeding immediately after the rains have begun. This is achieved by peculiarities in the “proximate factors” that actually bring birds into breeding condition. In contrast to other climatic regions, rain itself seems to play an important role as a proximate factor. Rain is the earliest possible Zeitgeber for a breeding season causally connected with the influence of rain on food supply. In the two species under close observation, the Zebra Finch and the Black-faced Wood-Swallow, it seems to be the sight of the falling rain that actually influences gonadal development and breeding behavior.

Several peculiarities in physiology and in behavior of central Australian birds are described that may contribute to achieving a quick response to the Zeitgeber for breeding: a constant gonadotropic activity of the pituitary gland, the lack of a juvenile refractory period, the ability to molt and breed simultaneously, and finally several behavior patterns that cement pair bond
and group formations, and that may help to promote mutual stimulation and synchronization of a pair or of a group.

LITERATURE CITED


Quelques Adaptations écologiques des Oiseaux des hautes Andes péruviennes

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Au Pérou, les Cordillères des Andes forment de puissantes chaines parallèles, au relief très complexe. En schématisant à l'extrême, on peut reconnaître deux Cordillères, l'une occidentale, l'autre orientale, entre lesquelles s'étendent des hauts plateaux d'altitude voisine de 4,000 m, parfois plus élevés. Dans le Sud du Pérou, cet étage andin s'étend sur une superficie énorme par suite de la puissance des chaines qui atteignent leur amplitude maximale à cette latitude.

Ces circonstances géographiques ont déterminé dans l'étage haut andin un climat très rude et sévère, auquel ont dû s'adapter les oiseaux qui l'ont colonisé.

Ces oiseaux ont dû bien entendu avant tout s'adapter à l'altitude elle-même, qui entraîne une raréfaction de l'air, donc une baisse de la tension d'oxygène. Pour lutter contre cette asphyxie véritable, les oiseaux présentent une série de modifications physiologiques encore mal connues, mais qui doivent être du même ordre que celles que présentent les Mammifères. Ces adaptations ne sont cependant pas primordiales. Au cours de leurs vols migratoires, certains oiseaux partis de régions basses sont capables de voler à très grande altitude, donc d'accomplir un travail physique très intense dans une atmosphère raréfiée, sans présenter de gêne apparente.

Les adaptations dont ont dû se rendre capables les oiseaux des hautes Andes appartiennent beaucoup plus au domaine écologique. Le milieu haut andin—l'altiplano des Péruviens—est en effet très sévère, notamment dans le Pérou méridional, beaucoup moins humide que les secteurs plus septentrionaux des Andes.

Comme beaucoup de climats montagnards, le climat andin se caractérise par ses basses températures (la température moyenne annuelle de Vinococaya, localité située à 4,380 m d'altitude, à l'Ouest du lac Titicaca, n'est que de +1°,9), et surtout par d'énormes écarts de température journaliers: à une température diurne de +20° correspond souvent un minimum nocturne de −15°; cette amplitude de variation est maximale pendant la saison sèche, aucune précipitation ne venant alors tempérer le refroidissement nocturne. Les effets de l'insolation accentuant encore ce phénomène, il n'est pas rare d'enregistrer des températures de +50° pendant le jour au niveau du sol (le thermomètre étant bien entendu protégé du rayonnement direct qui ne manquerait de fausser les mesures).

Le régime des pluies comporte certes une saison pluvieuse, qui correspond à l'été austral et s'étend de novembre à mars, au cours de laquelle tombent...
de 800 à 1,200 mm d'eau, parfois plus; mais en dehors de cette période sévit une sécheresse accusée, encore aggravée par l'insolation très intense à cette période de l'année et par les vents violents qui balayent en quasi permanence les hauts plateaux. Les effets combinés du froid, de l'aridité et de l'insolation déterminent donc un ensemble de facteurs écologiques limitant très étroitement la colonisation des hautes Andes par les êtres vivants.

Cette influence s'est manifestée dans le couvert végétal. Les hautes Andes ne comportent aucune plante arborescente, sauf quelques rares exceptions. Le paysage végétal les plus répandu est constitué par une steppe à graminées (surtout Festuca), la puna des Péruviens; dans les lieux mieux protégés, s'étendent des associations broussailleuses comparables à un maquis pauvre et bas.

Ces conditions du milieu physique et du milieu végétal ont donc imposé des conditions très sévères aux animaux, et singulièrement aux oiseaux qui ont tenté la colonisation des hautes Andes du Pérou.

L'avifaune est dans l'ensemble d'une grande pauvreté, en raison du tri très sévère imposé par les facteurs du milieu. Cette pauvreté est particulièrement frappante quand on la compare à la grande richesse faunistique des contreforts orientaux des Andes, une des régions les plus riches du globe.

Cette faune n'est de loin pas répartie d'une manière uniforme tout le long des hautes Cordillères. Elle se concentre dans les lieux les plus favorables, ce qui fait que la distribution des espèces est dans la quasi totalité des cas largement discontinue. Le fractionnement en populations locales des souches initiales a eu une énorme importance dans l'évolution des espèces et la spéciation. Ce type d'évolution n'est d'ailleurs de loin pas propre aux oiseaux, car il se retrouve dans d'autres groupes de Vertébrés et en particulier parmi les Rongeurs.

Il faut par ailleurs remarquer que la réduction du nombre de phylums établis sur les hauts plateaux fait que par suite du manque de concurrence vitale, certains d'entre eux ont littéralement "éclaté" au point de vue évolutif et ont donné lieu à une radiation adaptative très caractéristique, chacune des espèces occupant une niche écologique différente (ce phénomène apparaît notamment parmi les Fringillidés du genre Phrygilus).

ADAPTATIONS RUPICOLES

Les adaptations les plus importantes des oiseaux andins sont donc d'ordre écologique. C'est aux conditions de l'habitat consécutives à l'altitude bien plus qu'à l'altitude elle-même que les oiseaux ont dû s'adapter.

Ces exigences sont de divers ordres et nous ne pouvons de loin pas les évoquer toutes ici. Nous nous contenterons de retracer brièvement celles qui ont trait à la biologie de la reproduction. Si nous faisons abstraction des oiseaux d'eau, particulièrement diversifiés sur les hauts plateaux en raison de l'abondance et de la variété des habitats aquatiques, nous constatons que plusieurs tendances se sont manifestées parmi les oiseaux quant au choix de
leur mode de nidification, constituant autant de solutions différentes à un même problème: la lutte contre les basses températures, les grandes variations thermiques journalières et les intempéries.

Une partie importante des oiseaux est devenue rupicole, mettant à profit un milieu éminemment favorable. Comme l’a dit Weberbauer (1945), aux limites de la vie végétale, le désert pierreux et les rochers constituent des oasis de chaleur dans un désert froid. Ceci est également vrai pour les animaux, et en particulier pour les oiseaux. Le rocher jouit en effet de constances thermiques extrêmement bénéfiques, car il se réchauffe plus vite que le sol meuble, et peut donc jouer le rôle d’un véritable volant thermique. De plus le rocher créé une multitude de microclimats particulièrement favorables.

Le meilleur exemple d’adaptation stricte au rocher se rencontre parmi les Trochilidés dont l’habitat caractéristique se trouve au voisinage des grandes falaises. Les espèces qui, au Pérou, ont peuplé l’étage haut-andin ne sont pas nombreuses, et ne comptent que les Oreotrochilus (melanogaster, estella), les Chalcostigma (olivaceum), Colibri coruscans, espèce à vaste répartition qui déborde la région andine, et Patagona gigas, plutôt caractéristique de l’étage tempéré.

Oreotrochilus estella, dont nous avons eu l’occasion de retracer la biologie dans le Sud du Pérou (Dorst, 1962b), aménage presque toujours son nid en étroit contact avec les parois rocheuses. Sur 143 nids étudiés, pas moins de 108 (soit 76 pour-cent) étaient placés contre le rocher; alors que 15 (10 pour-cent) seulement étaient construits dans des arbustes juste au pied des falaises, 18 (13 pour-cent) dans des Puya raimondii, gigantesques Broméliacées dont les feuilles dures protègent parfaitement contre les intempéries (ces plantes n’offrent d’ailleurs pas de grandes possibilités aux oiseaux en raison de la réduction extrême de leur distribution à travers les Andes): 2 de ces nids (1 pour-cent) se trouvaient dans des buissons non protégés directement par une avancée rocheuse. Comme l’a déjà observé Pearson (1953), les Oreotrochilus n’hésitent même pas à nicher dans de véritables grottes (cavités naturelles, anciennes galeries de mines) où règne une obscurité quasi totale. Ce milieu, à première vue étrange pour un Oiseau-mouche, est évidemment très favorable au point de vue thermique.

La construction du nid contre le rocher, dont on décèle déjà des tendances chez certains autres Trochilidés, notamment chez ceux des hauts plateaux mexicains (Lampornis clemenciae) étudiés par Wagner (1952), est donc devenu le mode habituel chez les Oreotrochilus. Ils bénéficient ainsi pleinement de l’influence favorisante de ce microclimat et notamment d’une bonne exposition du soleil. Ce dernier facteur est particulièrement important. Les heures les plus froides sont évidemment comme partout celles qui précèdent et suivent immédiatement le lever du soleil. Le thermomètre descend alors très fréquemment aux environs de 0° à -5° C. Or le soleil, vif à ces altitudes, permet un réchauffement sensible de toutes les surfaces jouissant d’une bonne exposition aux heures matinales. Les conditions thermiques deviennent
ainsi immédiatement favorables, le refroidissement de l'aube est en quelque sorte "escamoté" par suite du rayonnement direct. La comparaison des courbes de variations de températures prises sous abri (températures météorologiques) et celles qui traduisent les variations au flanc d'une falaise est particulièrement suggestive. Le réchauffement est même encore beaucoup plus sensible par suite du rayonnement direct, que nous n'avons pas pu mesurer, mais qui entraîne un réchauffement presque immédiat.

En relation avec ce fait écologique important, la grande majorité des nids fixés au rocher se trouve dans des falaises orientées vers l'Est. L'orientation des falaises étant distribuée au hasard et permettant donc des comparaisons ayant une valeur statistique, sur 108 nids construits au contact du rocher, 75 étaient placés contre des falaises orientées vers le secteur Est (70 pour cent), contre 33 au flanc de falaises orientées vers d'autres secteurs. Nous devons cependant remarquer que si le soleil a une action bénéfique aux premières heures du jour, il devient néfaste plus tard dans la journée, dès 8:00–9:00 A.M. C'est pourquoi tous les nids d'Oreotrochilus découverts au flanc de falaises étaient placés dans des sites protégés du soleil à partir de cette heure par une avancée de rocher en surplomb. Les nids sont ainsi placés d'une manière très précise de manière à bénéficier du rayonnement direct au lever du soleil, mais d'en être protégés dès que le rayonnement devenu trop violent risque d'avoir des effets pernicieux.

L'exemple des Trochilidés est particulièrement démonstratif, car il témoigne de la précision avec laquelle les oiseaux ont su s'adapter au rocher. Ils ne sont cependant pas les seuls à avoir adopté les falaises comme lieux de nidification, car cet habitat est également fréquenté par de nombreux Rapaces (Buteo poecilopterus, Phalacrocorax albopterus), des Ardéidés (Theristicus brachypterus), des Columbidés (Metriopelia melanoptera), des Psittacidés (Bolborhynchus aurifrons), et des Passereaux (Oreochelidon andecola).

**AUGMENTATION DE LA TAILLE DES NIDS**

La grande taille des nids aménagés par beaucoup d'oiseaux andins ne peut manquer de frapper l'observateur. Qu'il s'agisse d'oiseaux nichant dans des habitats rocheux ou au contraire d'oiseaux mettant à profit les quelques plantes arborescentes des hauts plateaux (en particulier les Rosacées du genre Polylepis et les Broméliacées Puya raimondii), on ne peut manquer de souligner le gigantisme des nids, hors de proportion avec la taille des oiseaux qui les construisent.

Ces particularités sont évidentes dans le cas des Trochilidés, dont le nid atteint une taille considérable, notamment chez les Oreotrochilus. La hauteur et la largeur minimales sont d'environ 75 mm, mais très souvent elles atteignent jusqu'à 150 mm. Le nid des Colibris des régions basses qui forme souvent une simple coupe de très petites dimensions, aux parois minces, est donc en singulier contraste avec ceux des espèces propres aux hautes Andes.

Les dimensions des nids des Passereaux sont dans le même rapport, en
particulier chez *Zonotrichia capensis* et divers *Phrygilus* (*Ph. gayi* entre autres).

Les oiseaux andins se font également remarquer par l'épaisseur des matériaux à haut pouvoir d'isolant thermique qu'ils entassent pour protéger leur couvée du froid. Ces matériaux comprennent de fins débris végétaux, notamment des fragments de frondes de Fougères (*Asplenium, Polystichum*) si abondantes au pied des falaises, de fruits surmontés d'aigrettes, de laine de mouton, de poils de Viscaches, de plumes amassées de manière à former un matelas épais limitant ainsi au maximum la déperdition de chaleur. Les œufs et les jeunes sont donc placés dans des conditions optimales, au fond d'une coupe bien isolée au point de vue thermique. L'aménagement d'un tel nid est également bénéfique aux adultes qui y trouvent refuge pendant la nuit, ce qui est particulièrement important dans le cas des espèces poecilothermes (*Oreotrochilus*; Pearson, 1953).

Certains oiseaux ont même poussé l'aménagement de nids calorifugés beaucoup plus loin, comme c'est le cas des Furnariidés du genre *Asthenes* notamment *Asthenes d'orbignyi*, assez commun sur les hauts plateaux du Sud du Pérou. Ces oiseaux disposent des amas de branchettes soigneusement entrelacées, atteignant communément de 50 à 60 cm de hauteur et un diamètre d'environ 40 cm, hors de proportion par rapport à la taille de l'oiseau. A l'intérieur de cet amas, les *Asthenes* aménagent un couloir d'accès menant à une chambre d'incubation centrale, dont les parois sont revêtues d'une épaisse couche de fins débris végétaux, de laine et de poils, offrant ainsi un abri remarquablement douillet aux jeunes et aux adultes qui s'y retirent pendant la nuit, même en dehors de la saison de reproduction.

**NIDIFICATION HYPOGÉE**

De nombreux autres oiseaux ont en revanche choisi un mode de nidification hypogée. Sans doute l'aménagement de véritables terriers n'est-il de loin pas propre aux oiseaux de hautes Andes, car il se rencontre dans le monde entier et est même caractéristique de certaines familles. Mais l'extension qu'il a prise sur les hauts plateaux parmi les types aviens variés montre qu'on peut le considérer comme une adaptation à la vie dans le milieu andin, où les lieux de nidification sont rares et où l'aménagement de galeries souterraines constitue une excellente solution au problème de l'isolation thermique (Dorst, 1962a).

Alors que l'amplitude journalière des variations de température dépasse souvent largement une trentaine de degrés, la température interne des terriers des oiseaux est le plus souvent d'une constance remarquable, ses limites de variations ne dépassant pas 2–3°. Ce mode de nidification évite donc les effets de l'insolation si forte au milieu du jour et du refroidissement nocturne si intense, réalisant l'économie d'une quantité d'énergie considérable aux oiseaux ayant adapté ce mode de nidification. D'après des travaux récents de Kendeigh (1961), la vie sous terre économiserait jusqu'à 13 pour-cent de
l'énergie chez les oiseaux nord-américains étudiés par cet auteur et l'économie est sans aucun doute encore plus considérable dans le cas des oiseaux andins, en raison des circonstances si particulières de leur habitat.

La nidification hypogée a par ailleurs l'avantage de mettre les couvées à l'abri des prédateurs et des intempéries, la grêle et la pluie étant fréquentes pendant la saison de reproduction.


Plusieurs catégories peuvent être distinguées selon l'aménagement interne des galeries. Certains oiseaux ne disposent aucun matériau de protection à l'intérieur de leurs terriers. Tels sont en particulier les Colaptes andins (*Colaptes rupicola*), qui nichent en colonies, principalement le long des berges creusées par les rivières dans le sol alluvionnaire meuble; alors que ce mode de nidification n’est que tout à fait occasionnel chez leurs congénères nord-américains (*C. auratus, caffer, chrysoides*), il est devenu le cas général chez l’espèce andine, ce qui mesure l’adaptation de ceux-ci au milieu haut-andin.

Ces Colaptes creusent des galeries s’ouvrant par une ouverture de 7–10 cm de large, sur une hauteur de 9–15 cm, se continuant par un tunnel de mêmes dimensions souvent de plus d’un mètre, aboutissant à une chambre d’incubation sphérique, de quelque 30 cm de diamètre. Aucun matériau de protection n’est déposé dans cette galerie, les œufs et les jeunes reposant sur le sol nu.

Il n’en est pas de même chez certains Passereaux, et en particulier chez les *Upucerthia*, parmi lesquels nous avons pu étudier en détail *Upucerthia validirostris*. Cet oiseau niche au fond de galeries profondes en général de plus d’un mètre, constituées par un tunnel d’accès de 15 cm de hauteur sur 10 de largeur, aboutissant à une chambre d’incubation d’une vingtaine de cm de diamètre. Le fond est garni d’une épaisse couche homogène sans structure définie, faite de débris végétaux, d’une texture comparable à de la paille hachée. Ces matériaux sont essentiellement formés de débris de Graminées (surtout *Festuca*) prélevés dans les pampas avoisinantes, réduits en fragments mesurant de 3 à 5 cm. Ce matelas isole les œufs du sol, bien que s’imprégnant d’une forte humidité.

Un stade d’évolution plus avancé encore s’observe chez certains autres oiseaux, et en particulier chez les Tyrannidés du genre *Muscisaxicola* dont nous avons pu observer une espèce assez commune sur les hauts plateaux du Sud du Pérou méridional, *M. rufivertex*. Ce Tyran terrestre niche dans des galeries souterraines au fond desquelles il construit un véritable nid, comparable à celui de certains Fringillidés. Ce nid se compose d’une assise basale faite de matériaux assez grossiers, sur laquelle repose une coupe faite de matériaux plus fins, comportant notamment des brindilles végétales et des
flocons de laine, de manière à constituer une protection très efficace contre le froid.

Ce mode de nidification associe donc les avantages d'un terrier et ceux d'un nid véritable, ce qui assure à la couvée les conditions optimales pour le développement des jeunes.

**RÉDUCTION DU TAUX DE REPRODUCTION**

Le mode de nidification des oiseaux andins qui reflète l'influence du milieu si particulier des étages les plus élevés des Cordillères, ne représente que quelques unes des adaptations à côté de beaucoup d'autres aussi bien physiologiques qu'écologiques. En dépit de ces adaptations au milieu les oiseaux andins témoignent cependant d'un taux de reproduction nettement inférieur à celui de leurs proches parents établis dans les régions basses plus chaudes. Cela se manifeste notamment par une diminution du nombre d'œufs par couvée. Le cas des oiseaux à vaste répartition est particulièrement démonstratif. C'est ainsi que, parmi les Fringillidés, *Zonotrichia capensis* ne pond que 2 œufs sur les hauts plateaux, alors que la ponte normale est de 4–5 œufs dans les régions basses. Cette loi paraît générale parmi tous les oiseaux des hautes Andes, en plein accord avec la règle selon laquelle les oiseaux vivant dans des climats froids ont des pontes moins nombreuses que ceux de pays chauds.

Les conditions sévères de l'habitat se reflètent par ailleurs dans les périodes d'incubation plus longues sur les hauts plateaux, et une croissance des jeunes notablement ralentie. Cela se vérifie notamment dans le cas des Trochilidés: chez les *Oreotrochilus estella*, la durée d'incubation est de 22–23 jours, alors qu'elle est de 12–14 jours chez *Selasphorus rufus*; les jeunes prennent leur envol à 30–40 jours, alors qu'ils se trouvent au même stade à environ 20 jours chez l'autre espèce.

En dépit de ces ralentissements, les oiseaux témoignent cependant de facilités d'adaptation remarquables, qui leur ont permis de coloniser les hautes Andes au climat rude et hostile à toute vie animale.

**SUMMARY**

*Some Aspects of Bird Ecology on the Peruvian High Andes*

On the Peruvian high plateaus and on the upper slopes of the Andes above 3,500–4,000 m, the rough Andean climate is characterized by low mean temperatures, excessive daily temperature fluctuations, and a long dry season during the austral winter combined with bright sunshine. The vegetative cover is therefore scanty and includes no arborescent plants.

Birds show various adaptations to this harsh environment, particularly those adaptations connected with low oxygen pressure, ecology, and breeding biology.

In search of suitable habitat, most Andean birds have become rupicolous. Hummingbirds, notably *Oreotrochilus estella*, build their nests close to rocks, with 75 percent of all nests in such situations, and some even in caves or
large crevices. Some 70 percent of the nests so found were facing east, taking advantage of sunrise warmth. Many other birds live under similar conditions, among them some raptors, ibises, doves, parakeets, swallows, and other passeriform birds. Many of the nests in these situations are constructed large enough to afford both adequate shelter and insulation from the extreme temperatures.

Other nest sites—such as burrows dug in sandy pits or steep riverbanks—are used year after year. Such burrows provide protection against rain, low nocturnal temperatures, excessive diurnal temperature extremes (30° C outside; only 2–3° C inside), and predators like Andean foxes. Inside, *Colaptes rupicola* and others lay eggs on bare earth, *Upucerthia validirostris* and others on a vegetal "mattress," and *Muscisaxicola rufivertex* even constructs a nest inside the chamber.

Birds show a very scattered distribution correlated with suitable habitat frequency. The open pampas support very low population densities. These increase as the shelter and vegetation increase, with a concomitant decrease in territorial defense.

Even with these adaptations for such extreme living conditions, Andean birds show a lower fecundity, expressed in smaller clutch sizes. Longer incubation and nestling periods, as well as slower weight increases, further reflect adaptive responses to this rigorous environment.

TRAVAUX CONSULTÉS


Desert Adaptations in Birds

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The experimental studies of the past 10 years on temperature tolerance and water balance (Dawson, 1954; Bartholomew and Cade, 1956; Salt, 1952; and others) have provided a good basis for judging some of the abilities and limitations of birds in meeting desert conditions of high temperature and restricted moisture supply. Some of these investigators, particularly Bartholomew and Dawson, have on occasion interpreted their findings as showing that birds have no unusual physiologic adaptations for these particular conditions. In respect to the conservation of fluids, nothing as striking has come to light as the ability demonstrated in desert heteromyid rodents (Schmidt-Nielsen and Schmidt-Nielsen, 1952) in which conserving mechanisms are sufficiently perfected to permit metabolic water almost alone to sustain the animal in good condition. Seeming disappointment in not finding like features in birds has led, I believe, to minimizing the significance of the lesser physiologic differentials which were discovered. The significance of these emerges especially when, in the field, we detect mortality in birds confronted with desert conditions and realize that small differences in ability to maintain water balance and to tolerate heat could have been critical to their survival. Furthermore, it is evident that we have tended to overlook certain physiologic preadaptations of birds to the desert extremes mentioned and as a consequence may have expected more spectacular adaptive modifications than the situation actually demands.

Two very general preadaptations and three that are somewhat more restricted, in that they do not apply necessarily to all birds, may be brought to notice:

1) The temperature of the body is, as is well known, sustained at the highest level of that of any animal group, a situation evidently related to the general success of birds as organisms of high activity and especially related to flight and coordination. The consequence of this is that the temperature gradient from the core area of the body (King and Farner, 1961) through the “shell” area and feathers to the environment is not destroyed or reversed until the ambient temperature is in the order of 105° to 107°F. Not until that level is reached is a bird at rest called upon to employ vigorously its special cooling mechanisms, especially evaporative cooling and water loss through the respiratory system. Thermal neutral points characteristically are somewhat lower, but even if metabolic efficiency diminishes somewhat before environmental temperatures reach 105°, birds generally are not under much stress from heat until the normal thermal gradient is eliminated. Compared with mammals, an unfavorable reverse gradient is estab-
lished at much higher ambient temperatures, and it is also less steep under most desert conditions. Moreover, there is a shorter period of each desert summer day when the reverse gradient is in effect (Fig. 1). Thus, the period of the day in which environmental shade temperatures exceed body temperatures may be 8 hours in a mammal with body temperature of 98° to 99° but only 4 hours for a bird—any bird. Indeed, for a number of days in summer, a bird will not reach the critical reversal point at all, whereas the mammal will reach it every day over a 3-month period.

2) A related preadaptation frequent in birds but still not established as present in a large spread of species is tolerance of hyperthermia, in which elevation of body temperature some 7°F. above normal can generally be tolerated (Bartholomew and Dawson, 1958). This is not confined to desert species but it is apparently absent in some nondesert birds (Salt, 1952). Moreover, this hyperthermia permits maintenance of a thermal gradient of the normal direction, up to or above 110°.

3) The kidney of birds, like that of mammals, has the ability generally to discharge concentrated nitrogenous waste and other electrolytes. Also, birds are able, as are reptiles, to transform much of the urea to precipitated uric acid and urates. Accordingly, much of the nitrogenous waste is discharged as semisolids with very little water required for transport and flushing. This low water usage in excretion is fundamentally superior to that in mammals generally and would seem to parallel the concentrated discharge of nitrogenous waste of heteromyid rodents, which has been regarded properly as a special desert adaptation.

4) Most species of birds retain the high mobility characteristic of the class. With their power of flight they have the basic capacity to adopt a regime of daily movements of substantial length to and from the limited water sources of the desert. Or they may engage in nomadism, shifting about to avail themselves of the transitory and irregular water supplies or moisture sources typical of arid lands.

5) Birds as a group are in high proportion insectivorous, much more so certainly than rodents and lagomorphs. Intertwined with the prevalence of insect diet is the general capacity for rapid movement. Accordingly, many
groups of birds, by feeding on insects, tap a moist food source. In desert areas, the very effective adaptive water-conserving mechanisms of insects have largely solved for many species of birds their water balance problem.

Reflecting on these very generally stated preadaptations and disregarding for the time being the refinements and the side effects entailed in these physiologic matters, it is not, I contend, surprising that spectacular new mechanisms have not evolved in birds in response to problems of high temperature and water balance. An animal species may not be expected to change in evolution any more than it has to in order to meet an environmental situation with reasonable success. The selection pressures on desert birds in view of their preadaptations may be presumed to be of such an order that nonspectacular refinements in their existing physiologic operations filled the need.

If this be granted, what evidence can we bring out that the refinements are significant? Selection can and does work on small differentials both of structure and function. And desert-dwelling species do have tight water budgets and narrow limits between operating temperature and lethal high temperatures.

Dawson (1954) in his study of two closely related types of brown towhee found that neither the desert species, Pipilo aberti, nor the coastal representative of P. juscus can stand exposure for 2 hours to the midday summer sun such as they might encounter in the desert. However, these two species merely avoid such sun and heat by seeking the shade of dense plant growths available in their respective habitats and reducing their activity in the midday period. But the desert species shows better ability to withstand high environmental temperatures that range above its body temperature than does its coastal counterpart (excluded from this comparison are the eastern races of juscus which have not been subjected to experimentation and may have different capacities from the coastal birds). However this may be achieved, whether through increased ventilation of the respiratory system or by other means, Dawson’s records of water loss show what appear to me to be meaningful differentials as air temperature exceeds 107.6°. From this level up to 113°, aberti showed (Fig. 2, below) increased water loss, as expected, but at the same rate of acceleration that prevailed below 107°, whereas juscus at 107° began using water at a much increased rate, indicating its stress under these circumstances. Indeed, it could not be tested above 110° because it would die in the experimental test chamber at this level. It is clear that aberti can and does sit out midday heat of 115° or more in its habitat, with some augmentation of water loss, whereas juscus would not be able to do so, even by using water at an extravagant rate. To be sure, Dawson cautions that we cannot be sure that this differential shown experimentally is entirely innate. There may be some element of acclimation involved, although this would not seem to account for all of the difference shown.
Another significant statistic that Dawson brought out is that at about 103° aberti conserves its water better than fuscus, using 18 percent less. Since this situation holds at an air temperature representative of much of the summer daytime period, and one under which some activity is carried on, it reflects an ability to save very materially on the water budget. I would hold that such a differential is a meaningful adaptive differential. Indeed, it hardly can be characterized as merely a lesser refinement.

The species Pipilo fuscus occurs in border sympatry at the desert edge in southern California with Pipilo aberti. Here we have found it confined in the Little San Bernardino, San Jacinto, and Santa Rosa mountains to areas in canyons where there is permanent water. May not the differentials in heat tolerance and efficiency of water use dictate this limitation and be the reason why fuscus does not here occupy the desert proper and invade beyond these water sources? Pipilo aberti, although often having access to water in the desert valleys, does occur in some places where it is wholly absent in summer. Both species are primarily seedeaters, but they can and do use insects and moist plant foods (Marshall, 1960:54-55) and must by this means augment their metabolic water and balance, or come close to balancing, their water budget. It then becomes a matter of the small degrees of efficiency as to whether this is fully balanced, especially during heat stress, without recourse to surface water. In fact, in the field, one apparently has
to resort to such water in the desert summer climate, whereas the other does not.

In another pair of closely related species, some significant differences in response to high temperature have been shown by Salt (1952). These are the finches *Carpodacus mexicanus* and *C. cassini*. The first is a widespread and successful year-around occupant of the desert. It is dependent on sources of free water or succulent fruit, as shown by an abundance of observations and by experimental verification (Bartholomew and Cade, 1956). This species has resorted to its mobility to solve its water problems and not to physiologic water-conserving devices. However, *mexicanus* does clearly tolerate high desert temperatures, with water utilization, whereas its relative *cassini* cannot. *Cassini* migrates to the desert lowlands in winter, but in summer it is restricted to the dry interior mountains at elevations where shade temperatures rarely reach 90°. Salt tested *mexicanus* and *cassini* in dry air (12 percent relative humidity) for metabolic rate (oxygen consumption) and showed that above 86° *mexicanus* brings into play respiratory cooling devices whereas *cassini* does not; the latter merely depressed its metabolic rate and died when the air temperature was 104° over a 1-hour period. Obviously *cassini* does not have emergency cooling mechanisms such that it can cope with air temperatures at or above its body temperature, whereas *mexicanus* does. The latter, as observed, withstands desert summer extremes of 115° or more.

Salt’s experiments have the further significant feature that all birds were acclimated to a common weather condition before being subjected to the experiments that demonstrated these differentials. We cannot escape the conclusion, then, that substantial innate differences are involved and that *mexicanus* has significant physiologic adaptations to deal with desert summer heat which *cassini* does not possess. Desert populations of *mexicanus* may be no better adapted for this than populations of the same species that occupy coastal lowlands; but even if this is so, it is clear that they are, compared to their congeneric relatives, desert adapted. Salt concludes that *mexicanus* “has a body-cooling system which represents a compromise between conservation and maximum cooling power. As a result, it is able to withstand high temperatures so long as the vapor pressure of the air remains fairly low. . . . Compared with the other two species [*cassini* and *C. purpureus*], it can operate efficiently in hotter climates than the Cassin finch and more efficiently in drier climates than the purple finch.”

I turn now to some related field observations in which the lethal effects of desert temperatures and drought have been noted. These observations comprise instances of selection in operation. Each year across the deserts of the lower Colorado River basin of the southwestern United States and northwestern Mexico move great numbers of migrant birds, passing between their mesic or even humid and cool breeding grounds and the wintering ranges in the mountains or mesic areas of the mainland of Mexico. Especially in the
fall migration period, the desert crossing of some 500 to 700 miles is undertaken by many species of warblers and flycatchers during severely dry and hot weather.

In the late summer of 1950 in the Joshua Tree National Monument, a party from the Museum of Vertebrate Zoology gave particular attention to this fall migration. From 22 August to 3 September the typical high daytime temperatures of the desert summer prevailed. At our camps at 4,500 to 5,000 ft elevation, midday temperatures were in the range from 100° to 105°; but lower down, a few miles away, temperatures were reaching 115°.

### Table 1.—Record of Condition of Fall-migrant Passerine Birds

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Specimens Taken</th>
<th>Number of Birds in Poor Condition</th>
<th>Known-age Distribution of Birds in Poor Condition</th>
<th>Minimal Weight Expressed as an Approx. Percentage of Normal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Empidonax traillii</td>
<td>11</td>
<td>2</td>
<td>2 adults</td>
<td>79</td>
</tr>
<tr>
<td>Troglodytes aedon</td>
<td>5</td>
<td>1</td>
<td>1 immature</td>
<td>62</td>
</tr>
<tr>
<td>Vireo gilvus</td>
<td>15</td>
<td>2</td>
<td>1 immature</td>
<td>79</td>
</tr>
<tr>
<td>Vermivora celata</td>
<td>13</td>
<td>4</td>
<td>4 immatures</td>
<td>65</td>
</tr>
<tr>
<td>Vermivora ruficapilla</td>
<td>11</td>
<td>3</td>
<td>1 imm.; 1 ad.</td>
<td>70 (had died)</td>
</tr>
<tr>
<td>Dendroica auduboni</td>
<td>2</td>
<td>1</td>
<td>1 immature</td>
<td>85</td>
</tr>
<tr>
<td>Dendroica nigrescens</td>
<td>8</td>
<td>2</td>
<td>1 imm.; 1 ad.</td>
<td>71</td>
</tr>
<tr>
<td>Oporornis tolmiei</td>
<td>8</td>
<td>2</td>
<td>2 immatures</td>
<td>82</td>
</tr>
<tr>
<td>Wilsonia pusilla</td>
<td>12</td>
<td>5</td>
<td>2 imm.; 2 ad.</td>
<td>70</td>
</tr>
<tr>
<td>Phenucticus melanoccephalus</td>
<td>13</td>
<td>1</td>
<td>1 immature</td>
<td>71</td>
</tr>
<tr>
<td>Passerina amoena</td>
<td>4</td>
<td>1</td>
<td>?</td>
<td>Dead and desiccated</td>
</tr>
</tbody>
</table>

**Totals** 102 24 15 imm.; 6 ad.

Each day. Migrant passerine birds were crossing through these lower areas, and many of them were collected there or in the higher levels soon after they had crossed the lower regions. Not until 3 September did a thunderstorm of the preceding night break the period of heat stress.

All small passerine birds that we obtained were weighed and usually, as they were prepared, the condition of their fat reserves and any abnormal aspects of the breast musculature were noted. The experiments on water deprivation in House Finches show that loss of weight to a level 70 to 80 percent of normal brings the bird to the lethal point. Similarly, in our field observations we found that warblers weighing 70 to 80 percent of normal were either dead or obviously weakened.

For example, Nashville Warblers (Vermivora ruficapilla) in good condition but not heavily supplied with fat ranged in weight from 7.4 to 8.0 g, but birds with conspicuous fat ranged up to 10.0 g. Individuals that weighed only 6.8 and 6.4 g were 10–15 percent below normal lean weight and showed obvious depletion of musculature. One weighing 5.3 g had just died at what represents about 70 percent of the weight of a bird in good condition.

In Table 1 are shown the 11 passerine species of which we took some specimens that showed evidence of poor condition during the heat-stress
period. These birds had all crossed areas of open desert and had encountered several days and possibly a week of daytime temperatures over 105°. Probably they were often subjected to much higher temperatures, for effective shade would not readily have been found.

Our most vivid observation was that of a Rufous Hummingbird (*Selasphorus rufus*) on 1 September. In the heat of the early afternoon this bird was seen from our camp flying low to the ground up an open wash. It dropped to the ground, resting, then took wing but dropped again. Finally it reached the shade of our camp and was so weakened that we could catch it by hand. It could not be revived and died within an hour. It was very thin and weighed but 2.5 g. Another bird, similarly exhausted, appeared the next day and weighed only 2.3 g; these birds were at least 20 percent under normal, nonfat weight. We had in the first instance seen the bird actually fail during a migratory flight in hot sun through an area without water or nectar sources. Other members of this species taken 2 weeks later were in some instances well supplied with body fat, which constituted a substantial food and water reserve.

It is manifestly improper to draw conclusions concerning the specific causes that had brought a large proportion of these desert migrants to death or to a point where no recovery could be expected. Many disease situations and nutritional inadequacies will cause loss of weight and reduction of the breast musculature. Severe conditions of heat, low humidity, and water loss may only be contributing factors in the morbidity of such birds and not the underlying ones. Still, if these environmental conditions are involved, as they seem to be, in the final determination of life or death, they must have considerable selective influence.

In this connection, the following general correlations suggest the significance of the extreme environmental conditions. We rarely found a lightweight, weakened bird in this desert area outside the heat-stress period. Only 1 of the 11 species listed in Table 1 was detected in poor condition more than 3 days following the substantial rain and cooling that set in on 3 September 1950. In the heat-stress period, small desert-dwelling, and evidently desert-adjusted or adapted species, such as gnatchatchers (*Polioptila*), Gray Vireos (*Vireo vicinior*), Black-chinned Sparrows (*Spizella atrorcularis*), and Bewick Wrens (*Thryomanes bewickii*), were in no instance found in a morbid state.

If the failing migrants had possessed favorable physiological differentials of the order seen between the species pairs of towhees and finches earlier discussed, they might well have survived the desert crossing in the heat-stress period. Such differentials might have been a lesser water requirement, as in *Pipilo aberti*, or a greater tolerance for high temperature for brief daytime periods, as in that species and in *Carpodacus mexicanus*. A differential might have consisted of a better response for premigratory fat deposition, which could have provided better reserves to cope with the short-term extremes encountered in the crossing.
The fact that the migrant species discussed do suffer heavy losses is evidence certainly of some substantial inadequacies in desert adaptation among them. One may ask why, if these species suffer mortality of this high rate in many or most years, have not the unfit elements in them been quickly eliminated or reduced to a very low level. This desert migration route has certainly been followed for many centuries under similar conditions. The answer may lie in the balance of opposing selective forces. Variants in these species toward an improved physiology for desert life might be less satisfactory or incompatible under conditions on the mesic breeding grounds. One might indeed envision a balanced polymorphism in one of these migrant species in which one morph excels in desert crossing and the other in some aspect leading to improved survival or success on the nesting ground. The balance of forces may in any one year shift for or against the capacity for desert crossing during heat stress. If such a species can chance upon a physiologic combination that will permit it to cope well with the contrasting demands, it would then, of course, move to a single, higher adaptive peak rather than straddle two lower peaks or climb one or the other temporarily through polymorphism. We suspect that the flycatchers Contopus richardsonii and Nuttallornis borealis have done so, as we have not found them in any difficulty in August. But probably many species have not yet found the step-by-step stairway leading up the superior peak.

**SUMMARY**

Successful occupancy of deserts is possible for many groups and species of birds without the development of striking special adjustments because of the existence of several preadaptations in their physiology. Chief among these are high body temperature, which reduces the periods when the normal thermal gradient from body to exterior is obliterated or reversed, and ability to discharge concentrated nitrogenous waste with little water loss. Other features which are widespread and predispose birds to desert existence are a tendency readily to withstand elevation of body temperature several degrees above normal, high mobility which makes nomadism and movement to and from limited water sources possible, and widespread insectivorous habit by which the insects supply a large proportion of the birds' water budget.

Correlation of experimental work on water balance and temperature tolerance with field observations on tolerance indicates the probable importance to survival of the physiological differentials that have been demonstrated. Observations of species that apparently lack these favorable physiologic adaptations during the heat-stress period of the autumnal migration through the Joshua Tree National Monument reveal many individuals succumbing or in a weakened state. Had these migrants from mesic areas possessed slightly improved temperature tolerance and better cooling and water-conserving mechanisms, they might well have shown much less mortality than the 24 percent suggested by the field records.
LITERATURE CITED


Ist die Mortalitätsrate adulter Ficedula hypoleuca wirklich unabhängig vom Lebensalter?

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In seinem bewunderungswürdigen Buch The natural regulation of animal numbers vertritt Lack (1954) die seitdem wohl allgemein anerkannte Meinung, dass bei freilebenden Vögeln—im Gegensatz zu Mensch, Haustieren und einigen anderen Tierarten—die jährliche Mortalität in allen Lebensjahren gleich gross sei. Derselben Ansicht ist auch Meunier (1960). Jedoch deuten beide bereits auf die Grenzen dieser These hin; denn so alte Exemplare, wie sie nach ihr bei vielen Arten—wenngleich selten, so doch regelmässig—auftreten müssten, finden sich offensichtlich in der freien Natur nicht. Der andererseits zu fordernde Anstieg der Mortalitätsrate mit höherem Lebensalter liess sich aber bei Vögeln bislang auch nicht nachweisen. Diese Frage des Gleichbleibens oder der Veränderung der Mortalitätsrate bei zunehmendem Alter sei im folgenden an unserem vom Trauerschnäpper (Ficedula hypoleuca Pallas) im nördlichen Deutschland gesammelten Material geprüft.

MATERIAL UND METHODE


Die Gesamtberingungszahl bis 1961 einschliesslich von rund 27 000 (genau erfasst 26 388 = 23 798 pull. + 2 590 meist ♂ ♂ ad.) Ficedula hypoleuca erbrachte bis 1962 einschliesslich—unter insgesamt 1 600 Rückmeldungen—1 436 in einem späteren Jahre als brütende ♂ ♂ wiedergefangene Stücke.


**Tabelle 1—Die Untersuchungsgebiete**

<table>
<thead>
<tr>
<th>Bezeichnung</th>
<th>Pflanzensoziologische Association</th>
<th>Grösse in ha</th>
<th>Nisthöhlenanzahl</th>
<th>Nisthöhlenendichte: Stück je ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Moorurwald&quot; (Abt. 61)</td>
<td>Betuletum pubescentis</td>
<td>10,4</td>
<td>176</td>
<td>16,9</td>
</tr>
<tr>
<td>&quot;Birkenbruch&quot; (Abt. 61 + 58)</td>
<td>Betuletum pubescentis</td>
<td>8,8</td>
<td>67</td>
<td>7,6</td>
</tr>
<tr>
<td>&quot;Erlenurwald&quot; (Abt. 45)</td>
<td>Alnetum glutinosae</td>
<td>10,5</td>
<td>226</td>
<td>21,5</td>
</tr>
<tr>
<td>&quot;Joneck&quot; (Abt. 70 + 74)</td>
<td>Querceto-Betuletum</td>
<td>10,2</td>
<td>175</td>
<td>17,2</td>
</tr>
<tr>
<td>&quot;Schnäbel&quot; (Abt. 78 + R 2)</td>
<td>Querceto-Betuletum</td>
<td>17,2</td>
<td>236</td>
<td>13,7</td>
</tr>
</tbody>
</table>


Da es—wie bei Freilanduntersuchungen häufig—unmöglich war, die Versuchsbedingungen vollkommen ideal zu gestalten, seien die unten dargelegten Ergebnisse aus dem behandelten Teilgebiet zunächst als Beispiel und vorläufiger Beitrag zur angeschnittenen Frage mitgeteilt sowie mit einem gewissen Vorbehalt bezüglich der unbedingten zahlenmässigen Exaktheit der angegebenen Prozentsätze. In allen wesentlichen Zügen werden jedoch die in dieser Arbeit gezogenen Schlussfolgerungen durch die bereits begonnene Auswertung des Gesamtmaterials bestätigt.

**RESULTATE**

Die 338 Rückmeldungen nestjung beringter und brütend wiedergefangener...
Berndt und Sternberg: Die Mortalitätsrate adulter *Ficedula hypoleuca*

Tabelle 2—Wiederfundsahlen der als Nestlinge beringten ♀♀ von *Ficedula hypoleuca* nach Altersklassen im Drömling

<table>
<thead>
<tr>
<th>Jahr des Wiederfanges</th>
<th>1-jährig</th>
<th>2-jährig</th>
<th>3-jährig</th>
<th>4-jährig</th>
<th>5-jährig</th>
<th>6-jährig</th>
<th>Summe</th>
</tr>
</thead>
<tbody>
<tr>
<td>1959</td>
<td>55</td>
<td>20</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>80</td>
</tr>
<tr>
<td>1960</td>
<td>39</td>
<td>27</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>71</td>
</tr>
<tr>
<td>1961</td>
<td>43</td>
<td>42</td>
<td>25</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>114</td>
</tr>
<tr>
<td>1962</td>
<td>26</td>
<td>19</td>
<td>21</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>73</td>
</tr>
<tr>
<td>Summe</td>
<td>163</td>
<td>108</td>
<td>52</td>
<td>13</td>
<td>2</td>
<td>0</td>
<td>338</td>
</tr>
</tbody>
</table>

♀♀ setzen sich aus 163 1-jährigen, 108 2-jährigen, 52 3-jährigen, 13 4-jährigen und 2 5-jährigen zusammen (Tab. 2).

Die Beringungszahlen der einzelnen Jahre und damit das Ausgangsmaterial für die Wiederfunde aus den verschiedenen Altersklassen waren jedoch nicht stets gleich gross (von 901 bis 5 014 variierend; Tab. 3, Zeile c); es muss daher eine Korrektur der Wiederfundsahlen derart erfolgen, dass die Zahl der Funde auf eine einheitliche Altersklassen-Beringungszahl umgerechnet wird, und zwar am besten auf die Durchschnitts-Beringungszahl aus allen Altersklassen. Um nun im einzelnen für die Wiederfund-Jahre 1959 bis 1962 zu ermitteln (Tab. 3, Zeile b), wieviel Exemplare als Ausgangsmaterial für die Altersklasse der 1-jährigen Vögel überhaupt zum Wiederfang zur Ver-

Tabelle 3—Wiederfundsahleinkorrektur, Mortalität und Überlebensrate bei den ♀♀ von *Ficedula hypoleuca* im Drömling, bezogen auf die Beringungszahlen im Drömling

<table>
<thead>
<tr>
<th>Altersklasse 1-jährig</th>
<th>Altersklasse 2-jährig</th>
<th>Altersklasse 3-jährig</th>
<th>Altersklasse 4-jährig</th>
<th>Altersklasse 5-jährig</th>
<th>Summe</th>
</tr>
</thead>
<tbody>
<tr>
<td>a tatsächliche Wiederfundsahlen von 1959–1962</td>
<td>163</td>
<td>108</td>
<td>52</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>c Summe</td>
<td>5014</td>
<td>4486</td>
<td>3331</td>
<td>2012</td>
<td>901</td>
</tr>
<tr>
<td>d auf die Durchschnitts-Beringungszahl von (15744 ÷ 5 =) 3149 korrigierte Wiederfundsahlen</td>
<td>102</td>
<td>75</td>
<td>49</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td>e Mortalität</td>
<td>26%</td>
<td>35%</td>
<td>59%</td>
<td>70%</td>
<td>100%</td>
</tr>
<tr>
<td>f Überlebensrate</td>
<td>74%</td>
<td>65%</td>
<td>41%</td>
<td>30%</td>
<td>0%</td>
</tr>
</tbody>
</table>
füngung standen, müssen wir die von 1958 bis 1961 einschliesslich beringten Nestjungen zusammenzählen und entsprechend für die 2-jährigen diejenigen von 1957 bis 1960, für die 3-jährigen von 1956 bis 1959, für die 4-jährigen von 1955 bis 1958 und für die 5-jährigen von 1954 bis 1957 (Tab. 3, Zeile b). Das sind jeweils 5 014, 4 486, 3 331, 2 012 bzw. 901 (Tab. 3, Zeile c), auf die sich also die in Tabelle 3, Zeile a angegebenen Wiederfundsahlen beziehen. Legen wir nun für alle Altersklassen gleichmassig die durchschnittliche Altersklassen-Beringungszahl von $(5 014 + 4 486 + 3 331 + 2 012 + 901 = 15 744 : 5 =) 3 149$ zu Grunde, so ergeben sich als korrigierte Wiederfundsahlen 102 1-jährige, 75 2-jährige, 49 3-jährige, 20 4-jährige und 6 5-jährige, was insgesamt 252 Wiederfunden entsprechen würde (Tab. 3, Zeile d). Im folgenden werden zunächst nur diese Zahlen weiter verwendet. Zur Berechnung der durchschnittlichen jährlichen Mortalität—von uns "Durchschnittsmortalität" genannt—wenden wir folgenden Grundsatz an: Bei stabilier Population entspricht die Durchschnittsmortalität dem Anteil der Erstbrüter an der Population, und zwar unabhängig davon, ob die Mortalität in den einzelnen Lebensjahren gleich oder verschieden ist. Unter der Voraussetzung eines Bestandsgleichgewichts muss nämlich die Zahl der in eine Brutpopulation neu eintretenden Erstbrüter jeweils gleich der Summe der aus allen Altersklassen wegsterbenden Individuen sein.

Bei Zugrundelegung dieser Formel

$$\text{Durchschnittsmortalität} = \frac{\text{Erstbrüter}}{\text{Gesamtpopulation}}$$

ergibt sich für die untersuchte braunschweigische Ficedula-hypoleuca-Population $m = 102/252 = 0,40$ bzw. eine Durchschnittsmortalität von 40% und dementsprechend eine Durchschnittsüberlebensrate von 60%.

Für diese und die folgenden Fragen kann durch die Ab- und Zuwanderung beringter und unberingter alter ♀♂ kein nennenswerter Fehler entstehen, da bislang im weiblichen Nomadisieren bezüglich des Alters weder qualitative noch quantitative Unterschiede gefunden werden konnten (Berdnt, 1960 und unpubliziert). Da wir außerdem festgestellt haben (unpubliziert), dass in diesen Untersuchungsgebieten schon weitgehend auch die einjährige ♀♂ zur Brut schreiten, kann sich auch kein wesentlicher Fehler dadurch ergeben, dass die Einjährigen noch nicht voll erfassbar wären.

Um die Frage nach der Abhängigkeit bzw. der Unabhängigkeit der Mortalitätsrate im adulten Stadium vom Lebensalter beantworten zu können, berechnen wir im folgenden die Mortalität von jedem einzelnen Lebensjahr zum nächstfolgenden—von uns "Altersklassen-Mortalität" genannt—and gleichzeitig die sich im Zusammenhang damit ergebende Überlebensrate—dementsprechend als "Altersklassen-Überlebensrate" bezeichnet. Aus der Tabelle 4 erweist sich, dass die Mortalität der Ein- und Zweijährigen ± niedriger (26 bzw. 35%) und die der Drei-, Vier- und Fünfjährigen ± höher (59%, 70% bzw. 100%) als die Durchschnittsmortalität von 40% liegt. Die Mortalität ist also nicht nur von Jahr zu Jahr verschieden, sondern steigt mit zunehmendem Lebensalter immer weiter an. Das Umgekehrte ist selbstverständlich der Fall bezüglich der Überlebensrate (74%, 65%, 41%, 30% bzw.
Dafür, dass der Mortalitätsprozentsatz von den Dreijährigen zu den Vierjährigen nicht noch stärker ansteigt, kann die Kleinheit des Zahlenmaterials aus diesen älteren Jahrgängen verantwortlich sein.

Alle oben angegebenen Prozentsätze über Durchschnittsmortalität, Altersklassen-Mortalität bzw. Überlebensrate dürften jedoch nicht voll den tatsächlichen Verhältnissen entsprechen, sondern eine gewisse Korrektur benötigen. Unter den Wiederfängen befinden sich nämlich eine Anzahl von Exemplaren, die in entfernteren Versuchsgebieten nestjung beringt sind, also aus einer anderen Population stammen, deren Beringungszahlen bei der Umrechnung der Fundzahlen nicht mit zu Grunde gelegt sind. Diese Wiederfänge dürfen aber auch keineswegs fortgelassen werden, da sie die Verluste ausgleichen, die die Untersuchungspopulation durch Abwanderung nomadisierender Weibchen in die anderen Versuchsgebiete—also nicht durch Tod, wie bei der Mortalitätsberechnung sonst fälschlich angenommen würde—erleidet.

Um Näheres über die Fehlerquelle der Nichtberücksichtigung der Anzahl der auswärts beringten Nestlinge zu erfahren, legen wir in Tabelle 5 versuchsweise die Beringungszahlen der Nestjungen aller Gebiete für die korrigierende Umrechnung der tatsächlichen Wiederfunde in den Drömlings-Gebieten zu Grunde. Als hierdurch gefundene Mortalität ergibt sich für die Einjährigen 34%, die Zwei­jährigen 44%, die Dreijährigen 69%, die Vierjährigen 80% und die Fünfjährigen 100%. Die Mortalität steigt also von Altersklasse zu Altersklasse in völlig entsprechender Weise an, wie es sich oben bei Zugrundelegung der alleinigen Beringungszahlen aus dem Drömling zeigte; nur liegt die zuletzt gewonnene Reihe (Tab. 5, Zeile e) stets etwa um 10% höher als die zuerst gewonnene (Tab. 3, Zeile e). Da für die Wiederfunds­zahlen im Drömling in Tabelle 3 eine zu geringe, in Tabelle 5 aber eine zu hohe Zahl an beringten Nestlingen zu Grunde gelegt ist, muss Tabelle 3 eine geringere, und zwar eine zu geringe, bzw. Tabelle 5 eine höhere, und zwar eine zu hohe Mortalität zeigen. Da ungefähr die Mitte den richtigen Wert darstellen dürfte, ergibt sich als Mortalität für die Einjährigen (aus 26 bzw. 34%) etwa 30%, für die Zwei­jährigen (aus 35 bzw. 44%) etwa 40%, für die Dreijährigen (aus 59 bzw. 69%) etwa 65%, für die Vierjährigen (aus 
Tabelle 5—Wiederfundszahlenkorrektur, Mortalität und Überlebensrate bei den ♀♀ von Ficedula hypoleuca im Drömling, bezogen auf die Beringungszahlen aller Untersuchungsgebiete des Grossraumes

<table>
<thead>
<tr>
<th>Altersklasse</th>
<th>Altersklasse</th>
<th>Altersklasse</th>
<th>Altersklasse</th>
<th>Altersklasse</th>
<th>Summe</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-jährig</td>
<td>2-jährig</td>
<td>3-jährig</td>
<td>4-jährig</td>
<td>5-jährig</td>
<td></td>
</tr>
<tr>
<td>a tatsächliche Anzahl der Wiederfunde</td>
<td>163</td>
<td>108</td>
<td>52</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>c Summe</td>
<td>13893</td>
<td>13917</td>
<td>11980</td>
<td>9278</td>
<td>6686</td>
</tr>
<tr>
<td>d auf die Durchschnitts-Beringungszahl von (55754 ÷ 5 = 11151 korrigierte Wiederfundszahlen)</td>
<td>130</td>
<td>86</td>
<td>48</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>e Mortalität</td>
<td>34%</td>
<td>44%</td>
<td>69%</td>
<td>80%</td>
<td>100%</td>
</tr>
<tr>
<td>f Überlebensrate</td>
<td>66%</td>
<td>56%</td>
<td>31%</td>
<td>20%</td>
<td>0%</td>
</tr>
</tbody>
</table>

70 bzw. 80%) etwa 75% und für die Fünfjährigen 100% (Tab. 6). (Unser Gesamtmaterial enthält jedoch auch 4 Funde sechsjähriger ♀♀; daher wird in Wirklichkeit noch nicht die Mortalität der Fünfjährigen, sondern erst die der Sechsjährigen 100% erreichen, was in der erwähnten Gesamtbearbeitung aller Wiederfunde näher untersucht werden soll.)

Als Durchschnittsmortalität ergibt sich bei Zugrundelegung des Gesamtberingungsmaterials (Tab. 5): 130/282 = 0,46 bzw. 46%. Nehmen wir auch hier die Mitte zu dem oben gefundenen Wert von 40%, so erhalten wir

Tabelle 6—Korrigierte Altersklassen-Mortalität und Altersklassen-Überlebensrate der ♀♀ von Ficedula hypoleuca im Drömling

<table>
<thead>
<tr>
<th>Lebensjahr</th>
<th>Altersklassen-Mortalität</th>
<th>Altersklassen-Überlebensrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Jahr</td>
<td>ca. 30%</td>
<td>ca. 70%</td>
</tr>
<tr>
<td>2. &quot;</td>
<td>ca. 40%</td>
<td>ca. 60%</td>
</tr>
<tr>
<td>3. &quot;</td>
<td>ca. 65%</td>
<td>ca. 35%</td>
</tr>
<tr>
<td>4. &quot;</td>
<td>ca. 75%</td>
<td>ca. 25%</td>
</tr>
<tr>
<td>5. &quot;</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td>Durchschnittsmortalität</td>
<td>ca. 43%</td>
<td></td>
</tr>
<tr>
<td>Durchschnittsüberlebensrate</td>
<td></td>
<td>ca. 57%</td>
</tr>
<tr>
<td>Mortalitäten-Mittel</td>
<td>52%</td>
<td></td>
</tr>
<tr>
<td>Überlebensraten-Mittel</td>
<td></td>
<td>48%</td>
</tr>
</tbody>
</table>
Eine korrigierte Durchschnittsmortalität von etwa 43% (Tab. 6); diese ist—ebenso wie die oben errechnete—höher als die Mortalität der Ein- und Zweijährigen und niedriger als die der Drei-, Vier- und Fünfjährigen.

Als Massstab für die Beurteilung der einzelnen Altersklassen-Mortalitätssätze im Laufe des Lebens erscheint uns jedoch anstelle der Durchschnittsmortalität das "Mortalitätenmittel" geeigneter zu sein; wir versteht darunter das arithmetische Mittel aus den verschiedenen Prozentsätzen der Altersklassenmortalität. Wenn wir hierbei den Prozentsatz des auslaufenden 5. Jahres (100%) nicht mitrechnen und infolgedessen die Summe von (30 + 40 + 65 + 75 =) 210 durch 4 (Altersklassen) teilen, so erhalten wir ein Mortalitätenmittel von 52%, entsprechend einem Überlebensrates-Mittel von 48% (Tab. 6).

Hiernach geurteilt, liegt nun die Mortalität der Einjährigen sehr stark und die der Zweijährigen auch beträchtlich unter dem Mortalitätenmittel des ganzen Ficedula-hypoleuca-Lebens, während sich dann die Mortalität der Dreijährigen schon merklich und die der Vierjährigen noch stärker über das Mittel erhebt, und die Fünfjährigen (in dieser Population) wohl alle wegstehen. (Wie oben erwähnt, enthält unser Gesamtmaterial jedoch auch vier 6 Jahre alte ♂♂.)

**DISKUSSION**


![Graph](image)

**ZUSAMMENFASSUNG**

Die Weibchen einer Brutpopulation von *Ficedula hypoleuca* im nördlichen Deutschland bei Braunschweig wurden mit Hilfe des Beringungsverfahrens 4 Jahre lang auf ihre Mortalität untersucht. Die Auswertung aller 338 Wiederfunde nestjung beringter Weibchen aus 5 benachbarten Untersuchungsgebieten ergab eine durchschnittliche jährliche (Adult-) Mortalität ("Durchschnittsmortalität") von 43%. In den einzelnen Altersklassen war die Mortalität verschieden gross, und zwar stieg die "Altersklassen-Mortalität" von etwa 30% im 2. Lebensjahr über etwa 40% im 3., etwa 65% im 4. und etwa
75% im 5. auf 100% im 6. Lebensjahr. Das arithmetische Mittel aus den Mortalitätsraten der Altersklassen vom 2. bis 5. Lebensjahr ("Mortalitätenmittel") war 52%. Die Mortalität der Einjährigen und Zweijährigen lag unter, die der Dreijährigen, Vierjährigen und Fünfjährigen über dem Mortalitätenmittel. Anscheinend erreichten die Vögel im 2. und 3. Lebensjahr ihre körperliche und geistige Höchstleistung, während im 4. Lebensjahr der Höhepunkt des Lebens überschritten wurde. Danach dürfte eine erhöhte Anfälligkeit gegen Krankheiten und Feinde das Wegsterben auch der ältesten Individuen bis spätestens im 6. Lebensjahr bewirkt haben. Die Chance eines 4-jährigen Weibchens, 5 Jahr alt zu werden, ist nur \( \frac{1}{2} \) bis \( \frac{1}{3} \) so gross wie die eines 1-jährigen, 2 Jahre alt zu werden.

Die ermittelte Mortalitätskurve von *Ficedula hypoleuca* entspricht grundsätzlich derjenigen von *Homo sapiens*, die nur eine durch Domestikation (einschließlich der medizinischen Wissenschaft) bedingte Sonderausprägung der allgemein gültigen Mortalitätserscheinungen darstellen dürfte.

**SUMMARY**

*Is the Mortality Rate of Adult Ficedula hypoleuca Really Independent of Age?*

The female segment of a breeding population of *Ficedula hypoleuca* in northern Germany near Brunswick was tested as to its mortality during 4 years by means of the ringing method. The result of the evaluation of all 338 recoveries of females ringed as nestlings from 5 neighboring test districts (Table 1) was an average annual adult mortality ("Durchschnitts-Mortalität") amounting to ca. 43 percent. In the different age classes (Table 2), the mortality was not constant (Tables 3, 4, 5, and 6). The "age-class mortality" ("Altersklassen-Mortalität") rather rose from ca. 30 percent in the 2nd year of life to ca. 40 percent in the 3rd, ca. 65 percent in the 4th, ca. 75 percent in the 5th, and finally 100 percent in the 6th year of life. The arithmetic average of the mortality rates in the age classes from the 2nd to the 5th year of life ("mortality-average" = "Mortalitätenmittel") was 52 percent. The mortality of the yearlings and 2-year-olds was lower, and that of the 3-, 4-, and 5-year-olds was higher than the mortality average. The birds appeared to reach their maximum viability in the 2nd and 3rd year of life, whereas the culminating point was already exceeded in the 4th year of life. Thereafter, an increased susceptibility to illnesses and enemies is likely to have brought about dying of even the oldest individuals, at the latest in their 6th year of life. The chance of a 4-year-old female bird reaching 5 years of age is only \( \frac{1}{2} \) to \( \frac{1}{5} \) of that of a yearling reaching 2 years of age.

The mortality curve of *Ficedula hypoleuca*, as found out, in principle corresponds to that of *Homo sapiens*, the latter representing only a special expression of the general mortality phenomena formed by domestication, including medical science (Fig. 1).
ZITIERTE LITERATUR


Hatching Losses of Common Goldeneyes in the Finnish Archipelago

**PEKKA GRENQUIST**

*Game Research Institute, Helsinki, Finland*

The Game Research Institute in Finland has carried out yearly censuses of the waterfowl population in the Finnish archipelago since 1949 (Grenquist, 1961). In connection with these, the nesting success of the Common Goldeneye (*Bucephela clangula*) in the southwestern archipelago was recorded in the years 1954–61 at Trollö, Gullkronafjärden, in about 50 boxes placed in position in the beginning of the 1950's.

Since undue disturbances would have had an adverse influence on nesting success, each box was examined not more than twice during incubation and only once after hatching in order to obtain the necessary data on nesting and nesting success. For the same reason, incubating females were not leg-banded or wing-tagged, nor were they removed from the nest if they were brooding. The boxes were examined as rapidly as possible. They were cleaned and repaired in August and were thereafter left untouched, no measures being taken against competitors for boxes such as the Goosander (*Mergus merganser*), the Stock Dove (*Columba oenas*), squirrel (*Sciurus vulgaris*), or any other animal.

The statistical data used in this paper are mainly from Trollö. The data have been supplemented by observations made at Kimito (Kemiö) in 1957–61 and at Pettu, Finby, in 1959–60, both closer than Trollö to the mainland of southwest Finland. Intensive studies on the biology of the Goldeneyes of the archipelago have been in progress since 1961.

The average clutch size, calculated from 53 clutches in which incubation was completed during 1954–61, and for which the original egg number was known, was 10.34, with a coefficient of variation of 8.6 percent. The respective figures for all 63 clutches in which incubation was begun were 10.22 and 8.7 percent. The average number of young hatched was 9.62, with a coefficient of variation of 9.3 percent, in those 53 clutches in which incubation was completed. Particularly if compared with the total number of eggs laid (Table 1), hatching losses were negligible in the clutches in which incubation was completed as well as in those in which it was only started. Of the 1,554 eggs laid at Trollö in the period 1954–61, 50.6 percent produced a hatched duckling, in 6.2 percent incubation was not completed, 0.8 percent showed a dead duckling inside the egg, 1.9 percent were addled eggs, and 40.4 percent of the eggs were totally unincubated. For a clutch of 10 eggs this meant that 5 eggs would hatch, 4 would remain unincubated, and 1 would be lost for some other reason.

Extensive losses due to failure of incubation are not unknown in the Goldeneye. Deserted, unincubated clutches are well known in the Finnish archi-
pelago. The same holds true for the mainland, but the situation seems to be rarer than in the archipelago. Brander (in litt.) mentions that, on the whole, the nesting success of the Goldeneye was satisfactory in the 1950's in Urjala, on the southwestern mainland, but that nesting failed completely in 1959, most boxes containing full or almost full clutches of unincubated eggs. In an article on the Goldeneye as a breeding species in Sweden, von Essen (1947) reports a great number of deserted clutches remaining every year in the boxes, in most cases consisting of unincubated eggs. Quantitative data on nesting success or on the number of unincubated eggs are scarce, however. Linkola (1962) has treated a body of data collected in Keski-Häme, comprising 50 clutches of Goldeneye eggs. The percentage of hatched young was 56, figure that agrees closely with the result obtained at Trollö. Game biologist P. Koivisto, of the Evo Research Station, belonging to the Game Research Institute, has given the following statistics for the area around Evo for the years 1950–55 and 1958–59: Out of a total number of 640 eggs laid, 74 percent hatched and 20 percent were deserted; it is not known whether the deserted eggs were unincubated in all cases, as were those (40.4 percent = 628 eggs) at Trollö. Fredga (1962) reports very satisfactory hatching success in an experimental area in Värmland, Sweden (Table 2).

Although the data in Table 2 are incomplete, a comparison between Tables 1 and 2 reveals that hatching success has been more satisfactory on the mainland than in the archipelago. At Trollö, nesting has actually succeeded in only 3 years out of 8.

**Table 1.—Incubation and Hatching at Trollö 1954–61 as a Percentage of the Number of Eggs Laid**

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>No. Brooding Females</td>
<td>6</td>
<td>11</td>
<td>10</td>
<td>7</td>
<td>12</td>
<td>15</td>
<td>18</td>
<td>11</td>
<td>90</td>
</tr>
<tr>
<td>No. of Eggs Laid</td>
<td>65</td>
<td>130</td>
<td>166</td>
<td>222</td>
<td>242</td>
<td>192</td>
<td>257</td>
<td>280</td>
<td>1,554</td>
</tr>
</tbody>
</table>

** Fate of Eggs **

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Ducklings hatched</td>
<td>77</td>
<td>80</td>
<td>45</td>
<td>33</td>
<td>46</td>
<td>75</td>
<td>53</td>
<td>33</td>
<td>787</td>
</tr>
<tr>
<td>Incubation interrupted</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>—</td>
<td>—</td>
<td>12</td>
<td>8</td>
<td>97</td>
<td>6.2</td>
</tr>
<tr>
<td>Duckling dead</td>
<td>—</td>
<td>3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2</td>
<td>1</td>
<td>12</td>
<td>0.8</td>
</tr>
<tr>
<td>Inside egg</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>30</td>
<td>1.9</td>
</tr>
<tr>
<td>Eggs unincubated</td>
<td>9</td>
<td>3</td>
<td>42</td>
<td>66</td>
<td>51</td>
<td>22</td>
<td>31</td>
<td>56</td>
<td>628</td>
</tr>
</tbody>
</table>

**Table 2.—Hatching Success (Percent) for Three Goldeneye Management Areas**

<table>
<thead>
<tr>
<th>Year</th>
<th>'50</th>
<th>'51</th>
<th>'52</th>
<th>'53</th>
<th>'54</th>
<th>'55</th>
<th>'56</th>
<th>'57</th>
<th>'58</th>
<th>'59</th>
<th>'60</th>
<th>'61</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trollö, Finland</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>77</td>
<td>80</td>
<td>45</td>
<td>33</td>
<td>46</td>
<td>75</td>
<td>53</td>
</tr>
<tr>
<td>Evo, Finland</td>
<td>94</td>
<td>22</td>
<td>71</td>
<td>93</td>
<td>52</td>
<td>88</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>77</td>
<td>88</td>
<td>—</td>
</tr>
<tr>
<td>Värmland, Sweden</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>78</td>
<td>72</td>
<td>82</td>
<td>—</td>
</tr>
</tbody>
</table>

* Data from Fredga (1962).
Competition for nest boxes by the Goosander and the Stock Dove, in causing direct losses in the form of unincubated eggs, as shown by the Trollö statistics, amounts to a relatively small 6 percent. It is quite usual in the archipelago for the Goosander and the Goldeneye to lay their eggs in the same box. Such nests are then always deserted by the Goldeneye. If incubation is performed and successfully concluded by the Goosander, the young of the Goldeneye usually hatch first and jump down without any adult bird calling outside the box. These instances have not been included in the Trollö statistics, which concern hatching losses only. Of the 628 unincubated Goldeneye eggs in the years 1954–61, 21 eggs (= 3 percent) remained unincubated in six boxes containing eggs of both the Goosander and the Goldeneye. In other areas of the archipelago, losses caused by the Goosander may exceed the figure reported above.

If the Stock Dove makes its first nest at approximately the same time as the Goldeneye lays her eggs, as it usually does, and if this is made in the same hole or nest, the Stock Dove gains the upper hand in many cases. For instance, the dove may make its nest of twigs on top of the eggs of the Goldeneye and begin incubation as soon as the first egg has been laid. Four such nests were found at Trollö, and the losses of Goldeneye eggs (14) constituted 2 percent of the total loss due to failure to incubate. In certain cases, the Stock Dove has clearly made its nest on already-deserted Goldeneye clutches, as at Pettu in 1960, where Stock Doves incubated their eggs in two natural holes, covering 10 and 14 eggs of the Goldeneye, respectively.

Other species competing with the Goldeneye for nesting holes in the archipelago are the Jackdaw (Coloeus monedula), the squirrel, the Tawny Owl (Strix aluco), and the Starling (Sturnus vulgaris). The Jackdaw occupies old nests of the Black Woodpecker (Dryocopus martius) in the alder stands on the shore, other natural holes, and any available boxes so early that the Goldeneye, which usually nests later, can seldom use them. Brander (1958) has found eggs of the Goldeneye beneath Jackdaw nests on the mainland, which means that “subtenancy” has followed the same course as described above in the case of the Stock Dove. Starling nests, made on large presumably deserted clutches of the Goldeneye, have also been found in the archipelago of Pettu, Finby.

There seem to be relatively few direct losses from failure to incubate owing to competition for nesting holes with species that breed earlier or at the same time as the Goldeneye, i.e. the squirrel, the Tawny Owl, the Jackdaw, the Goosander, and the Starling. The harmful effect of these species from the point of view of Goldeneye management lies in the fact that they occupy most of the natural holes, principally those of the Black Woodpecker, as well as the boxes, which are probably the most attractive nesting places to the Goldeneye. Moreover, when simultaneous egg laying occurs in the same nesting hole, this must have a decidedly adverse effect, perhaps particularly on female Goldeneyes that have not previously nested.
A closer examination of hatching and hatching losses at Trollö in 1954–61 reveals that losses, both absolute and relative, have increased with the increasing number of eggs laid. It even seems that the greatest losses have taken place 2 years after the best hatching successes. The hatching peak of 80 percent in 1955 was followed by a marked loss of 33 percent in 1957, and the peak of 75 percent in hatching success in 1959 by a low of 33 percent in 1961. Statistics collected in Finland and Sweden (Table 2) show that the peak losses vary locally but, according to reports of the Game Research Institute for both the archipelago and the mainland, great losses have occurred as the result of unincubated eggs. This has happened more often than usual during recent years and has been simultaneous with a rapid increase in the Goldeneye population caused by intensified provision of boxes throughout the country in the 1950’s.

It thus seems that an explanation of the great losses from unincubated eggs may be the abundance of young Goldeneye females, or even of 2-year-old females, that are choosing boxes for egg laying and incubation for the first time. Von Essen (1947) supposes that the above-mentioned desertion of clutches is an indication that they are unfertilized and produced by sexually immature females. At the end of May 1960, Mr. Koivisto and I collected a total of 50 deserted and unincubated eggs in Pettu. Three of them, or 6 percent, were unfertilized. During approximately the same period in 1961, 86 eggs similarly deserted were taken in Pettu; this time, 37 percent of them were unfertilized (Koivisto, in litt.).

It is obvious that in game-management areas expressly provided with boxes for the Goldeneye, such as at Trollö and Pettu, which are situated on the migration routes of the species in the archipelago, young Goldeneye females gather in certain years in greater numbers than usual. On account of the shortage of natural holes in the trees and competition on the part of old female Goldeneyes and other nidicolous species, many young females attracted by such boxes, which best correspond to their innate nesting-site requirements, have competed for the same box. Observations made both at Trollö and elsewhere have shown that this situation has raised the number of eggs in a single box to over 20, 30, or even 40; in such cases the eggs have remained unincubated. In the boxes examined during 1954–61 at Trollö, the number of unincubated eggs per box varied between 1 and 23. The mean number of eggs per box was 8.5, with a coefficient of variation of 67.8 percent, the latter about eight times greater than for clutches in which incubation was completed. It has sometimes been observed that two females were in the box, while a third was waiting her turn on the cover. This behavior very much resembles the box visits of 1-year-old birds; these, however, are made mainly toward the end of the incubation period of the sexually mature females (see also Kokko, 1958). Such a situation can also lead to fights between the egg-laying females. One or two dead females have even been found in the same box (Brander, in litt.; reporters of the Game Research
Institute), and it seems probable that fights during the egg-laying period have been the reason for deaths in certain cases. Some clutches, deserted during incubation, have contained embryos varying in age by as much as 1–3 weeks, as well as completely unincubated eggs, which indicates that the eggs were laid by several females.

The Goldeneye, which originally nested in natural holes on river and lake shores in the northern coniferous forest zone, has hardly any innate adaptations to enable females nesting for the first time to master all the complicated situations they may encounter in competing for nesting holes at overcrowded nesting sites.

**SUMMARY**

In 1954–61, 53 clutches of *Bucephala clangula* averaged 10.3 eggs ($CV = 8.6\%$) where brooding was concluded, and the mean size of broods hatched was 9.6 ($CV = 9.3\%$). For 1,554 eggs, 50.6 percent hatched, 6.2 percent had incubation interrupted, 1.9 percent were not fertilized, and 40.4 percent were unincubated. In this rapidly increasing population in response to nest-box construction, peaks of hatching success (80 and 75 percent) in a given year were twice followed by low hatching success 2 years later (33 and 33 percent). The disturbance caused by several young females laying eggs in the same boxes as older females of their own species, Goosanders, and Stock Doves is thought to be an explanation of the low hatching success in overcrowded nesting areas in the archipelago.

**LITERATURE CITED**

Population Control in Red Grouse (*Lagopus lagopus scoticus*)

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The aim of this paper is to summarize ideas presented in a much longer account by the author and his colleagues (see Jenkins, Watson, and Miller, 1963), and also to consider these ideas in relation to previous important contributions. The purpose of the study described was to understand grouse population dynamics, i.e. the relation between recruitment plus immigration and mortality plus emigration.

Red Grouse (*Lagopus lagopus scoticus*) in Scotland and northern England have attracted attention from ecologists and game biologists for more than half a century. A committee was appointed, as long ago as 1905 under the Board of Agriculture and Fisheries, to promote an investigation conducted entirely at the expense either of the members of the committee or of private enquirers. A scientific and secretarial staff was maintained for about 6% years on an income totaling £700 per annum, and with this meager budget the results obtained were remarkable and compare very favorably with the results of modern investigations. A comprehensive report was published (Committee of Inquiry . . ., 1911) consisting of two volumes. The primary object was simply to investigate the subject of “grouse disease,” and the major conclusion was as follows. Food shortage, usually consequent on heavy snow, causes large numbers of grouse to congregate on restricted feeding areas, where they become overcrowded and foul the ground with parasitized droppings. As a result, they ingest excessive numbers of parasites, chiefly *Trichostrongylus tenuis*. These parasites weaken the bowel wall and allow intestinal bacteria to enter the bloodstream with a consequent toxemia. The birds are then unable to survive at the end of winter when food is scarcest, or to endure the strains of the nesting season; and they die “of privation acting on a constitution already weakened by the consequences of strongylosis” (op. cit., p. 302) in an emaciated condition known as “grouse disease.”

This work has been referred to frequently in the literature, recently by Chitty (1954) and Lack (1954). Lack notes that the account of Leiper and Wilson in the report suggests a typical host–parasite interaction resulting in population oscillations, but that this was not the whole story. His summary of the evidence presented by the Committee is that “the critical factor in the onset of grouse disease is not merely the population density of the grouse, but their numbers in relation to food supply, and that strongylosis sets in when the birds are weakened by food shortage.” Lack suggests that predators might mitigate the effects of disease, if present in normal numbers, but notes

that disease occurred in the last part of the eighteenth century before predators were "largely eliminated." Since he states that "food shortage keeps the population at a lower level when the parasite is present than when it is absent," Lack's conclusion clearly is that parasitic disease is an important factor controlling grouse abundance; and one would suppose that if the parasite were eliminated and other things remained the same, grouse would usually be more numerous.

Chitty (1954) also reviews the literature concerned with grouse disease, and emphasizes two different points. The first is that evidence of disease being associated with population decrease is no proof that the population would not in any event have suffered heavy losses. Therefore the Committee of Inquiry was not justified in concluding that parasitic diseases were necessarily responsible for declines in grouse numbers. Since infected populations did not always decrease, Chitty enlarges on the Committee's important suggestion that there must also have been changes in the power of resistance of the host. Chitty's second point is that Leslie and Berry (in Committee of Inquiry . . ., 1911) noted that "it is only where the parent birds are unhealthy that the young stock seems to be seriously reduced by bad weather during the breeding season." He shows that similar evidence has been produced by other students of gamebirds, and he concludes that the probability of survival of the young of such animals is largely predetermined by the physiological condition of their parents. This view would be reconciled with Lack's if the condition of the adults depended on the degree of parasitic infestation and on the food supply.

During most of the three decades following publication of the report of the Committee of Inquiry, Red Grouse were abundant in Scotland; but during and after the Second World War there was a decline in grouse numbers. This was serious for owners of land where grouse were shot, since shooting rentals were an important source of income. Accordingly, the Scottish Landowners' Federation decided to finance an enquiry into the decline of Red Grouse, with the cooperation of Aberdeen University and the Nature Conservancy. This enquiry was started in Glen Esk in November 1956 on some first-class grouse moors owned by the Earl of Dalhousie, and was financed by the Scottish Landowners' Federation, by public subscription, for 3 years. After 1960 the research was entirely taken over by the Nature Conservancy, with the formation of the Unit of Grouse and Moorland Ecology.

Notwithstanding the results obtained by the Committee of Inquiry, it was decided that the research should initially be entirely empirical, starting with a fundamental population study. This involved regular counts of grouse on two 400-hectare (1,000-acre) study areas at different altitudes (low, at about 300 m, and high, at about 650 m), together with the collection of such routine statistics as sex ratios, clutch sizes, chick survival, estimates of mortality, and so on. In addition to the counting, many birds were marked.
with plastic tabs; and studies of the social structure of grouse populations have been an integral part of the work.

Bag records suggest that the fluctuation in grouse numbers recorded during the study was probably typical of events during the recent history of the area (Fig. 1). The number shot did not correspond exactly with the crop available for exploitation, since there was a tendency in years of low numbers for fewer to be shot than was justifiable (Fig. 2). This may be typical of the harvesting of gallinaceous game birds (cf. Hickey, 1955). Nonetheless, changes in the size of the bag did follow general changes in the size of the summer grouse population.

THE REGULATION OF BREEDING NUMBERS

The changes in numbers through each season followed a typical pattern, at least on the main (low) study area (Fig. 2). There was no gradual decline from the summer peak to the following spring. Instead, sudden changes in numbers were separated by long periods when numbers were constant. The chief changes on the main study area (Fig. 2) were in autumn and again in late winter. Shooting coincided with the period of autumn change. In
1957 the number shot was sufficient to account for the total population change at this season, but in the other years it was always considerably less than the total coincident population change. In fact, the agreement in 1957 between the number shot and the total decrease was probably due to coincidence, and it seems clear that the level of winter numbers is not determined by the stock left at the end of the shooting.

In 1957, 1958, and 1961, spring numbers were high, about one pair to two hectares, following late-winter decreases on the low area of 26 percent, 21 percent, and nil, respectively. In 1959 and 1960, the spring population was low with one pair to about four or more hectares, following decreases of 45 percent and 30 percent. However, there was no constant relationship between the size of the late-winter decrease and the spring population density: In 1961, for instance, when the decrease on the low area was nil, the decrease on the nearby high area was about 33 percent, and yet both areas had similar high spring numbers.

The extent of the late-winter decrease, which is presumably geared to conditions at that season, is thus clearly not the main factor in determining the size of the spring population. Barring accidents, there is usually little change in the number of established, territory-owning grouse between September or October and the following spring. The breeding density thus appears to be conditioned initially by the factors controlling territory size in the previous autumn. The late-winter decrease in numbers could be accounted for by the expulsion of unestablished surplus birds previously tolerated as interlopers or vagrants by the territory owners; since their number may vary from autumn to autumn, there are corresponding changes in the size of the late-winter decrease.

More observations are needed on the late-winter decrease, and unfortunately in 2 years of detailed study—1961 on the low area and 1962 on a new area—there was little change in numbers at this season. However, these observations have shown that, during early and midwinter, territories are defended only in the early mornings on fine days, while in late winter they

![Diagram](image-url)
are defended continuously. During the early and midwinter period, the grouse population on the breeding ground consists of two classes of birds, territory owners, at this stage mainly cocks, together with other surplus individuals, mainly hens, that do not own territories. The surplus birds feed on the territories when these are undefended; when chased off by the territory owners, the interlopers find sanctuary in small flocks on interspaces between the territories. These interspaces may be described as communal areas, in contrast to territories. The communal areas are unoccupied after the late-winter decrease, when the population consists entirely of territory owners.

Apparently, the autumn decrease occurs through the dispersal of birds that cannot obtain a territory, or find sanctuary in a communal interspace, and the late-winter decrease involves the dispersal of surplus birds previously found on communal areas. Observations so far suggest that the population size at midwinter is more or less stable, despite a constant turnover among transient members of the flocks on communal areas. Presumably, the population size is limited by the number of territories, plus the capacity of the communal interspaces in early and midwinter, although established pairs may also occasionally be displaced in the late-winter decreases.

After the late-winter decrease, the adult sex ratio usually stayed the same each year until August, when young and old became indistinguishable. However, the ratios differed in different years, being about equal in 1957, 1960, and 1961, but unequal, at about 1.5:1, in 1958 and 1959 on the low area. Once the spring population size was determined in February, the sex ratio remained the same despite changes in numbers or substitutions among the residents. Cocks remained unmated despite the presence of transient unattached hens. Between April and late May 1959 the population on the high area dropped by one-third through the exodus of about 100 birds of both sexes, yet the sex ratio remained the same. The sex ratio could not have been determined merely by the numbers of birds of each sex that happened to be available. Instead, it must have been imposed on the population, presumably by some environmental condition such as the availability of food for one or two birds on a territory. Spring sex ratios may have been determined by the quality of the territories in late winter when the last flocks dispersed and sexual activities became most vigorous. When the quality of the principal food, heather (Calluna vulgaris), was good, most or all of the territories might have supported hens, with a consequently equal sex ratio; but when the food was poor, many territories might have been unable to support hens, with a consequent disproportionate loss of hens in late winter and an unequal sex ratio. Hence, while the autumn decrease was mainly due to the expulsion of surplus young birds of both sexes, the birds displaced in the late-winter decrease may sometimes have been mainly hens, plus any surplus cocks that had been tolerated in the nonterritorial flocks during early winter.
In 1958 and 1959 there was no change in population size between spring and autumn, despite a summer increment from breeding (Fig. 2), but in 1957 and 1960 the population in autumn was larger than in spring. Winter population losses in 1958 and 1959 differed from those in other years in that heather was locally spoiled by frosting in early spring or late winter. This was probably due to freezing of the soil water combined with low atmospheric humidity and a high rate of transpiration. Consequently, the heather became dehydrated and turned brown, and grouse did not eat it. Heather growth was not measured in these years, but it was estimated visually at not less than 120 random-sample points on each of ten study areas in the autumn of 1959, and compared with the respective percentage changes in grouse numbers between the spring of 1959 and that of 1960. There was a highly significant correlation, large increases in population being associated with good shoot growth \( P < 0.001 \). The results of a similar comparison for the next 12-month season did not show a significant correlation, possibly because there was a narrower range of variation in heather condition between study areas; but it seems reasonable to suppose, as a basis for future studies, that variations in grouse breeding densities are correlated with variations in heather condition in the previous autumn. In other words, grouse territory sizes may depend initially on the food supply in autumn; and in this case it is the food supply in autumn that exerts the primary control on breeding density in the following spring.

The hypothesis, therefore, is that a maximum limit to the spring population, i.e. the maximum number of territories, is imposed by the quantity and quality of edible food available in the previous autumn. At that time the territory size of the cocks becomes adjusted to their food supply, and if the winter is mild, as in 1960–61, with no adverse effect on the heather, the population remains constant through to the next breeding season, when each territory supports a breeding pair. In this case, the actual spring population is the same as the maximum. If the food fails in the winter, the number of territories may be unaffected, but there will be a high proportion of unmated cocks and few breeding pairs. The late-winter decrease, consequently, can be attributed largely to the dispersal or death of females.

**Breeding Success**

In addition to the actual numbers of chicks reared, important measures of breeding are clutch size and hatching success. These three statistics were all found to vary in different years in such a way that the five seasons could be classified in two groups—"good breeding seasons" in 1957, 1960, and 1961, and "poor breeding seasons" in 1958 and 1959. There were slight differences in mean clutch size associated with altitude, but on the low area the mean clutch in a good year was about 8 eggs, hatching success about 90 percent, and the mean number of young reared per adult female about 4–5 (Table 1). By contrast, in a poor year the mean clutch was about 6
or 7 eggs, hatching success about 70 percent, and the number of young reared was about 1 or 2. Either most of the young in each brood were reared, or few or none of them; and most of the deaths occurred within the first week or two after hatching.

Highly significant correlation coefficients (Table 2) suggest that the similarities in the annual fluctuations of so many relatively independent observations are unlikely to be due to chance. The correlation matrix (Table 2)

Table 1.—Performance of Grouse on the Glen Esk Study Areas, 1957–61

<table>
<thead>
<tr>
<th></th>
<th>LOW AREA</th>
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<th>HIGH AREA</th>
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</tr>
</thead>
<tbody>
<tr>
<td>A. Mean wt. adult cocks shot Aug.–Sept. (g)</td>
<td>695</td>
<td>679</td>
<td>661</td>
<td>707</td>
<td>706</td>
<td>692</td>
<td>676</td>
<td>657</td>
<td>704</td>
</tr>
<tr>
<td>B. Mean wt. adult hens shot Aug.–Sept. (g)</td>
<td>612</td>
<td>587</td>
<td>578</td>
<td>618</td>
<td>614</td>
<td>613</td>
<td>588</td>
<td>579</td>
<td>619</td>
</tr>
<tr>
<td>C. Adult survival 1 Apr.–11 Aug. (%)</td>
<td>93</td>
<td>67</td>
<td>59</td>
<td>97</td>
<td>89</td>
<td>No data available</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>D. Young/breeding hen on 12 Aug.</td>
<td>3.8</td>
<td>2.3</td>
<td>1.0</td>
<td>5.4</td>
<td>3.8</td>
<td>1.8^b</td>
<td>0.8^b</td>
<td>0.6^b</td>
<td>2.3^b</td>
</tr>
<tr>
<td>E. Hatching success (%)</td>
<td>88</td>
<td>72</td>
<td>70</td>
<td>95</td>
<td>88</td>
<td>91</td>
<td>92</td>
<td>76</td>
<td>95</td>
</tr>
<tr>
<td>F. Mean clutch size</td>
<td>7.9</td>
<td>6.9</td>
<td>6.1</td>
<td>8.1</td>
<td>7.8</td>
<td>7.2</td>
<td>6.2</td>
<td>5.3</td>
<td>7.3</td>
</tr>
<tr>
<td>G. Hens per cock during last spring count</td>
<td>0.86</td>
<td>0.73</td>
<td>0.65</td>
<td>0.91</td>
<td>0.99</td>
<td>—</td>
<td>0.71</td>
<td>0.81</td>
<td>1.14</td>
</tr>
<tr>
<td>H. Adult survival 1 Jan.–31 Mar. (%)</td>
<td>83</td>
<td>69</td>
<td>59</td>
<td>81</td>
<td>72</td>
<td>No data available</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I. Breeding density (birds/40 ha)</td>
<td>33</td>
<td>34</td>
<td>19</td>
<td>14</td>
<td>31</td>
<td>32</td>
<td>40</td>
<td>20</td>
<td>13</td>
</tr>
<tr>
<td>J. Late-winter decrease (%)</td>
<td>20</td>
<td>21</td>
<td>46</td>
<td>30</td>
<td>0</td>
<td>—</td>
<td>37</td>
<td>55</td>
<td>69</td>
</tr>
</tbody>
</table>


^b Chick survival on the high area has been calculated in terms of young : 1 old since no data are available for the sex ratio in 1957.

shows that adult survival in summer is significantly related to adult survival between January and March. Since adult and juvenile survival in summer are also significantly related, breeding success may be correlated with events occurring before the eggs are laid. Breeding success is correlated with spring sex ratios but not with spring breeding density and the late-winter decrease.

This leads to a second hypothesis, that breeding success is determined by the same factors that influence the sex ratio of the breeding adults, namely the quantity or quality of the food in late winter. These factors also affect the subsequent survival of the adults; and presumably the connection between adult survival and breeding success depends on the condition of the adults and their brooding behavior. Hence, the conclusion from the study in Glen Esk is the same as Chitty’s (1954) and subsequently Siivonen’s (1957),
namely that the survival of the young is predetermined by the physiological condition of their parents. An interesting point in the Glen Esk study is that breeding success was not positively correlated with breeding densities. Good and poor breeding occurred when grouse were both numerous and scarce in spring. The explanation of this with the present hypothesis is that breeding success depends on conditions immediately prior to breeding, while the size of the breeding population may depend on other factors operating 6 months or more previously.

Table 2.—Correlation Coefficients between Data from Table 1

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
<th>I</th>
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<tbody>
<tr>
<td>LOW AREA</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>+0.974**</td>
<td>+0.927*</td>
<td>+0.946*</td>
<td>+0.920*</td>
<td>+0.971**</td>
<td>+0.967**</td>
<td>+0.800</td>
<td>+0.037</td>
<td>-0.652</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td></td>
<td>+0.980**</td>
<td>+0.951*</td>
<td>+0.963**</td>
<td>+0.983**</td>
<td>+0.962**</td>
<td>+0.866</td>
<td>-0.021</td>
<td>-0.551</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td></td>
<td></td>
<td>+0.968**</td>
<td>+0.984**</td>
<td>+0.970**</td>
<td>+0.858</td>
<td>+0.916*</td>
<td>-0.133</td>
<td>-0.377</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td></td>
<td></td>
<td></td>
<td>+0.973**</td>
<td>+0.959**</td>
<td>+0.846</td>
<td>+0.876</td>
<td>-0.182</td>
<td>-0.374</td>
<td></td>
</tr>
<tr>
<td>E</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+0.933*</td>
<td>+0.854</td>
<td>+0.842</td>
<td>-0.280</td>
<td>-0.333</td>
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</tr>
<tr>
<td>F</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+0.907*</td>
<td>+0.920*</td>
<td>+0.073</td>
<td>-0.580</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td></td>
<td></td>
<td></td>
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<td>-0.677</td>
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<td>H</td>
<td></td>
<td></td>
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<td>+0.085</td>
<td>-0.257</td>
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</tr>
<tr>
<td>A</td>
<td>+0.973**</td>
<td>+0.952*</td>
<td>+0.868</td>
<td>+0.969**</td>
<td>+0.037</td>
</tr>
<tr>
<td>B</td>
<td></td>
<td>+0.987**</td>
<td>+0.778</td>
<td>+0.975**</td>
<td>-0.080</td>
</tr>
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<td>D</td>
<td></td>
<td></td>
<td>+0.746</td>
<td>+0.941*</td>
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</tr>
<tr>
<td>E</td>
<td></td>
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<td>+0.870</td>
<td>+0.179</td>
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<tr>
<td>F</td>
<td></td>
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<td></td>
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<td>+0.061</td>
</tr>
</tbody>
</table>

* The letters A, B, C, etc. refer to the same statistics as in Table 1. Values of the correlation coefficient for different levels of significance are: ** 1 percent = 0.959; * 5 percent = 0.878; 10 percent = 0.805.

Mortality and Population Control

Even in poor breeding years there were many more grouse at the end of each breeding season than were present on the area the next spring (Fig. 2). In other words, recruitment from breeding produced more birds than subsequently stocked the area, thus creating a surplus. Data from subsidiary study areas suggest that this was probably true elsewhere. Even in 1957 when shooting on the low area resulted in a loss equal to the total autumn decrease, Fig. 2 suggests that there was some immigration from outside before the decrease was complete. Similarly, when the late-winter decrease occurred, another surplus was produced. Some of these surplus birds colonized neighboring areas, particularly during the shooting season. However, there is no reason to suppose that the study areas were different from other optimum habitats, and it seems to be characteristic of preserved grouse
moors for there to be a surplus of nonterritorial birds during winter and spring. Such birds do not remain on the heather areas after February, or rather they are not detectable by our counting methods which are believed to be fairly precise (Jenkins, Watson, and Miller, 1963). They appear to live on marginal ground at the moor edge, such as in fields, or on grassy places within the moor. In 1959, following the 45 percent late-winter decrease on the low area, grouse were seen in flocks in such places in the spring, up to 27 birds inhabiting some grassy fields; and a succession of birds was continually seen on such marginal areas as grassy stream banks within the moor. However, it is only in years with very big surpluses that these birds are obvious; otherwise they may easily be overlooked.

Presumably, surplus birds expelled from the optimum habitats constantly revisit them, and most eventually die there. Mortality on the low area varied seasonally, being least in 1960 when numbers were lowest and in 1961 when the population was expanding, and highest in 1958 and 1959 when the population was declining (Jenkins, Watson, and Miller, 1963). Nonetheless, the decline was not primarily due to mortality since, paradoxically, the greatest mortality each year occurred during periods when numbers were stable; and mortality was usually insufficient to account for the sudden losses during the autumn and late-winter decreases. In 3 years out of the 4, however, the estimate of total annual adult mortality including shooting, based on the total number of birds actually found dead, was within 20 percent of the total loss of adults during the same period, estimated through counting. The exception, 1957–58, can be accounted for through exceptional circumstances involving very heavy shooting (Jenkins, Watson, and Miller, 1963). Thus, mortality on this study area could usually be accounted for through the elimination of birds made surplus at the times of population dispersal.

During early winter and until February, most mortality was due to predation. The chief predators were foxes (Vulpes vulpes), Golden Eagles (Aquila chrysaetos), and Hen Harriers (Circus cyaneus). Later in the year and particularly in spring, most deaths were due to disease, which means that the birds were emaciated and infested with parasites. The trichostrongyles associated with grouse disease are eaten with the heather, and the maximum number of deaths from disease coincides with their emergence in spring. Although grouse sometimes had large numbers of parasites in winter, relatively few died then. The degree of parasitism did not, however, determine the condition of the birds, and the infestation increased from 1957 to 1959 independent of the condition of the grouse. In 1957 and 1958 the average numbers of trichostrongyles in diseased birds were about 2,000 and about 4,000 respectively, while in 1959, the average number in healthy birds was 4,000. The number of worms could not, therefore, have been the cause of disease, and the condition of the birds must have depended primarily on something else, possibly on their nutrition.
There was apparently a remarkable change in parasitic infestation in July 1959. Until mid-August the average number of worms was 8,000–10,000 per bird, and only 1 in 41 birds examined had no parasites. After mid-August, 7 of 12 examined had few or no worms, and thereafter the rate of infestation stayed low throughout 1960 and 1961. This is hard to explain unless it is assumed, as seems reasonable, that most birds dying from disease were surplus birds and not from the resident breeding population. Presumably by mid-August 1959 most of the surplus, highly parasitized birds had been eliminated; and birds dying subsequently were territory owners with low infestations of trichostrongyles. This introduces the idea that a high position in the social structure of the population confers immunity to disease and, incidentally, to other causes of mortality, notably predation; and this has been confirmed by observation (Jenkins, Watson, and Miller, 1963). Including all the deaths observed during the study, predation and disease accounted for approximately equal proportions of the total mortality; and it seems that surplus birds that were not removed in winter by predation were eventually eliminated by starvation and parasitism in spring.

These ideas to some extent reconcile those put forward by Lack and the Committee of Inquiry. It seems that food shortage does indeed cause some grouse to congregate on restricted areas, but these birds are surplus individuals that fail to obtain territories during times of seasonal dispersal. They collect in flocks on marginal ground where they become parasitized and toxemic. The critical factor, however, is not the degree of parasitism but, as Lack suggests, the population density in relation to the food supply. If they were more common, predators might mitigate the effects of disease, since there might then be no population surplus, or a smaller proportion of the surplus might be left for elimination by disease. However, there is some evidence (unpublished) that the density of predators was affected by the numbers of surplus grouse, and that predator numbers were not entirely controlled by human persecution. Many predators have undoubtedly been eliminated in the interests of game preservation, as Lack (1954) describes; but if they had survived, it is arguable that they would have exploited surplus grouse rather than limit the size of grouse breeding populations. Lack’s other conclusion, that parasitic disease is an important factor controlling grouse abundance, clearly does not find support; nor is it true that, if the parasite were eliminated, grouse would thereby be more abundant. It seems likely that fluctuations in grouse numbers are initiated by variations in their food supply. Red Grouse may be particularly susceptible to food shortage since they are largely dependent on a single plant species for food. When this food fails, a large proportion of the local population may be doomed to perish. Individuals in poor condition might be particularly susceptible to parasitic infestation, but in the absence of parasitism they would be expected to die anyway.
ACKNOWLEDGMENTS

The study in Glen Esk was conducted by a team consisting of A. Watson, G. R. Miller, D. E. Pinnock, and D. Jenkins, under the direction of Professor V. C. Wynne-Edwards. We acknowledge with gratitude the courtesy of the Earl of Dalhousie in allowing the study on his moors. The author appreciates the improvements in this paper made by his colleagues.

SUMMARY

This is a review of some more detailed papers describing population studies of Red Grouse on 400-hectare study areas in northeast Scotland.

Breeding densities may depend primarily on the food supply in the previous autumn when the territories are established, and be modified by the quantity and quality of food remaining on the territories at the end of the winter. Breeding success may be determined mainly by the quantity and quality of the food on the territories in late winter. This affects the reproductive behavior of the adults, with consequent variations in clutch size, hatching success, and chick survival. Apparently, grouse numbers are not controlled primarily by any extrinsic mortality factor, nor by inadequate recruitment through poor breeding. Whether good or bad, breeding always resulted in the production of more birds than stocked the area the following spring. Thus, there was a population surplus in winter.

The significance of “grouse disease,” assigned an important rôle in the literature, is assessed. Birds dying through parasitism appear to be mostly surplus individuals that cannot obtain territories, and are doomed anyway.

LITERATURE CITED


Committee of Inquiry on Grouse Disease. 1911. The grouse in health and disease: being the final report of the Committee of Inquiry on Grouse Disease. London. 2 v., 512 and 151 p.


Population Dynamics of Leach’s Petrel, *Oceanodroma leucorhoa*

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According to a hypothesis proposed by Wynne-Edwards (1955), the populations of most seabirds and several species of large birds of prey are not regulated directly by the food supply, as seems to be the case with many birds (Lack, 1954:141-153). He suggested instead that these populations are limited by behavioral or physiological characteristics which diminish the reproductive potential and thereby reduce pressure on the food supply. He proposed that these birds have managed to substitute objects of intraspecific competition, such as territory or social position, in place of the basic limiting factor, food (Wynne-Edwards, 1959).

Since 1955, I have been studying Leach’s Petrel (*Oceanodroma leucorhoa*), mainly by banding individuals in a single breeding colony at Kent Island in the Bay of Fundy, in an attempt to test the applicability of Wynne-Edwards’ hypothesis to this species. This paper is a progress report on that study.

**FEEDING EFFICIENCY AND THE SINGLE-EGG CLUTCH**

The characteristic that most clearly reduces the reproductive potential of seabirds is the small clutch size, which the Procellariiformes show in extreme form. These birds, from the albatrosses to the storm petrels, lay only one egg per year.

To test whether or not this is due to an inability to rear more than one nestling, in 1956 we added a nestling to each of two nests of Leach’s Petrel. Each added nestling was very similar in weight and stage of development to its nest mate. Increases in the weight of all four at the beginning of the experiment indicated that the parents did not discriminate between their own offspring and the introduced nestling. A storm on 8 August, nine days after the beginning of the experiment, resulted in a distinct loss of weight in all four nestlings, presumably because they were not fed on that date. In both nests the introduced nestling then declined in weight until 12 August, when observations had to be discontinued until 10 September. On the latter date, both introduced birds were found dead, as well as one of those originally present. This survival of one nestling in two nests is lower than the normal survival proportion.

While the smallness of the sample makes this experiment inconclusive, it suggests that ordinary weather variation prevents these birds from raising

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1 Contribution No. 29 from the Bowdoin Scientific Station, Kent Island, Grand Manan, New Brunswick, Canada.

2 This study was supported in part by a grant (No. 5575) from the National Science Foundation. Student assistants received aid from Undergraduate Research Participation Grant No. 11869 from the National Science Foundation.

more than a single young in a season. This hypothesis is supported by the fact that it is not uncommon to find young petrels in undisturbed burrows in an emaciated condition, weak and sluggish and with lowered body temperature. Some of these birds survive, but the majority do not. It seems unlikely that these are all cases where one parent has been killed. It must be remembered, however, that the Bay of Fundy is close to the southwestern limit of the range of the species in the Atlantic, where conditions may be marginal and the population seems to be declining. It should also be noted that nestlings of this species, like those of many other tube-noses, ordinarily become very fat and then lose weight before leaving the nest. They often reach weights of 80 g, and individuals weighing 90 and 92 g have been found, nearly twice the 48-g weight of breeding adults. No nestlings have been known to leave the nest successfully without this preliminary fattening, which thus appears to be essential to normal development.

In view of the fact that this species is known to feed on euphausid crustaceans, which are abundant enough to form the food base for enormous populations of marine organisms, it might be expected that enough food could be obtained to raise more than one offspring each year. However, the method of feeding used by this species and, in general, by other storm petrels is very inefficient as compared with the filter feeding at various depths used by other plankton eaters. These birds catch their food while in flight and are therefore limited to the very small proportion of the food organisms which is at or just under the surface. Diurnal vertical migrations of food organisms may further oblige them to do much of their feeding at night (Palmer, 1962:233). This method of feeding is also inefficient in that a separate action is needed to capture each individual prey organism. The method would seem to require the expenditure of so much energy in proportion to the amount of food obtained that there might be only enough left over to support a single growing nestling.

The general population decline in the southwestern part of the Atlantic range of Leach’s Petrel is a further indication that the food supply may play a direct role in limiting the population of the species. The Kent Island population has gradually declined in the past decade. The populations on the other islands in the Grand Manan Archipelago are, in general, less than one-tenth as large as when reported by Gross in 1935 (Huntington, 1959). Populations along the Maine coast are apparently declining, too (Palmer, 1949). The possibility that a decline in the food supply may be involved is strengthened by the observation that commercial herring catches have tended to decline in this area in recent years; Leach’s Petrel and the herring, Clupea harengus, share a similar copepod-euphausid food base (Bigelow and Schroeder, 1953). Of course, this particular point is not valid if the herring decline is due mainly to predation.

The storm petrel feeding method by itself would seem to prevent excessive exploitation of the food supply. The plankton population may not be im-
C. E. Huntington: Population Dynamics of Leach's Petrel

mune to depletion by predation, but it will surely be in no danger from birds that merely pick up some of the individual organisms that come within a centimeter or two of the surface. The petrels' competition comes largely from filter feeders and other animals that are supported by the water and can feed at various levels below the surface. Predation by the petrels presumably plays a part in limiting the number of prey organisms available to the petrels at any given time, but does not significantly affect the total population of the prey species. In other words, there is no feedback effect from the petrel population as predators to the population of their prey. Therefore, the petrels can gain no advantage from substituting nest site or territory for food as an object of competition, even if they could.

RELATIONSHIPS BETWEEN SEPARATE COLONIES

Whatever the role of the food supply may be, predation has certainly played a conspicuous part in the recent decline of this species' population off the coasts of Maine, New Brunswick, and Nova Scotia. Predation by mammals introduced by man has wiped out thriving colonies, such as the one on Nova Scotia Seal Island; predation by the increased numbers of Herring Gulls (Larus argentatus) and Great Black-backed Gulls (Larus marinus) may be significant in some places, too. Destruction of one colony can have an indirect effect on other colonies that are not directly in contact with the predators, if the colonies depend on each other for recruitment of breeding stock. The evidence from banding of adults and nestlings indicates that the colonies are interdependent in this way.

A substantial interchange of breeding birds between islands is apparently accomplished largely by birds breeding for the first time. About 50 percent of the birds banded while nesting at Kent Island return the year after their first capture, and about 70 percent return in the year after each subsequent capture, indicating that the process of nesting creates a strong bond to the nesting locality in most individuals. This bond is a precisely directed one; about 70 percent of all these returns are found in the same nest burrow where they were previously caught; the remaining 30 percent are found within 30 m of the old burrow. The birds banded as nestlings present a wholly different picture. Only about 0.5 percent of them have ever been recovered. Like the adults, these have all been at the island where they were banded (Gross, 1947), but this result is attributable to the limited distribution of petrel-banders. The implications of this finding are that there is no strong tendency for these birds to return to breed at the island where they were reared and that therefore there is an extensive interchange of birds between the various colonies. If the reproductive efficiency of the colonies in the center of the range of the species is greater than that of the peripheral colonies, thanks to a more favorable environment, then a net export of first-time breeders from the center to the periphery would be necessary to maintain a stable total population.
Recent observations by Leslie M. Tuck, the author, and others indicate that off the coast of Newfoundland there are colonies of Leach’s Petrel vastly larger than any known elsewhere in the Atlantic. On 27 and 28 July 1960, Tuck and I counted the occupied burrows on seven square plots, each 3 m on a side, on Gull Island, off Witless Bay, Newfoundland. The average density was just slightly over one occupied burrow per sq m. The fact that numerous burrow entrances were in sight wherever we could see the ground in the island’s woods gives me confidence in the extrapolated estimate of 400,000 occupied burrows for the whole island. This island is not unique, and it seems probable that Newfoundland has a breeding population of millions of Leach’s Petrels. The evidence available to me from personal observations and the literature suggests that no colonies of more than a few thousands of these birds exist in other parts of the Atlantic. Therefore, it would appear that the Newfoundland colonies must have a tremendous influence on the others through the interchange of individuals.

POSSIBLE BASES OF SELECTION

Given this centrifugal influence of the Newfoundland colonies, one would expect that whatever factors exert selective pressure at these central colonies would be important in determining the characteristics of the Atlantic population as a whole. If the availability of nest sites is a critical factor at the central colonies, the less successful individuals in this competition might be expected to emigrate to the peripheral colonies, where they might be subject to a different and harsher kind of selective pressure, due to less favorable feeding conditions. This situation, coupled with a gregarious habit, would appear to set the stage for the kind of substitution of limiting factors suggested by Wynne-Edwards.

When one looks for evidence of vigorous nest-site competition at the densely populated colonies, however, he does not find a clear picture. Eggs laid on the surface of the ground are likely to indicate crowding among burrow-nesting tube-noses. I have found such an egg once in a place on Kent Island where the ground was riddled with burrows. In our traverse of about three-quarters of a mile through the woods of Gull Island, Newfoundland, Tuck and I found four petrel eggs on the surface. This suggests competition for nest sites, at least in some places, but there is also evidence suggesting that there was room for many more birds. Twenty-two out of a total of 89 burrows investigated on Gull Island and 8 out of 24 on the neighboring Great Island were empty. Many, but by no means all, of these were apparently still being dug, presumably by prebreeders. Certainly the islands offered ample opportunities for petrels to find burrows or dig new ones close to other members of the species without moving to another island.

On the basis of these fragments of evidence, at least, it is my conclusion that Leach’s Petrel does not provide support for Wynne-Edwards’ hypothesis of population regulation by substitution of other goals for food as objects
of competition. Instead, Leach's Petrel appears to have occupied an ecological niche based on an inefficient feeding method which prevents it from threatening its own food supply and directly limits its reproductive potential; therefore, it could gain no advantage from any such substitution.

SUMMARY

Experiments with added nestlings and observations of seemingly undernourished nestlings suggest that Leach's Petrel cannot ordinarily find food enough to rear more than one nestling and sometimes not even one, at least in a breeding colony near the limits of its range. The population decline in the marginal parts of its range is due partly to predation, but is so widespread as to suggest that a change in the food supply is also responsible. The situation may be complicated by extensive movements from one colony to another, especially by young birds moving from the relatively crowded Newfoundland colonies to the smaller marginal colonies, where natural selection would be expected to operate more harshly and food shortage might be the agency for eliminating birds originally selected on the basis of unsuccessful nest-site competition. However, availability of nest sites does not seem to be a limiting factor, even at the largest and most crowded colony known.

LITERATURE CITED

The Determination of Reproductive Rates in Paridae

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In his interesting and stimulating book, *The Natural Regulation of Animal Numbers*, Lack (1954) advances the idea that, with each animal species, the reproductive rate is determined by natural selection, and that its mean value will therefore always be the highest one that can be attained under the prevailing circumstances. Since in nearly all species of birds, parents have to take care of their young for some time after hatching of the eggs, the average size of a bird’s clutch corresponds with the largest number of young that the parents can cover or for which they can provide enough food. The breeding season is timed to the period during which conditions permit the species to raise young most successfully; this is, in general, the period when food is most abundant.

In some groups of birds, such as the Columbidae, the clutch has a fixed size. In many passerines, however, we find, among the pairs constituting a population, a notable variability in clutch size as well as in the number of broods that are reared per season. A sound knowledge of the factors, by which this variability is caused, is of the greatest importance in obtaining a clear insight into the population dynamics of a species. For many years these factors were one of the subjects of my ecological studies on populations of tits in the Netherlands (Kluyver, 1950, 1951, 1952).

**GENETIC DETERMINATION**

The first question that arises is whether or not genetic or other inherent differences may exert some influence on the variability of the reproductive rate in a population. That genetic factors are responsible for the fixation of clutch size in certain birds can hardly be doubted. In species such as tits where, as I will show later, environmental factors cause important variations in the reproductive rate, it is open to discussion whether or not genetic and other inherent factors may in addition play a part in this variability.

In my three study areas, together covering about 800 ha, the entire population of the Great Tit (*Parus major*), the species I studied most intensively, runs to about 250 pairs a year. Every year I try to ring all of the parents and nestlings. Consequently, I am well familiar with many parent–offspring relations. However, in these populations many birds are to be found that have immigrated from nearby areas and that therefore are of unknown origin. For this reason, our populations are not sufficiently isolated to be used for a study of genetic differences.

Nevertheless, there are two lines along which it may be possible to obtain evidence of the influence that genetic factors may exercise on the variability of the reproductive rate in a population.
Many ringed individuals and even many pairs of ringed birds are found in the populations of consecutive seasons. In these ringed individuals we can study the presence or absence of a constancy in the reproductive rate.

For 111 ringed females, which lived in the same wood and which all had successfully reared their first brood, I recorded the number of clutches in consecutive seasons. The data obtained in this way indicate that with 59 females the number of clutches, either one or two per season, remained constant, whereas with 52 females it did not remain constant. This small difference between frequencies of constancy and inconstancy, being not significant, suggests that the production of either one or two clutches does not rest on innate factors.

With respect to the size of the clutch, it is not useful to make a comparison between a first and a second clutch which are produced by a pair of tits in the same year, as the mean size of the clutch decreases in the course of the season. Therefore, we have to compare sizes of first clutches in consecutive years, and we have to find out whether or not their difference is smaller in the clutches produced by a single female than it is in the clutches produced by two nonidentical females living in about the same habitat. I found that this is hardly so. This means that our data do not support the supposition that the difference in clutch size of nonidentical females might rest on a genetic difference. It might be due to differences in the ecology of the two seasons.

The second line for investigating the role played by genetic factors in the determination of the reproductive rate is a more indirect one.

Lack, in considering the evolution of the reproductive rate in birds, propounds the thesis, and herein I agree with him, that natural selection in a population must lead to the increase of those genotypes that, on the average, have the highest recruitment. By recruitment we mean that part of the seasonal progeny of a pair reaching maturity, i.e. in tits that part of the ringed nestlings recovered next year in the breeding season at their nest. The rate of recruitment of a pair is not always proportional to its fecundity. Lack (1948) established, e.g. for the Starling (Sturnus vulgaris), that in the case of very large broods more fledglings succumb in the first year of life than in normal broods. This difference in resistance is so strong that in large broods even fewer young reach maturity than in normal broods. Lack is of the opinion that in this way the action of natural selection on the genetic factors that are responsible for a clutch of normal size is demonstrated. Lack's idea—that natural selection in the population must lead to a preponderance of that class of females whose reproductive rate leads to the highest recruitment—is only acceptable if the variation in the reproductive rate which is present in the population is itself determined, or at least codetermined, by genetic factors. This means that, in case recruitment does not appear to be highest in the class of females that is most frequent in the population, dif-
ferences in genetic constitution are unlikely to take part in the variability of rates of reproduction that are present in the population.

I have split the data of my populations of Great Tits into classes of females (= mothers) with a seasonal brood size—first and second brood to-

Fig. 1
H. N. Kluyver: Reproductive Rates in Paridae

gether—of 1–4, 5–6, 9–10, etc. The lower part of Fig. 1 shows the frequency of each of these categories, females producing 7–8 fledglings in a season being most numerous and the number of the other classes decreasing in both directions.

The crucial point is whether the class that is most numerous coincides with the class in which seasonal recruitment is highest, as it did in Lack's Starlings. If so, the line representing the frequency of classes in the population and the line representing their rates of recruitment will show a certain similarity of shape. The latter line must also have its top in the class of 7–8 fledglings.

The middle part of Fig. 1 shows this rate of recruitment, expressed per 100 mothers of each class. The lowest rate of recruitment, 30 per year, is found in the class of females with the lowest reproductive rate (1–4 fledglings per mother), and the rate of recruitment gradually increases with the reproductive rate to a value of 144 per year in the class of 17–21 fledglings per mother. The class of mothers that has 7–8 fledglings per season has a rate of recruitment of only 53 per season. Recruitment is highest in the class having the most fledglings per season, which class comprises only a very small part of the population. As the rate of recruitment does not reach its highest value in the class of females that is most numerous in the population, natural selection does not work along this line. Consequently, it does not appear probable that genetic factors play a part in the variability shown by the rate of reproduction.

Yet the argument is incomplete. Although natural selection does not work along the line of recruitment, it might work along another line; it might affect the length of life of the parents. As tits not only breed in their first year but also in their later years, longevity of the individual must be considered as important a quality for the population as a high recruitment.

We will later see that the rearing of a first brood consisting of a large number of nestlings prevents many pairs from proceeding to a second clutch in the same year. Might a high seasonal reproductive rate not exhaust the reserves of a bird so deeply that it also shortens the length of its own life? If so, natural selection might favor the development of the classes with a genetically determined low reproductive rate to some extent, and in this way the preponderance of the class with merely 7–8 fledglings per season would become understandable.

My recoveries of ringed mothers in the next breeding season give an adequate answer to this question. The highest line in Fig. 1 shows the percentages of ringed mothers recovered in the next breeding season. This provides a suitable measure for their length of life. The outcome is quite clear: A better survival of the females that had few young does not exist. This means that natural selection does not work along this line either.

To sum up: Size of the clutch and number of clutches per year present hardly any constancy in the individual birds, and neither recruitment nor
parent survival are spread in the population as we would expect them to be, if the reproductive rate was genetically determined.

These facts indicate that differences in reproductive rate are not the product of any natural selection working in the direction of a definite reproductive rate. These differences must be due to phenotypic factors. Each individual tit has the innate capacity to modify its reproductive rate: Presumably this capacity is the product of natural selection having worked in the direction of adapting reproductive rate to the conditions of the environment.

**ENVIRONMENTAL DETERMINATION**

Outside the tropics, birds start nest building and egg laying in spring, i.e. in the season of increasing daylength, and they do it earlier in a warm spring than in a cold one. Are such physical factors the only so-called proximate factors that give the signal for the start of these activities and that in turn insure nestlings being present in a period of sufficient food supply?

**Importance of Food Supply**

With all tits, the food consists mainly of several kinds of insects which, in the breeding season, predominantly comprise defoliating caterpillars.

Two *Parus* species, the Crested Tit (*P. cristatus*) and the Coal Tit (*P. ater*), breed exclusively in coniferous woods. The reasons why they avoid deciduous woods I have to leave out of consideration now.

A uniform woodland of Scotch pine (*Pinus sylvestris*) is a common habitat for these tit species; for two other tit species, the Great and the Blue tit (*P. caeruleus*), it is a marginal habitat. The latter two species prefer deciduous woods, especially oak woods, with a rich undergrowth and with a well-developed canopy. Such a wood is an optimum habitat for both of them. Differences in population density shown by the Great Tit as well as by the Blue Tit in coniferous and in deciduous woods are certainly due to differences in adequate food resources. This at least is true if enough nesting sites are at the tits' disposal, as is artificially realized in my study areas by the erection of nest boxes. In a natural wood, a surplus of suitable nesting sites in rotten stumps and branches is usually to be found.

Nearly all caterpillars living in deciduous wood hatch from eggs during the period in which the buds of the deciduous trees begin to expand and the trees rapidly burst into foliage. This means that in this and the immediately following period the quantity of tit food rapidly increases. In May, caterpillars of *Tortrix* and *Cheimatobia*, for example, usually are extremely abundant and provide much food for young tits. In general, in Scotch pine woods, caterpillars are usually less abundant than in oaks. Larvae of some Scotch pine moths, such as *Eriopis, Evetria*, and *Cacoecia* species, do not hatch, however, in spring, but in the preceding autumn. In the autumn these larvae are already feeding on the needles, and when the larvae enter their winter rest, they have already reached a certain size. Early in spring these
larvae emerge. They then feed on the pine needles of last year, and that is why these larvae in early spring reach a size that makes them attractive to the parent tits as food for their young. That is the reason why, in early May, pines probably have as many caterpillars of the right size for feeding young tits as do oaks. Soon after that, however, tit food is much more abundant in oaks.

In oaks as well as in pine woods, I put trays for catching caterpillar droppings, the number of larger droppings being a reasonable comparative measure of the number of larger caterpillars present in the trees. "Larger" in this case means "large enough" to be attractive for the parent tits to feed to their young. The main point of difference between oaks and pines is that caterpillars in the oak wood show a sharp peak from the end of May to early June. This peak is wanting in the pines. Later in the season, caterpillars are usually only slightly more abundant in oaks than in pines.

Tits nesting near the boundary between deciduous and coniferous woodland certainly are accustomed to forage predominantly in the habitat where they can find food more easily. Systematic observations on the foraging of color-ringed individuals of the Great Tit living in such a border area showed, in late May and early June, a clear preference for the deciduous wood, whereas in July this preference was still present, but much less pronounced (Table 1).

We will now consider the question of how far such differences in the amount of available food may affect such aspects of the breeding biology as breeding season, nesting success, etc.

Start of Breeding

The pine-wood species, viz. the Coal and Crested tit, most often start earlier with laying than the species that are mainly found in deciduous woods. An early start in a coniferous wood is in agreement with the larger size of the caterpillars that are found in this kind of wood in spring.

In the Netherlands, the habitat of the Crested and Coal tit consists exclusively of Scotch pine. It is much more uniform than that of the Great Tit and Blue Tit, which live predominantly in deciduous woods, consisting of a mixture of oak, beech, birch, and many other trees and shrubs. Nevertheless, coniferous tits show more variability in the initial date of the breeding season than the Great and Blue tits.

I calculated the standard deviations of the average initial dates recorded
in a period of 15 years. In the Blue Tit, which is almost wholly limited to
deciduous woods, the standard deviation is, nearly every year, smaller than
in the Great Tit, which lives in both habitats. In the two conifer-residing
tits, however, it is nearly always larger, which means that the initial dates
show a greater spread.

With respect to the Great Tit itself, the same difference exists between a
population living in a pine wood and a population in a deciduous wood.
Again, the former population shows a greater spreading of the initial dates
than the latter. This I ascribe to the slower increase of food supply in the
pine wood.

This close correlation between the moment at which laying starts and the
increase of the food supply strongly suggests that, next to other factors such
as daylength and air temperature, it is the amount of food that gives the tits
the signal to start their laying.

**Population Density**

The coniferous woods, being poor in food supply, were very thinly pop¬
ulated by tits, the average population of the three most common species,
Great, Blue, and Coal tit, together amounting to 2–5 pairs per 10 ha. In
these woods many of my boxes were unoccupied every year. The population
of my only oak woods study area was much denser. About 60 pairs per
10 ha were to be found in it, when sufficient nest boxes were available.

I divided this wood into a section with many boxes, in fact with a super¬
abundant number (just as in the pine woods) and a section with few.
Nearly all of the boxes in the latter section were occupied by Great Tits,
which dominate in the quarrels for nesting sites, whereas in the former sec¬
tion a number of boxes were occupied by Blue Tits and some of the boxes
were unoccupied.

**Clutch Size and Nesting Success**

It developed that in the Great Tit, to which I will limit my further consid¬
erations, the size of the first clutch is higher in the whole of the oak wood,
i.e. where caterpillars are abundant, than in the pine woods where food is
scarce. The tits in the oak wood have adjusted the size of their clutch, just
as they have the time at which they start laying, to the abundant food sup¬
ply which will be present in the nestling period. In the oak wood many
clutches contain 12 and more eggs; in the pines such large clutches are
nearly absent. The mean size of first clutch amounts to 10.5 in oaks and
9.2 in pines, this difference being statistically significant. Apart from that,
four other symptoms indicate the poorer supply of tit food in pines, viz. (a)
the number of feedings that the nestlings receive from their parents, (b) the
growth rate of the nestlings, (c) the survival rate of the nestlings, and (d)
the frequency of so-called runts in the nest.

Growth rate and number of feedings per nestling (the latter recorded with
an automatic recorder) are known for the first brood. Oak-wood nestlings are more frequently fed and grow faster than pine-wood nestlings. The fact that the number of nestlings per brood is usually higher in oak woods than in pine woods emphasizes the importance of this observation. Nesting success, i.e. survival rate of nestlings, is measured in this study as the percentage of eggs which, in a period of 15 years, have developed into nestlings able to leave the nest. In the pine woods, broods are always less successful than broods raised in the oak woods. Average nestling survival amounts to 73 percent in pines and to 90 percent in oaks, despite the fact that the clutch in the oaks is higher. Moreover, an experiment in which the clutches in the pine woods were artificially reduced resulted in an increase of nestling survival. This points to a competition among the nestlings, which is most probably a competition for food. Runts, i.e. nestlings that lag behind in development, are more common in pines than oaks. Such runts are most often the latest-born nestlings. Although runts are always begging for food, parent tits tend to feed the more advanced young, size and weakness of the runt making it subordinate. Consequently, if food is scarce and the older and stronger young are also begging continuously, especially the latest-born young gets too few feedings and eventually it dies of starvation. In unsuitable, marginal habitats such as pine woods, this mechanism provides that there is no complete scramble for food among the young, in which all of them would then receive less food, become weakened, and eventually die; there is only a contest in which at least some of the young can survive well. In oak woods, food is abundant enough for successfully rearing all of the young.

All aspects of breeding biology which we studied comparatively in oaks and pines show, therefore, that broods in the pine woods are less successful. This confirms the conclusion that food supply is the factor that primarily governs the rate of reproduction.

This, however, is not the whole truth. As the breeding season progresses, mean size of clutches decreases, both in oaks and pines. Second clutches, started in June or July, consist of fewer eggs than first clutches started in April. This seasonal decrease of clutch size proceeds more rapidly in oak woods than in pine woods; but at the end of the breeding season the positions are reversed, for then the clutch size is higher in pine than in oak woods.

Second Clutches

Next to average clutch size, an important feature is the percentage of pairs that proceed to a second clutch. In pine woods, many pairs do so (in many years up to 50 percent), but in most oak woods only 20 percent proceed to a second clutch. Consequently, in the last part of the breeding season, reproductive capacity of the population is higher in pines than oaks.

However, the harvest of caterpillar pellets on trays showed that, even in
the season of the second clutch, an oak wood is richer in tit food than a pine wood. This is confirmed by the fact that second-brood oak-wood nestlings survive better than those in pines.

What might be the reason that pine-wood pairs of the Great Tit in this season are nevertheless on the average both more apt to undertake second clutches and lay more eggs per clutch than pairs living in oaks? In my opinion, an important point is that population density is higher in oaks than pines. A dense population prevents many pairs from producing a second clutch. This is shown by the fact that tits have more second clutches in years when the population density is low than in top years. This holds good for both oak and pine woods. Moreover, the important influence of population density was clearly shown by an experiment. I reduced population density in a part of my oak wood to about the same level as in the pine woods by placing only few boxes at the tits' disposal. Consequently, the proportion of the pairs present producing a second clutch increased considerably.

What might be the mechanism that causes the relation between high population density and few second clutches? I suggest that we should look for this mechanism in the necessity of starting a completely new breeding cycle. Starting a new breeding cycle implies that a tit pair has once more to set up a territory. The territory that a pair occupies before it enters upon its first clutch completely loses its importance during the period in which the parents are feeding their young. In the latter period, the parents move out to places where they can most easily obtain the required amount of food, and in doing so they pay no attention to territorial boundaries.

The occupation and defense of a new territory, which, moreover, is often established at a different site, i.e. outside the original territory, requires a high amount of energy, especially in a densely populated area, where an immense effort is required to keep out all the many fellow tits wandering about with their young. In spite of that, a pair that proceeds to a second clutch must at least for a short time enter upon this task.

When we further realize that the birds have to set up this territory in a period of decreasing reproductive impulse, it becomes clear that in a dense population a smaller part of the pairs present will be fit for it, than in a thinner population.

We might ask which of the pairs present proceed to a second clutch, and which do not? As so many of my birds were banded, I am able to investigate whether and to what extent individual qualities (age of the partners and degree of success obtained with the first brood) might perhaps influence the decision of the pair to enter upon a second clutch.

With respect to the influence of the age of the breeding birds, observations on banded pairs show that in the class of yearling females a slightly smaller number of females proceed to a second clutch than in the class of the older females.

A more important influence on the frequency of second clutches is, how-
ever, exercised by the degree of success obtained with the first brood. Table 2 gives percentages of tit pairs proceeding to a second clutch in pine woods and in mixed-wood areas where the population density is rather low and where second clutches consequently are numerous. It appears that pairs whose first clutch consisted of many eggs are more apt to proceed to a second clutch than the pairs whose first clutch consisted of but a few eggs.

This indicates that those birds which early in the season laid a large number of eggs are apt to retain their reproductive capacity during a longer period than birds whose first clutch consisted of a smaller number of eggs. This conclusion seems to contradict the earlier-established fact that in oak woodland the first clutches are large, whereas second clutches are scarce in this habitat. For this deviating result, there are two reasons; the first is that the population density in the oak woods is so high that many pairs have to forego for that single reason rearing a second brood, and the second reason is that nesting success is very high in the oak wood.

The horizontal lines of Table 2 indicate the influence of nesting success, obtained with the first brood, on the percentage of second clutches. Following the horizontal lines for each first clutch in the table, we clearly see that more second clutches are started after a less successful first brood than after a first brood that resulted in a high number of fledglings.

My conclusion is that it is not the laying of a large number of eggs, but rather the rearing of a large number of nestlings that exhausts the endocrine secretions (which decide whether a second clutch will be entered upon or not) so markedly that a second clutch is omitted.

In oak woods many pairs rear a large number of young in their first brood. Next to a high population density, this is a supplementary cause for the scarcity of second clutches observed in this kind of wood.

**SUMMARY AND CONCLUSIONS**

Pairs of local tit populations show considerable variation in size of clutch and number of clutches per year.
No indication could be found that genetic factors, varying in different individuals, are responsible for these variations.

Tits have the capacity to modify their reproductive rate by adjusting their breeding season, size of clutch, and number of clutches to the conditions of the environment. The conclusion is that food supply is very important. No simple relation, however, exists between amount of food and reproductive capacity. A large food supply stimulates a high rate of reproduction, but it also causes a high density of population, which in turn inhibits reproduction to a certain extent. Moreover, a pair having had a high number of young in the early part of the breeding season is apt to be too exhausted to undertake another clutch later on in the season.

Apart from other factors, the combined action of food supply, population density, and physiological exhaustion of reproductive capacity gives rise to an intricate pattern of variability of reproductive rates in tits.

LITERATURE CITED

Survival in the Great Tit, *Parus major*

**Christopher Perrins**

*Edward Grey Institute of Field Ornithology, Oxford University, Botanic Garden, Oxford, England*

This work is part of a population study of the Great Tit that was started in 1947 under the direction of David Lack (see Lack, 1955, 1958; Lack, Gibb, and Owen, 1957). The purpose of the present paper is to investigate some of the factors affecting the survival of the young birds.

The work discussed here has been carried out on the Wytham Estate, 2 miles west of Oxford. About 600 acres of Wytham is woodland suitable for Great Tits. In Marley Wood, some 66 acres of Wytham, records of the breeding population of Great Tits and Blue Tits (*Parus caeruleus*) have been kept for 16 years. These data for the Great Tit (Fig. 1) indicate that there has been an increasing population during the years 1958–61, followed by a drop in numbers in 1962. These are the years that will be used for the main discussion in this paper. Fig. 1 also shows the data for a nest-box population at Veluwe, Holland, studied by Kluijver (pers. comm.). It will be noted that, although there are year-to-year differences in the fluctuations, there is a close resemblance in the overall pattern of fluctuation in the two areas, which are 300 miles apart. There is thus good reason to believe that the fluctuations in the Marley population reflect those in a much wider area.

The young Great Tits were ringed, and their weights on the 15th day after hatching recorded against their ring numbers. (The day on which the first young in the nest hatched is counted as day one, although more correctly it is day 0.5 [Gibb, 1950].) Gibb (1950) has shown that the weights of the young birds do not increase between the 15th day and the time of leaving the nest (about 19th or 20th day). Intensive trapping was carried out each winter to catch as many as possible of the young ringed in the previous summer. Table 1 gives the number of young that left the nest and the number that were later recovered (data analyzed up to 31 March 1962).

In this paper a bird that has survived is defined as one that is known to be alive 3 months after fledging. By this time the young birds are fully independent of their parents, and they have completed their first molt. I believe that each individual from then on stands a more or less equal chance of further survival with all the other yearlings.

**Movements of Birds**

It is necessary to know to what extent the Great Tits in Wytham tend to leave the wood, particularly as a large number of the young are never seen again. As shown later, certain classes of young disappear in higher proportions than others. I believe that this is due to a higher death rate, but it is important to be certain that it is not due to emigration. About 8,000 Great

Tits have been ringed during the study, and Fig. 2 shows the place of recovery of the 49 birds that are known to have left the Wytham Estate. Very few of these traveled much over 3 miles. Since 45 of these birds were ringed as nestlings, it is perhaps better to consider the recoveries in terms of nestlings alone. During the study, 5,784 nestling Great Tits have been ringed; and in addition to the 45 recoveries outside the estate, some 614 have been recovered inside Wytham. As those birds that had left had traveled so short a distance, many of these may have been roosting in Wytham at night; distances of 2 miles between feeding place and roosting site are known. The birds marked as known returns in Fig. 2 were caught outside

Fig. 1. Comparison of two nest-box populations of the Great Tit censused during the breeding season. Data from Veluwe, Holland, provided by Kluijver (pers. comm.).
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Table 1.—Number of Young Great Tits That Fledged Each Year and the Number Recovered at Least 3 Months after Fledging

<table>
<thead>
<tr>
<th>Year</th>
<th>No. Fledged</th>
<th>No. Recovered</th>
<th>Percentage Recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>1958</td>
<td>361</td>
<td>37</td>
<td>10</td>
</tr>
<tr>
<td>1959</td>
<td>824</td>
<td>107</td>
<td>13</td>
</tr>
<tr>
<td>1960</td>
<td>739</td>
<td>223</td>
<td>30</td>
</tr>
<tr>
<td>1961</td>
<td>1,225</td>
<td>99</td>
<td>8</td>
</tr>
</tbody>
</table>

* Data analyzed up to 31 March 1962.

the wood in the winter, but were found back there the following spring. Likewise, two Blue Tits, ringed in Wytham, are known to have traveled 11 and 20 miles during the winter, but were found back in the wood the following summer.

Over three-quarters of the birds that were recovered outside the wood were found in winter, the time when it is known that many Great Tits may come around houses in their search for food. Most of these birds were killed by cats or by flying into windows and by other means associated with houses. The fact that most of these birds were recovered in this way means that one can be reasonably certain that the recoveries in Fig. 2 are representative of the movements of Wytham Great Tits as a whole, since these means of recovery are fairly equally spread over southern England.

![Diagram of recoveries of Great Tits outside Wytham.](image)

Fig. 2. Recoveries of Great Tits outside Wytham.
In recent years there have been large-scale autumnal movements of Great and Blue tits in England and on the Continent (Cramp et al., 1960). However, the evidence suggests that the majority of the birds involved were of continental origin, and there is no satisfactory evidence that British-bred Great Tits were involved at all. Analysis of the birds that moved out of Wytham gives no indication that birds moved out of the wood in one year more than in any other or in one direction rather than another. Moreover, it will be shown that the birds that disappeared were lighter than average, but the birds recovered outside the wood were heavier than the average weight for their brood, so they cannot have been representatives of the classes of young birds which disappeared.

**Young in the Nest**

Gibb (1950) showed that, in oak woodland, the caterpillars on which the tits feed their young are abundant only for 2-3 weeks and that the correlation between the date of the breeding season of the tits and that of peak abundance of the caterpillars is very close.

In any one year, two major factors affect the amount of food that the individual nestling receives. One is the number of young in the brood: The larger the brood, the less food each nestling receives. Each nestling consequently weighs less on the average in a larger brood than in a smaller one. Parallel results have been obtained on the number of feeding visits per chick in many species. Each nestling is fed proportionately less often in a larger than a smaller brood (e.g. Kendeigh, 1952; Moreau, 1947). In this study, the average difference in weight of nestling Great Tits in relation to brood size is about 3 g, each young bird in broods of 3-4 averaging 20 g and in broods of 12-13 young 17 g.

The second major factor is the period in the season at which the brood hatches. The later that the young hatch, the shorter is the period in the nest that is coincident with the flush of caterpillars. Gibb (1950) showed that the parents of the later broods fed the young less often. Table 2 shows the

<table>
<thead>
<tr>
<th>Year</th>
<th>Study Area</th>
<th>Mean Difference in Weight (g)</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1958</td>
<td>All Wytham</td>
<td>0.165</td>
<td>0.067</td>
</tr>
<tr>
<td>1959</td>
<td>All Wytham</td>
<td>0.056</td>
<td>0.020</td>
</tr>
<tr>
<td>1960</td>
<td>All Wytham</td>
<td>0.024</td>
<td>0.009</td>
</tr>
<tr>
<td>1961</td>
<td>Wytham except Marley</td>
<td>0.109</td>
<td>0.023</td>
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<tr>
<td>1961</td>
<td>Marley only</td>
<td>0.338</td>
<td>0.060</td>
</tr>
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</table>

*The figures listed here are the differences between the weights of young in different broods on their 15th day after hatching; they are cumulative, e.g. in 1958 young hatched on 1 May were weighed on 15 May and averaged 0.165 g more than young that hatched on 2 May (and weighed on 16 May) and 0.330 g more than young that hatched on 3 May (and weighed on 17 May), and so on. Figures in this table were calculated for young in broods of 7-8, and broods that were not of this size were adjusted for by a regression analysis (because weight of young also varies with brood size—see text).
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decline in weight per day for nestlings in broods of 7–8 occurring in the 4 years 1958–61. For example, in two broods that hatched 2 weeks apart in 1961, each chick in the earlier brood averaged 1¾ g more than each of those in the later one. The magnitude of the decrease in weight differed markedly in different years. I believe that the size of this decrease gives a good indication as to how well the food supply was holding out in that year.

The mean clutch size of the tits decreases throughout the season (Kluijver, 1951; Lack, 1958). This is undoubtedly a long-term adaptation to the increasing scarcity of food for the young, which makes it harder for the parents to rear them in the later part of the season.

As shown in the next section, mortality after leaving the nest is related to the food supply in the nest. However, not only do the young in smaller broods and in broods that hatch earlier in the season survive better after fledging, but a larger proportion of them successfully leave the nest. This is because more of the larger and the later broods are taken by predators (Table 3). It is reasonably certain that such broods are hungrier and more

Table 3.—Predation on Great Tit Nests in Wytham in Relation to Brood Size and Time of Season, 1959–61

<table>
<thead>
<tr>
<th>Year</th>
<th>Brood Size</th>
<th>No. Nests</th>
<th>No. Lost</th>
<th>%</th>
<th>No. Nests</th>
<th>No. Lost</th>
<th>%</th>
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<tbody>
<tr>
<td>1959</td>
<td>Up to 13 May</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3–6</td>
<td>9</td>
<td>0</td>
<td>0</td>
<td></td>
<td>25</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>7–10</td>
<td>23</td>
<td>0</td>
<td>0</td>
<td></td>
<td>14</td>
<td>3</td>
<td>21</td>
</tr>
<tr>
<td>11–15</td>
<td>17</td>
<td>0</td>
<td>0</td>
<td></td>
<td>20</td>
<td>5</td>
<td>25</td>
</tr>
<tr>
<td>1960</td>
<td>Up to 15 May</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2–5</td>
<td>13</td>
<td>1</td>
<td>8</td>
<td></td>
<td>20</td>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>6–8</td>
<td>24</td>
<td>2</td>
<td>8</td>
<td></td>
<td>34</td>
<td>5</td>
<td>15</td>
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<tr>
<td>9–14</td>
<td>28</td>
<td>5</td>
<td>18</td>
<td></td>
<td>21</td>
<td>6</td>
<td>29</td>
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<td>1961</td>
<td>Up to 10 May</td>
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<tr>
<td>2–5</td>
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<td>2</td>
<td>9</td>
<td></td>
<td>33</td>
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<td>21</td>
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<td>6–8</td>
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<td>9</td>
<td>21</td>
</tr>
<tr>
<td>9–13</td>
<td>35</td>
<td>6</td>
<td>17</td>
<td></td>
<td>26</td>
<td>6</td>
<td>23</td>
</tr>
</tbody>
</table>

*Dates in each year were chosen so that approximately half of the data fell into each half of the season. Similarly, brood sizes were chosen to give similar numbers of broods of small, medium, and large size. The data are slightly biased in favor of the large broods, as the very late broods are usually heavily preyed upon and most of them are small (clutch size decreases throughout the season). Noisy in the nest so that the predators (which are chiefly weasels, *Mustela nivalis*) find them more easily. Thus, more of the large and the late broods do not even leave the nest. As about 1 in 5 of the females of preyed-upon nests have been killed with their broods, selection against the laying of large or late clutches does not act only through failure to produce young, but also through some of the females not having another opportunity to breed.
SURVIVAL AFTER FLEDGING

Variations in weight of the young affect the survival of the birds after fledging. The percentage of young surviving in the different classes is shown in Fig. 3 and 4. As the recovered birds are only a proportion of those that survived, these percentages should be compared only with other percentages in the same year and not with those of another year, because various factors greatly affect the proportion of the total population that is caught each winter. Thus, the figures are comparable within years but not necessarily between years.

These graphs show that some classes of young birds were not recovered in as high a proportion as other classes. It is believed that those classes from which fewer were recovered had experienced a higher mortality. Two groups of graphs are shown in Fig. 3. The upper group is based on Table 2 and shows the average decrease in weight of the individuals of broods of 7–8 throughout the breeding season during each of the 4 years. The lower group shows the survival of the young in relation to their weight on the 15th day. It is clear from this figure that the heavier young survive better; hence, it is the young of both the large and the late broods which do not survive so well. In 1959 and 1960, when the data on weight decrease suggest that food was holding out reasonably well at the end of the season, the lighter young were not at such a disadvantage as they were in 1958 and 1961, when extra weight was of especial advantage. In 1959 only those young of 19 g and over seem to have had an equal chance of surviving, while in 1960 all young of 16 g and over survived equally well.

In the two sets of graphs in Fig. 4, the upper group repeats those of the previous figure. The lower group shows survival in relation to the date of hatching, the data being lumped into 3-day periods. The young that hatched earlier in the season survived better than those that hatched later. This observation fits with what is known about the food supply. There was proportionately less difference between the success of the chicks in early and late broods in 1959 and 1960, when the seasonal weight decrease was small, than there was in 1958 and 1961 when it was large; in 1959 and 1960 a reasonable percentage of the late-hatched young survived, while in 1958 only a very small percentage did so, and in 1961 perhaps none of the late chicks lived.

The above data show why the tits do not normally have second broods in oak woodland and what the limiting factor is that prevents them from having larger broods. There remains the problem of why the birds do not lay earlier than they do. In 1960 and 1961 (Fig. 4), the young that hatched at the beginning of the season appear not to have survived so well as those that hatched slightly later. It is not known whether the young of the very first broods of the season really are at a disadvantage, as the data are too few for this period. However, over the 16 years of the study 12.3 percent of the
young of the very early broods have been recovered, as opposed to 11.8 percent of the other young from the first half of the season. This suggests that the young from the very first broods survive about as well as those that come

Fig. 3. Survival of Great Tits in relation to weight, 1958-61. This figure shows two separate groups of graphs. The top group (drawn against the left and the upper axes) involves regression lines from the data in Table 2 and shows the mean weights of 15-day-old nestlings hatched at different times in the season, the position and length of the line against the upper axis showing the time and extent of the breeding season. The bottom group (drawn against the lower and the right axes) shows the percentage of each weight class of young recovered in relation to their weights in the nest. Because of a paucity of data, the weight classes 12–15 g, 16–17 g, and 21–22 g have been lumped and plotted as 13.5, 16.5, and 21.5 g, respectively.
later. Hence, the reason that all the tits do not breed in the very early period does not depend on survival of the young after hatching. It is even more difficult to understand why birds that breed in the second half of the

Fig. 4. Survival of Great Tits in relation to date of hatching, 1958-61. This figure shows two separate groups of graphs. The top group (drawn against the left and the upper axes) is the regression lines from the data in Table 2 and shows the mean weights of 15-day-old nestlings hatched at different times in the season, the position and length of the line against the upper axis showing the time and extent of the breeding season. The bottom group (drawn against the lower and the right axes) shows the percentage of young later recovered in relation to their time of hatching. The data are grouped by 3-day periods, and the position and length of the graphs show the time and extent of the breeding season.
main period do not breed in what is now the first half, as there can be no reasonable doubt that they would rear more young if they did so.

I suggest that the tits do not breed earlier because the females cannot get into breeding condition any sooner than they do. There is little direct evidence for this, but the first-year females tend to breed slightly later than the older birds, and it seems reasonable to expect that the older birds, being experienced in feeding, will be able to get into breeding condition slightly earlier than the first-year ones. It is difficult to suggest any other possible factor that might be involved. Kluijver (1951) gives some evidence that individual birds tend to breed at the same time in the season in different years.

**WINTER POPULATIONS**

After the young have fledged, it is very difficult to trap them until the leaves have started to fall from the trees. By this time it is possible to discover how well the young have survived. This is done by finding the ratio of older to first-year birds in the population (it is possible to distinguish the two age classes by plumage). For example, in the winter of 1960–61, 399 first-year and 116 older birds were trapped, a ratio of 3.5 young per adult, an extremely high proportion of yearling as compared with older birds. The following winter, 1961–62, 127 first-year and 281 older birds were trapped, a ratio of 0.45 yearling per older bird.

When differences such as these occur, they are already apparent by early November, long before the cold weather starts. Evidently something happens to the young after they leave the nest and before the winter begins. The young birds have not emigrated in appreciable numbers, as is shown by the very few recoveries outside the wood. In addition, the birds that were recovered outside the wood tended to be heavier than the average for their broods, and thus are from the weight classes that have produced most known survivors rather than from those weight classes that have produced fewer. Therefore, it must be assumed that the birds that have disappeared have died within the wood, at some period between fledging and early November.

It seems likely that this mortality is caused by a paucity of food during the period when the young are learning to feed for themselves. Further, it seems likely that the numbers of birds present may greatly affect the amount of food available for each bird. In 1961, the year with a quite abnormally high tit population, the caterpillar population in Wytham was very low. In one part of the wood, Marley, the Great Tits bred at a density of 1.3 pairs per acre, but in the rest of the wood they bred at an average of 0.43 pair per acre, less than a third of the density in Marley. (This was probably due partly to a shortage of boxes in areas other than Marley, although this does not seem to have resulted in movement into Marley.) The nestlings in Marley averaged nearly a gram less in weight than the nestlings in the rest of the wood. Moreover, Fig. 5 shows that the weight decrease in relation to date was also more rapid in Marley than in the rest of the wood. Finally,
the proportion of birds recovered after 3 months was markedly lower from Marley than from the rest of Wytham in that year (being 5 versus 11 percent); and the lower graphs show that, considering birds of equal weight,
survival of young was poorer in Marley than it was in the rest of the wood. Kluijver (1951) has shown that there is little difference between the summer and winter mortality of adult Great Tits. In addition, he has indicated that the year-to-year variations in adult mortality, probably caused by differences in severity of winter, are not great. The above data on the differences in survival of the young in different summers suggest that this survival has varied more than the annual adult mortality.

No. juveniles per adult

<table>
<thead>
<tr>
<th>No. of birds in sample</th>
<th>48</th>
<th>57</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>49</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>51</td>
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<td></td>
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<td>58</td>
</tr>
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<td>60</td>
<td>61</td>
</tr>
</tbody>
</table>

Fig. 6. Ratio of first-year to older birds in winter population in relation to percentage change from the breeding population of the preceding season to that of the following season, e.g. the point labeled 58 shows that in the winter of 1958–59 there were some 1.6 young in the population for each older bird and that the breeding population in 1959 was 50 percent larger than that in 1958. All years in which there were less than 15 birds of known age have been excluded. Note: The 1961 breeding population had only 1.7 first year per older bird, not 3.5 as were present in the previous winter. The reasons for this are not fully understood, but at least part of the reduction in the numbers of first-year birds is due to there being insufficient nesting boxes in some parts of the wood.

The number of breeding pairs of Great Tits has varied markedly from year to year (see Fig. 1). The number of surviving young has also varied greatly. When the two sets of data are plotted against each other (Fig. 6), there is a close correlation between the two, high survival of young from one year leading to a high breeding population in the following year. Evidently, one of the major factors affecting the number of breeding birds in any one year is the number of young surviving from the previous year. An average 50 percent of the adults die each year and, if the breeding population has risen, it is because more young have survived than adults died; while if the population has fallen, it is because fewer young survived than adults died. While hard winters or other catastrophes may at times greatly reduce the
population of both yearling and older birds, no such phenomena occurred during the period of this study.

CONCLUSION

The adult Great Tits are raising as many young as they can, and the period after fledging in late summer or autumn is important to the survival of these young. It is during this time that the major variations in mortality occur, which in turn affect the level of the next year's breeding population. While from time to time hard winters reduce the population, in England at least, such winter conditions are not normally as important as those soon after the young have left the nest in midsummer.

SUMMARY

The weights of nestling Great Tits decrease as brood size increases because the parents are unable to feed each chick in a large brood as often as each chick in a small brood. Nestlings in late broods are lighter than those in early ones because food is scarcer later in the season. The weight of nestlings affects their chances of survival after leaving the nest. The number of young birds surviving the late summer months varies greatly from year to year. The number of surviving young seems to be the most important factor affecting the number of breeding pairs the following year.

LITERATURE CITED


Behavioral Response of Song Sparrows to Different Environmental Conditions

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A 3-year study (1960–62) of Song Sparrows (*Melospiza melodia*) in an archipelago showed extreme variation of population densities on different islands. The differences were consistent, and were related to the types of habitat that the respective island populations inhabited. The purpose of this paper is to show how the unique environmental conditions on one particular island, when contrasted with other areas, resulted in a very high population density, and facilitated behavioral adaptation on the part of the birds.

General Information.—The breeding range of Song Sparrows extends from central Mexico to Alaska, and from the West to the East Coast. Within this broad range, the species shows a high degree of adaptability to varying environmental conditions. Most of the eastern races migrate during the winter, while those along the West Coast, where the winters are mild, are mainly resident throughout the year.

In general, Song Sparrows are common breeders along forest edge, beaches, and riverbanks, in gardens and forest burns, and in fresh- and salt-water marshes, as well as in refuse areas with some vegetation. Marshall (1948) described several races of Song Sparrows inhabiting distinct, although contiguous, habitats in the San Francisco Bay area.

Certain characteristics of the environment are, apparently, essential to all races of Song Sparrows. They need the proximity of water, or at least moist habitat. They also need dense, although not very high, vegetation (shrubbery, high grass, hedges) for nesting sites, singing and perching posts, shelter, and concealment during their daily activities. Since they are primarily ground feeders, they also require exposed ground under the vegetation where some light can penetrate. Low and dense shrubbery, marsh vegetation, and high grass, which provides enough room for movement among the stems, meet their requirements. Dense forest, dry and low grassland, and vegetation that inhibits movement on the ground are usually avoided by Song Sparrows.

They have been described as holding “Type A” territories in the classification of territories by Nice (1941). This territory type includes mating, nesting, and feeding grounds, which are well defended previous to and during the breeding season. Although resident birds as a rule stay on their territories during the winter, the area of their activity is extended, and they are tolerant toward other members of the species as long as the strangers do not show signs of territorial activity.

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The work reported here was undertaken on a group of islands in the Gulf Islands archipelago, along the Pacific Coast of southern British Columbia, Canada. The investigation was concentrated on Mandarte Island with its peculiar habitat, while brief visits were annually and seasonally paid to the neighboring islands.

**Mandarte Island.**—The island is slightly more than 700 m long, and 100 m wide, with an area of 6.26 ha, excluding tidal zone. The southwest side of the island is bordered by steep cliffs 20–25 m high, while the northeast side, with cliffs of 3–4 m, is skirted by a rocky tidal zone 5–25 m wide at low tide. A groove in the sandstone block of the island divides it into two, nearly equal, longitudinal halves.

Three main zones of vegetation can be distinguished on Mandarte Island (Fig. 1). **Cliffs and rocky beach** comprise more than 20 percent of the island (Table 1). Along the southwest side where the cliffs are steep, two species of cormorants (*Phalacrocorax auritus* and *P. pelagicus*) maintain breeding colonies. This area is generally barren of any plants, although some soil, 2–25 cm deep, has accumulated around the cormorant nests. Crevices in the rocks around the island are inhabited by Pigeon Guillemots (*Cepphus columba*).

**Grasslands** cover extensive areas on both sides of the groove, separating it at most places from the cliff side. Although the soil layer is very thin and often interrupted by barren rock surfaces, it is very rich from being fertilized by the many Glaucous-winged Gulls (*Larus glaucescens*) that breed there. The grass has a vigorous growth during the mild and moist winter and spring
(Fig. 2), frequently reaching a height of 1–1½ m. It is composed mainly of 2–3 grass species, with a high seed production.

The shrubbery is spread along the 5- to 15-m wide groove uninterrupted. Only a few isolated patches of shrubs are scattered over the grassland, not more than 5 percent of the total shrub area. This zone is composed of several species of deciduous shrubs, 1–3 m high, most of them berry producers (Tompa, 1962). Although the foliage is dense, the vertical stems grow either in bunches, or are widely spaced, leaving the ground exposed for foraging and movements. The uneven contour and edge of the shrubbery provide excellent singing and perching posts for the birds (Fig. 3).

Fig. 2. Grassy plateau on the southwestern side of Mandarte, with an extension of shrubbery from the groove. Note the gulls over the grassland and the cormorant colony to the right. Islands in the background are No. 19 and 23 (see map in Fig. 4).

There is only one area on the island, ca. 0.25 ha, where there is enough soil to support a group of mixed trees, 10–25 m high. The trees are widely spaced, with a rich growth of shrubs and many fallen branches underneath.

The shrubbery is inhabited by Song Sparrows throughout the year. About 20–25 pairs of crows (*Corvus brachyrhynchos*), and a few Red-winged Blackbirds (*Agelaius phoeniceus*) breed on the island. Rufous Hummingbirds (*Selasphorus rufus*) are common throughout the summer. Amphibians and reptiles are absent; the only mammal is the Deer Mouse (*Peromyscus maniculatus*). Nest parasitism is excluded, and predators, dangerous to Song Sparrows, pay only occasional visits to Mandarte Island during the winters.
Neighboring Islands.—Other islands in the area can be arbitrarily divided into two categories by their habitat (Fig. 4):

Category I.—These are small islands, generally less than half of a hectare, that show superficial resemblance to Mandarte Island. They are mainly covered by low and arid grassland, or mats of succulent plants. At other places xeric, creeping shrubs run horizontally over the surface. Rocks are thickly covered by dry tolerant mosses and lichens, and one species of cactus. Taller vegetation, if any, is represented by small, isolated shrubs and single trees (Fig. 5).

Category II.—Islands in this group are over one hectare in size, and most of them are considerably larger than Mandarte. Most are covered by mixed woods, although some have extensive areas of grasslands. Where the forest is relatively open there is a rich growth of shrubs. Shrubby areas also follow the forest edge, along beaches in particular. Clearings and open fields at higher elevations are covered by low and arid grassland, resembling that on smaller islands, with scattered trees and shrubs. At lower elevations and in depressions, the vegetation is either scant with exposed sandy surfaces, or
Fig. 4. Map showing Mandarte Island in relation to neighboring islands. Islands No. 1 to 3 belong to Category I, No. 4 to 23 to Category II (see text).

Fig. 5. Habitat on a small island (No. 1). Note the low grass and the scattered shrubs and small trees. Island No. 9 in the background.
Fig. 6. Typical habitat on larger islands (No. 16). Song Sparrow territories follow the shrubby edge between the field and the forest.

there are small, boggy areas where the growth of grass is thick and well mixed with many different herbs (Fig. 6).

**POPULATION DATA IN RELATION TO HABITAT TYPES**

*Mandarte Island.*—Beginning in 1960, an extensive color-marking program of Song Sparrows has been carried out by the author on Mandarte Island. By 1961 more than 90 percent of the breeding population was banded, making an accurate survey of the population possible for 1961 and 1962 (Table 2).

<table>
<thead>
<tr>
<th>Status</th>
<th>1960</th>
<th>1961</th>
<th>1962</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male (breeding)</td>
<td>46–48</td>
<td>47</td>
<td>44</td>
</tr>
<tr>
<td>Female (breeding)</td>
<td>46–48</td>
<td>47</td>
<td>44</td>
</tr>
<tr>
<td>Unmated male (territorial)</td>
<td>4–6</td>
<td>5</td>
<td>17</td>
</tr>
<tr>
<td>Unmated male (floating)</td>
<td>?</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Totals</td>
<td>96–102</td>
<td>101</td>
<td>113</td>
</tr>
</tbody>
</table>

Territory defense in any year was restricted to the section of shrubbery that a male (or a pair) occupied. Grasslands were only defended immediately bordering that area, increasing the size of territories on the average by
not more than 20 percent. Territorial activity was the strongest previous to and at the beginning of the breeding season, and ceased during the molt period of adults in late summer. A revival of territorialism in the fall reached its climax in October, and coincided with the peak of autumnal emigration of the young (see below).

During periods of strong territorial defense in the spring and fall, the activity of birds was mainly restricted to the shrubbery, where singing, fighting, courting, and nesting occur. Even then, they frequently and regularly left their territories to take a bath at the beach, or to forage in the tidal zone and over the grasslands. When feeding nestlings, the parents collected food items from the grasslands as well as in the shrubbery. These feeding grounds were outside the area of territory defense. Neighboring males often fed close to each other, the bird nearer to its own territory being dominant over the other. Hence, the actual size of utilized area for feeding is considerably larger than the area defended, resembling home ranges of some other passerines and many small mammals (Table 3).

Table 3.—Defended and Utilized Area by Song Sparrows on Mandarte Island, at the Beginning of Three Breeding Seasons

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of Territories</th>
<th>Mean Area Defended (m²)</th>
<th>Mean Area Utilized (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1960</td>
<td>52–54</td>
<td>(320)</td>
<td>(445)</td>
</tr>
<tr>
<td>1961</td>
<td>52</td>
<td>320</td>
<td>445</td>
</tr>
<tr>
<td>1962</td>
<td>61</td>
<td>275</td>
<td>385</td>
</tr>
</tbody>
</table>

*While the area of defended grassland was ca. 20 percent of the area of shrubbery held by a male, the latter had no bearing on the total area utilized (Tompa, 1962).

Although adults remain on their territories during the winter, and vacant places are filled by young in the fall, from November to late February birds feed in any part of the island, mostly in the grassland and around the cormorant colonies. These sites are used as common feeding areas, where both adults and juveniles join in loose groups of 5–10, or more. Chasing is rare, never serious, and it reflects a peck order rather than the relative distance from individual territories.

Islands in Category I.—In addition to Song Sparrows, these small islands are also inhabited by White-crowned Sparrows (*Zonotrichia leucophrys*), which prefer more open and arid areas. Territories of the two species overlap, and often coincide. Grassy areas are mostly utilized by White-crowned Sparrows, while activities of Song Sparrows, including feeding, are more restricted to the small, scattered shrubs. The latter species also frequents the tidal zone for bathing and occasional feeding. Otherwise, their feeding areas are located within territory boundaries. These islands did not support more than 1–3 Song Sparrow pairs per season. (For comparison of territory sizes, see Table 4.)

Islands in Category II.—An accurate survey of breeding populations in
this category was difficult, if not impossible, because of the large areas involved, the sporadic occurrence of Song Sparrow habitats, and the lack of color-marked individuals (with the exception of those that emigrated from Mandarte Island). Complete data are available for only two islands, each less than 4 ha. One of them \((a)\) was evenly covered by open forest and, during the course of the study, supported 9–11 territories averaging ca. 3,000 m², distributed over the island. The other island \((b)\) had nine territories along the beach in 1962, with a mean size of ca. 1,500 m². The center of the island was covered by dense coniferous forest. These birds, although mainly feeding within territory boundaries, also had access to a 5- to 25-m wide tidal zone at low tide.

**Table 4.—Territory Size of Song Sparrows on Mandarte Island, the Neighboring Islands, and Data from Other Authors**

<table>
<thead>
<tr>
<th>Locality</th>
<th>Year</th>
<th>Area (m²)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandarte (defended area)</td>
<td>1961</td>
<td>320</td>
<td>This study</td>
</tr>
<tr>
<td>Mandarte (utilized area)</td>
<td>1961</td>
<td>445</td>
<td>Tompa (1962)</td>
</tr>
<tr>
<td>Neighboring islands</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Category I</td>
<td>1960–62</td>
<td>ca. 1,000</td>
<td>This study</td>
</tr>
<tr>
<td>Category II (a)</td>
<td>1960–62</td>
<td>ca. 3,000</td>
<td>This study</td>
</tr>
<tr>
<td>Category II (b)</td>
<td>1962</td>
<td>ca. 1,500</td>
<td>This study</td>
</tr>
<tr>
<td>Other areas</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ohio (mainland habitat)</td>
<td>—</td>
<td>2,700</td>
<td>Nice, 1943</td>
</tr>
<tr>
<td>Minnesota (lake shore)</td>
<td>—</td>
<td>1,902</td>
<td>Suthers, 1960</td>
</tr>
<tr>
<td>San Francisco Bay</td>
<td>1953</td>
<td>416</td>
<td>Johnston, 1956</td>
</tr>
</tbody>
</table>

\(^a\) Averages for Ohio and Minnesota were calculated from data in the respective papers. Johnston’s data represent the highest density over 6 years of study.

On large islands, from \(\frac{1}{2}\) to 10 km², Song Sparrow territories were sporadic, depending on the density of forest and the vegetation cover of open areas. They had a linear arrangement along shrubby forest edges and beaches. On islands of this category, Song Sparrows were mostly restricted to shrubby places, while open grasslands, dense forests, or high forest canopies were utilized by other species more adapted to these habitats. Song Sparrow territories on the larger islands were comparable to those on the two islands described above, although some territories were probably considerably larger.

**Recruitment and Emigration.**—On Mandarte Island the ownership of territories during and just prior to the breeding season is normally decided by actual fights and chasing that followed intrusion. In most cases, the previous owner is the winner. Deceased adults are continuously replaced—by unmated males in the breeding season, and subsequently by young males after they have completed their postjuvenal molt. Final ownership of territories is settled only in the spring.

Emigration of young occurs in two phases. The first phase coincides with
the autumnal revival of territorialism, culminating in October. The autumnal emigration to other islands involved a minimum of 5 percent (maximum 43 percent, considering the total loss of young between August and November) of the young in 1960, and a minimum of 11 percent (maximum 36) in 1961, as shown by sight records and returns. Although most birds were recovered on Halibut Island, 1,300 m to the south, one bird was captured on James Island, more than 5 km to the west of Mandarte.

Although the exact proportion is not known, the number of young females emigrating in the fall is considerably higher than that of the young males. This might be explained by the fact that it is the male that establishes and holds the territory; the female simply settles down on it. Since in the fall most of the old females are still alive, young of this sex group have little chance to find vacant places and most of them leave. On the other hand, young males show much stronger site attachment, and there may be as many as 2–3 applicants for every vacant territory after the fall emigration.

As a result of this disproportionate emigration of sexes, both in 1961 and 1962 there was a slight shortage of females at the end of the winter on Mandarte Island. With or without territories, young males were, however, still in excess. This is then the time of the second phase of emigration. Many first-year birds, having spent the winter on neighboring islands, are trying to return to Mandarte at this time. Young females, because of the shortage of this sex group on the island, do not meet any difficulties in settling down immediately on already established territories. Returning first-year males are, however, seldom successful. Most of them stay unmated, or depart again, this time permanently. The proportion of young that successfully returned in the spring represented 21 percent of the total young recruitment to the adult population in 1961, and 25 percent in 1962.

Although the possibility of 1–2 real immigrants to Mandarte Island cannot be excluded for any year, the chances are not very high. Most birds were banded on Mandarte, and the few that were not could be checked by their usual location.

DISCUSSION AND CONCLUSIONS

Nice (1941) defines “Type A” territories as “mating, nesting, and feeding ground for the young,” and writes later in the same paper: “Each pair supports itself and its young brood on its territory. But food is evidently not the whole reason for territory with Song Sparrows. . . .” Hinde (1956) also thought that in species in this category territorial behavior may “help to ensure an adequate supply of food for the young.” In this respect, Song Sparrows on Mandarte behave differently, when compared with neighboring areas. This difference is not only manifest in the utilization of common feeding areas outside the usual habitat, but also in the extremely crowded conditions in the shrubbery where the territories are held—a situation that implies behavioral adaptation. These differences in feeding areas and the increased
tolerance of individuals in the population are ultimately caused and made possible by ecological factors, which must be sought in those characteristics of the habitat that differ markedly between Mandarte Island and other areas.

One factor is the composition, structure, and complexity of the vegetation. Mandarte Island in this respect provides all the basic habitat requirements of Song Sparrows, and it is also simple, excluding many other species. On other islands, where the shrubbery is scattered over dry and low grasslands, its composition and structure often depending on the density of the forest, the habitat is increased in complexity. These areas are inhabited by several other species in addition to Song Sparrows, with similar but not identical habitat requirements. The territories may be overlapping or even coinciding, the inhabiting forms utilizing that component of the habitat to which they are the best adapted (cf. Svärdson, 1949).

Another important factor is the role of food. The presence of several thousand gulls and cormorants considerably improves the food conditions on Mandarte Island. This happens directly through leftover food material, and indirectly by causing a vigorous growth of the grass that increases seed production and by affecting the abundance and diversity of insect populations. The result is an easily accessible food supply throughout the year, which is outside the usual Song Sparrow habitat. There was no indication of any mortality of adults and nestlings during the study that could be attributed to food shortage on the island.

The combined effect of the structural elements of the habitat and the above-average food conditions put Mandarte Island in a unique situation in the area. That the possible disadvantages of the extremely high density (decreased clutch size, interference, etc.) were outbalanced by the advantages is not only indicated by low mortality rates (Tompa, MS), but also by the yearly effort of young birds wintering in neighboring areas with low densities to return there to breed.

The situation described above suggests that either (1) the Mandarte Island Song Sparrows do not fit into the group with “Type A” territories, and they resemble those with “Type B,” or (2) the original classification of territories is too stringent and the Song Sparrow does not specifically defend a feeding territory in the strict sense. It seems that the food value of “Type A” territories is only secondary for Song Sparrows. The primary function would then be to minimize both intra- and interspecific interference with pair-bond and nest-site establishment by adjusting the population level in accordance with the prevailing environmental conditions in relation to its basic habitat requirements.

SUMMARY

A study of Song Sparrows (Melospiza melodia) inhabiting an archipelago along the Pacific Coast of Canada showed very high population density on one island (Mandarte Island), when compared with neighboring islands. The
difference could be related to the respective habitat types that the island populations occupied. On Mandarte Island where all basic habitat requirements of Song Sparrows were satisfied, and there was an abundance of food outside their usual habitat, defense was restricted to only the shrubbery zone where mating and nesting occurred. Grasslands and the area of cormorant colonies were utilized as common feeding grounds throughout the year. This behavioral adaptation, and an apparent increase in tolerance toward crowdedness, has allowed for a significant decrease of average territory size and consequent increase of population density.

On neighboring islands where conditions were less suitable for Song Sparrows, the territories were large, and feeding normally occurred within territory boundaries.

The situation suggests that the Mandarte Island Song Sparrows do not hold feeding territories, and that for the species in general the food value of territories is only secondary, the primary function being to minimize interference with mating and nesting. Through habitat selection the birds are able to adjust their numbers to the existing environmental conditions.

LITERATURE CITED


Ecological Significance of Territory in the Australian Magpie, *Gymnorhina tibicen*

**Robert Carrick**

*Division of Wildlife Research, C.S.I.R.O., Canberra, Australia*

Much has been written on the possible significance of territorialism in birds and other animals; but, while some of the functions of territory appear self-evident enough, actual proof of their operation in nature has been difficult to obtain. In a comprehensive review of this subject, which cites the relevant literature to that time, Hinde (1956) was still able to write: "There is no direct evidence that territory limits the total breeding population in all habitats. . . . Territorial behaviour may reduce disease, but this is unlikely to be a significant consequence except in some colonial species. . . . The functions of territorial behaviour are extremely diverse, and the quality of the evidence available for assessing them is little different from that available to Howard." This last point is still substantially true, half a century after Howard. Wynne-Edwards (1962) has given a fully documented account of the territory habit, which he rightly interprets as no different in purpose from the other forms of social behavior that constitute the homeostatic machinery whereby populations of animals are widely dispersed and excessive increase of numbers, with consequent depletion of food and other resources, is prevented.

The two main questions arise from each side of the population equation, and each contains several others. **Firstly**, does territorialism reduce productivity (fecundity) significantly below the biotic potential of the species? To what extent does it do so, and how is the reduction achieved? Are adult females unable to breed through denial of suitable nest sites, mates, or food supply? Or is maturity prevented by lack of the necessary proximate stimuli, or even by inhibitory factors? **Secondly**, does territorialism buffer its adherents from important causes of mortality? Does it prevent or reduce the risk of starvation, i.e. what is the relation between territory and food supply? Does it confer safety from predators or protection from disease?

A main difficulty of research on this problem is that the effects of territorialism usually have to be inferred from the study of the territorial individuals alone; there is no nonterritorial element in the same species, or at least it is barely visible, to serve as a control and provide comparative data on natality and mortality under the two systems. This stems from the fact that those individuals that fail to attain territorial status are either excluded from the habitat that the species requires for food, shelter, and reproduction, and so they succumb, or else they live cryptically in and around the margins of the preferred habitat. In the case of the strongly territorial Australian Magpie (*Gymnorhina tibicen*), however, there is a large and obvious overflow.

population outside the wooded breeding territories that is not territorial, at least in the same sense as the breeding birds, and that can maintain its numbers without recourse to migration. This stems mainly from the fact that this species is primarily an insectivorous ground-surface feeder, but is versatile enough to explore other food sources and even resorts to carrion and pasture foliage when necessary. The controlled experiment that we would like to set up in so many other species exists naturally.

Fig. 1. Adult cock Australian Magpie (*Gymnorhina tibicen*) giving the aggressive carol at the boundary of its territory. Photo by E. Slater.

*G. tibicen* (Fig. 1) is a member of the Australo-Papuan family Cracticidae, allied to the Corvidae. It stands about 9 inches high; and its adult plumage pattern, with jet black underparts and white nape, rump, and wing-flash, advertises the fact that predation on it is unlikely to be important; so exposed habitats can be used. A reasonable solution to the problem of diurnal shelter from the elements, especially heat and wind, can usually be found even in open country, and these individuals resort to communal night
ECOLOGY: POPULATION STUDIES

roosts some distance from their feeding grounds. This magpie is a sedentary species, with conspicuous behavior; it is not shy and it is readily trapped. Its aggressive carol, energetic defense of the territorial boundary, and readiness to attack intruders, including ornithologists, further assist field study (Fig. 1). The immature first-year birds are distinguished by their grayish, not black, plumage, and the sexes by the grayish lower nape and rump and the shorter bill of the female. It nests typically in trees, but shows considerable adaptability.

Fig. 2. The central part of the study area at Gungahlin, Canberra. Open savannah woodland (Eucalyptus spp., exotic conifers, and deciduous trees) and adjacent pasture are the habitat for permanent breeding territories. Photo by C. Totterdell.

The scene of the present study is 5 sq miles of open savannah, woodland, and pasture (Fig. 2 and 3) around Gungahlin, the headquarters of the Division of Wildlife Research, C.S.I.R.O., outside Canberra, Australia. The native gums, among which Eucalyptus blakeleyi predominates, form sparse cover with ground feeding places throughout and around them; exotic trees, including conifers and elms, are planted more compactly, and offer equally acceptable nest sites to the magpie. The study area was chosen to include samples of breeding habitat with intervening open ground. The basis of this study is individual color banding of territorial birds and group banding of others; over 650 of the former, and 2,500 of the latter, have been banded during 1955–62. Adults and young in territories on the study area have been banded annually, and in the four winters 1957, 1958, 1960, and 1961, about
80 percent of the nonterritorial birds living in the treeless pasture habitat have been banded. Since 1955, some 220 territorial groups have been studied. The area of woodland cover around Gungahlin (Fig. 2), which contains two-thirds of the territorial breeding groups in the study area, has been most intensively studied; every magpie there is color banded, i.e. about 150 birds in 40–45 territories. Over 1,000 specimens for dissection have been taken from comparable open and wooded terrain several miles from the study area, and experiments involving manipulation of internal or external environment have been made mainly outside the study area. Counts of the territorial birds in the area, with identification of color-banded individuals, are made every 3 months, and the free-flying juveniles still present in February receive their color combination then.

This is a preliminary account of the main findings that relate to the ecological significance of territorialism. These results are based on extensive data from birds of known identity and history, and a full account of this study will be published in a future issue of *C.S.I.R.O. Wildlife Research*.

**SOCIAL ORGANIZATION AND USE OF HABITAT**

The Australian Magpie forms social territorial groups of 2–10 birds. Most territories fall within the 5- to 20-acre range, with an average of about 10
Fig. 4. The territories in the central part of the study area (Fig. 2). Most are occupied by permanent groups; the two types of marginal territory are shown at top left (inadequate cover) and bottom right (inadequate pasture); small arrows show where mobile groups attempted to nest, and the large arrow shows where flock birds invaded breeding territories in the hard winter and spring of 1957.
Robert Carrick: Territory in the Australian Magpie

acres, but smaller areas are held where surrounding pressure is strong, and larger ones at the margins of the territorial area where there is no neighboring group. A group of two birds is always adult cock and hen; there may be six adults in a group, with any combination of sexes but a maximum of three breeding individuals of either sex in one group. The average number of adults per group is three, and males seldom outnumber females. Bigamy is common, and trigamy occurs. There is no relation between the size and quality of the territory and the number of birds that occupy it. At any time a large territory may have a small group, and vice versa; groups can fluctuate in time within the range of 2–10 birds without change of boundary.

The upper limit of territory size is, by observation, the largest area that the group can obtain and hold effectively; the better territories contain far more nest habitat and shelter than the group can use, and may well contain a food surplus also, although this requires to be tested by experimental alteration of food level. In a few instances the constant lateral pressure at territory boundaries enabled a group to increase its area when a neighboring group departed, but this gain was later surrendered, presumably through inability to defend the larger area. The lower limit of territory size is set by the amount of feeding pasture required to sustain the group, for a much smaller area than this can contain superabundant cover. Thus, territory size is largely determined by group size, although it is difficult to see what determines the level of the latter, which is similar throughout the range of the black-backed and white-backed forms of *G. tibicen* in eastern Australia. It is tempting to suggest that the group is limited by the number of birds that the dominant member can control, but the Western Australian Magpie (*G. dorsalis*) differs in having groups of up to 26 birds, with as many as six adult males in some groups, that occupy territories of 30–150 acres, and there are apparently no flocks (Robinson, 1956).

In many changes of territory ownership, no healthy reigning group has been dispossessed, regardless of the size of its territory or the relative strength of opponent groups. The members of defending and attacking groups fight as a team, with the advantage strongly in favor of the former.

It is convenient to recognize five social categories based on the quality of habitat occupied by each (Fig. 4 and 5), but these form a graded series and the system is anything but static, for birds and groups in the poorer environments are continually striving to improve their position in the habitat scale. Groups compete for tree cover with adjoining pasture feeding areas, which results in the open and marginal woodland, and also some open pasture, becoming subdivided into territories that are held for periods and defended with a tenacity proportionate to their quality as places to breed and feed.

1) **Permanent** groups hold territories that provide an adequate or surplus amount of all requirements all the year round. There are many more trees than the small number of birds requires for shelter, roosting, or nesting, and seasonal weights give no indication of food shortage at any time. Birds
Fig. 5. The territories in a marginal part of the study area (Fig. 3). The marginal territory in the center was occupied in 1959 and 1960 by a cock with two hens; the dominant hen nested in the single hawthorn bush and the subordinate one made abortive attempts elsewhere; in 1961, this group succeeded to the permanent territory on the right, but interference by the dominant hen still prevented the subordinate one from breeding successfully. A group of two cocks and three hens found the center territory inadequate for breeding in 1961, despite an extension to include a dead tree. A similar variability of response was shown by the open groups at top left and top right, and only the latter nested on the artificial tray provided.
remain in these optimal territories all day and all year, and make no attempt to move. Virtually all successful breeding is done by these birds. A permanent group may contain birds of all ages.

2) Marginal groups occupy territories with an inadequate amount of either cover or feeding area. They form around one or two small trees or bushes (or even artificial nest sites such as telegraph poles or tall wireless masts) on the outskirts of better cover; also in open woodland poorly defended by the surrounding groups but with inadequate pasture for feeding at all seasons. Attempts to breed rarely succeed to the point of fledging. Marginal groups usually consist of adult birds only.

3) Mobile groups commute between a separate feeding area in the open and a nesting-roosting area among trees. The latter is held against the strong opposition of neighboring groups, and mobile groups exist mainly during the breeding season. Breeding always fails, usually at an early stage, and mobile groups do not contain first-year birds.

4) Open groups form in areas of treeless pasture that provide adequate feeding all year, except possibly during severe drought or hard frost. They roost in the denser woodland that is not otherwise used by this species; the daily flight is usually within a mile, and members of the same open group may go to different roosts. An open group can last several years, and some become mobile groups in spring. Open groups contain only adult birds, but they make no attempt to nest.

5) Flock birds are nonterritorial. They are birds of all ages and both sexes, and some may have bred as members of territorial groups now disbanded. They form loose flocks of a few up to several hundred individuals that feed in open pasture and roost in woods. More intensive study might well reveal that most flock adults are in fact in open groups with varying degrees of attachment to feeding area or constancy of membership, but more stable during the breeding season. The flocks show slight mobility throughout the year, and about half of the open terrain in the study area is occupied and the other half left untenanted by them at any one time. They do not attempt to nest.

**Changes of Status**

In this territorial system, there is considerable temporal and spatial stability of groups and individuals; in May 1962, 16 of the original 38 permanent groups present in 1955 still occupied the same territory, and 20 percent of males and 18 percent of females were in the territories where they were first banded as adults in 1955 or early 1956. These figures are rather low because they include losses from human activities that would not occur over most of the magpie's range. This stability is maintained by constant vigilance in a dynamic situation in which there is continual daily effort all the year round, with an upsurge of activity in July to October, i.e. before and during breeding, on the part of both groups and individuals to improve their social status.
Individual changes may result in increase, replacement, or decrease in the members of a group. Most birds leave their natal territory during their first year, some in the second, and a few in the third, but a small proportion continues to live and breed there. More females than males do this, and the oldest hen that has remained in the parental territory is now almost 7 years old, while the oldest cock is 3½ years old. It is exceptional for an adult to be added to an existing group, but this has occurred when a sick hen was unable to repel a flock hen that became established in the group before the resident hen recovered. Members of a group repel their own sex, but each sex supports the other once a contest is under way. When a vacancy is created, as by mortality, for either sex, a replacement by one or more birds of the same sex may occur; this is more usual in the case of females than males, presumably because of the greater ability of the latter to hold on to their territory. Mortality causes decrease in a group, and either sex may emigrate from a group in an inadequate territory to one in a better territory where there is a sex vacancy for it.

A group preformed in the flock, or one in occupation of a poor habitat, may succeed in forcing its way into a better habitat, thus creating a new territory. Loss of the dominant adult, usually the male, often leads to break-up and displacement of a group by a new one. A group seldom becomes too large, but in one case a group of 3 males, 4 females, and 3 immatures became subdivided and the adult male and female, which separated from the others, continued to occupy part of the original territory. Expansion of territory with change in the composition of the group can occur when a neighboring group goes out and the territory is not immediately claimed by an incoming group; unless the first territory is small, the group is not usually able to defend the expanded area effectively and has to surrender all or part of it eventually.

THE GONAD CYCLE AND BREEDING

In the Canberra region, egg laying extends from August through October, and some seasons start earlier than others. This is preceded by increased epigamic activity of adult males from July onward, when many immatures are evicted from territorial groups and many open and marginal groups make determined attempts to secure adequate tree cover for nesting. The female alone selects the nest site and builds the nest; copulation occurs only at her invitation. The clutch contains 1–6, average 3, eggs, and some re-laying after failure occurs in earlier seasons, but little in a normal one. The cock does not brood, but may feed the hen on the nest and may play a variable part in feeding the young.

Males of all ages and all environments and social positions have motile sperm in the breeding season. Testes are largest in adult males in permanent territories, and much smaller in territory or flock 1-year-olds. Where nutrition is adequate, as it always seems to be, physical environmental stimuli
alone appear capable of bringing the testis to maturity, after which age and social status in that order determine how far development will proceed. Testis size and sperm production do not appear to be affected by antagonistic relations between groups, or between a group and trespassing individuals, or within the group.

No 1-year-old female has been known to ovulate. Some 2-year-old hens breed, but even in permanent groups some females of this age or even older may not breed. In spring the ovary undergoes partial development in every case, and the final rapid increase in size of oocytes, with associated nest-building behavior, depends on the presence of certain critical stimuli as well as the absence of inhibiting factors. To attain ovulation, the hen must be a member of a social group in a territory that offers an acceptable nest site, but the threshold value of the latter in different individuals varies from a high tree to a low bush or post, and in one exceptional case the ground. Tradition is probably important, and preliminary experiments in open territories with artificial sites in the form of wooden trays on poles, bare or decorated with foliage, and with small trees, suggest that foliage as such sometimes has valency. Male stimulation of the female does not occur, for hens whose adult cocks were caponized with oestrogen implants and made effeminate to the point of building nests and soliciting, continued to build and lay (infertile eggs) normally on the same dates as control groups.

Even in the presence of adequate proximate stimuli, oocyte development and nest building can be inhibited by emotional factors, such as intrusion of a strange magpie of either sex into the territory, an undue amount of boundary fighting, or domination by another female of the same group. The psychosomatic effect of alien individuals, even on hens in first-grade permanent territories, has been observed as it occurred naturally in several situations, notably in 1957 when flock birds, which overran some territories (Fig. 4) during the frosty winter and were not evicted by spring, caused inhibition of nesting among the resident hens; this effect has been confirmed experimentally. The response of individual hens to similar stimulatory and inhibitory factors in the environment varies widely.

No open group has reached the stage of nest building. The breeding performance of mobile groups varies from failure to commence building to an occasional successful hatching, but, because of predation while the adult is absent at the feeding ground, no hen in a mobile group has been able to fledge its young. Those mobile hens that become sufficiently established to build and lay often lose their eggs from the direct attack of neighboring magpies; or else the eggs become addled, or eggs or nestlings fall to predators when the hens are engaged in boundary fights or are absent in the feeding area. The most common predator of eggs and nestlings is the Australian Raven (Corvus coronoides). Marginal groups often fail to nest, but a small percentage rear young to the free-living stage. It is the permanent groups that produce the annual increment to the population, but even their breeding
Table 1.—Numbers of *Gymnorhina tibicen* in the Gungahlin Study Area

<table>
<thead>
<tr>
<th>Status When Censused</th>
<th>Territory(^a) Aug.–Sept.</th>
<th>Flock(^b) May–July</th>
<th>Total in Population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>Percent</td>
<td>No.</td>
</tr>
<tr>
<td><strong>ADULT FEMALES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1957(^c)</td>
<td>92</td>
<td>36</td>
<td>161</td>
</tr>
<tr>
<td>1958</td>
<td>103</td>
<td>35</td>
<td>189</td>
</tr>
<tr>
<td>1960</td>
<td>112</td>
<td>39</td>
<td>178</td>
</tr>
<tr>
<td>1961</td>
<td>111</td>
<td>40</td>
<td>168</td>
</tr>
<tr>
<td><strong>AVERAGE DURING 1957–61</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>79</td>
<td>21</td>
<td>296</td>
</tr>
<tr>
<td>Females</td>
<td>107</td>
<td>38</td>
<td>174</td>
</tr>
<tr>
<td>Total adults</td>
<td>186</td>
<td>28</td>
<td>470</td>
</tr>
<tr>
<td>(Sex ratio (\delta:\Omega))</td>
<td>(43:57)</td>
<td></td>
<td>(63:37)</td>
</tr>
<tr>
<td>1st-year birds(^d)</td>
<td>ca. 15</td>
<td></td>
<td>ca. 70</td>
</tr>
<tr>
<td>Total population</td>
<td>ca. 200</td>
<td></td>
<td>ca. 540</td>
</tr>
</tbody>
</table>

\(^a\) Territory birds include all hens that have an opportunity to breed, i.e. permanent, marginal, and mobile groups.

\(^b\) Flock birds are nonterritorial individuals plus open groups.

\(^c\) Owing to improved methods of observation and trapping in subsequent years, the numbers for 1957 may be rather low.

\(^d\) Counts taken in midwinter.

Rate is reduced by aggression between groups and by sex dominance within groups, as well as by the usual factors not directly associated with social territorialism. The extent to which this system reduces breeding to one-quarter of the potential it would have in the absence of territorial capitalism of breeding sites and sociosexual aggression and dominance is shown in Tables 1 and 2.

**ANNUAL PRODUCTIVITY AND MORTALITY**

In a good breeding season about one juvenile magpie per adult territorial female reaches the free-flying stage in January, and the number is much

Table 2.—Degree of Breeding Failure Caused by Territorialism

<table>
<thead>
<tr>
<th>Year</th>
<th>1958</th>
<th>1960</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>Percent</td>
</tr>
<tr>
<td>Total number adult females in study area</td>
<td>292</td>
<td>100</td>
</tr>
<tr>
<td>Nonbreeding females in flocks</td>
<td>189</td>
<td>65</td>
</tr>
<tr>
<td>Failing females in territories, due to intergroup aggression</td>
<td>16</td>
<td>6</td>
</tr>
<tr>
<td>and intragroup dominance</td>
<td>13</td>
<td>5</td>
</tr>
<tr>
<td>Total reduction of nests</td>
<td>218</td>
<td>76</td>
</tr>
</tbody>
</table>
lower in poor seasons. The high survival of adult birds during the course of this study indicates that a low annual death rate, especially in the permanent territorial groups, is adequate to cancel the normal increase from natality.

Starvation has not been evident in this study, although birds of all ages in the wide range of habitats, but each with good feeding pasture, have shown significant differences of body weight throughout the year. The same is true of stomach contents and fat reserves.

Predation by crows and hawks occurs up to the free-flying stage, and is more severe in poorer cover, but natural losses among older birds, even including those due to feral cats, are not considered serious. The Peregrine Falcon (*Falco peregrinus*) has occasionally hunted the area and taken adult flock birds in the open. Immature *Homo sapiens* of all ages take a steady but small toll of nestlings, which are popular if illegal pets, and of adults, which afford target practice in the absence of other game and, in the case of the cock during the breeding season, engender retaliation for their unprovoked attacks on people. Territories on main roads consistently lose their juveniles, and an occasional adult, in traffic accidents, and rabbit traps and other human agencies also account for a small number of birds, mainly in territories.

Diseases of many kinds have been identified during this study, some of them lethal, and at least one is considered to be an important primary cause of death. This is *Pasteurella pseudotuberculosis*, which killed large numbers of flock birds during the cold wet winter of 1956, but, being contact-spread, did not cause a single death among the territory individuals, all of which were banded, in woodland closely adjacent to open pasture where dead and dying birds could be picked up daily at the height of the epidemic. The flock birds exposed to this infection showed no sign of debility, as compared with territory birds, that might have predisposed them to mortality, and the conditions that favor the disease appear to occur too infrequently for development of resistance to it. During the harder winter of 1957, the food on the more exposed pastures became unavailable, and many flock birds concentrated on softer ground and haystacks, where they picked up the spores of the fungus *Aspergillus*, which became a secondary cause of death of some importance that year. Both of these diseases and several others take a constant low-level toll of magpies.

**CONCLUSIONS**

Territorialism and associated sociosexual interactions limit breeding to about one-quarter of the adult population of *G. tibicen*.

Territorialism buffers that element of the population against important mortality from disease, and probably also protects it from predation.

The completeness of the territorial habit in *G. tibicen*, in which the social group lives permanently within its territory, indicates that the food supply
of this area is always adequate; nor is there evidence that flock birds come up against the food limit.

ACKNOWLEDGMENTS

I am much indebted to F. N. Ratcliffe and the Executive of the Commonwealth Scientific and Industrial Research Organisation, Australia, for enabling this study to be done. I am also grateful, among many others, to my wife, who has been mainly responsible for identifications of banded birds, to W. J. M. Vestjens, who has borne the brunt of the trapping and collection of specimens and breeding data, to Mrs. Amy Bernie for maintenance of records and analysis of data, to R. Mykytowycz for pathological examinations, and to I. C. Rowley and K. Keith for assistance during the earlier years.

During the discussion after this paper was read at the Congress, significant questions and comments were made by David Lack of Oxford and Richard F. Johnston of Kansas.

SUMMARY

A study of population ecology in the Australian Magpie (Gymnorhina tibicen) during 1955–62 at Gungahlin, Canberra, is based on 650 birds individually color-banded and 2,500 others banded; 220 territorial groups have been studied, and three field experiments done on proximate factors in the stimulation and inhibition of breeding. A preliminary account of the evidence on the ecological significance of territorialism is given in this paper.

Open savannah woodland and adjacent pasture are permanently occupied by breeding groups of 2–10 birds, with a maximum of 3 adults of each sex; an average territory is 10 acres. Similar social groups also hold marginal territories that are deficient in feeding pasture or tree cover for shelter and nesting. Open treeless pasture supports a large nonbreeding element, including former breeders, in the form of slightly nomadic flocks and some territorial groups that may become mobile in spring between separate feeding and breeding areas. Successful breeding is virtually confined to the permanent groups, and productivity is low; territorialism reduces breeding to one-quarter of its potential. Groups and individuals in the poorer habitats make constant efforts to improve their status; the causes of changes in the composition or status of groups are described.

Testes mature in all situations, but the response of individual females to the environmental situation is more variable. The adult ovary requires adequate stimuli from group status and suitable nest site. It can be inhibited by sociosexual factors, such as conflict with neighboring groups or intruders in the territory, or by dominance within the group, which cause a psychosomatic reaction involving ovarian repression.

In this species, territorialism has led to a high degree of numerical and spatial stability. It buffers the permanent occupants of the preferred habitat from important disease mortality, and probably also from predation.
LITERATURE CITED


Dichte und Dynamik von Brutpopulationen zweier deutscher Waldgebiete 1949–61

SEBASTIAN PFEIFER

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Wer sich heute mit der Frage der Dichte von Brutpopulationen beschäftigt, wird feststellen, dass die ersten quantitativen Untersuchungen aus relativ neuer Zeit stammen. Meines Wissens war es in Europa der Finne Palmgren (1928, 1930, 1931, 1933), der in einigen Waldbereichen seines Heimatlandes die Dichte der dort lebenden Vogelarten erforschte. Er stellte je nach Biotop Dichten zwischen 0,6 und 5,3 je ha fest. Schiermann (1930, 1934) erfasste nach der bekannten Probeflächenmethode die Siedlungsdichte der Vögel in brandenburgischen Kiefernwäldern und im Gebiet des Unterspreewaldes. Die Siedlungsdichten schwankten in Brandenburg zwischen 0,32 und 2,36 je ha, im Spreewald zwischen 0,32 und 2,84 je ha. In Brach- und Ödlandschaften zwischen 0,06 und 0,07 je ha. Auf einem Berliner Friedhof zählte der gleiche Autor (1939) 16,3 je ha.

Steinbacher (1942) stellte im Frankfurter Zoologischen Garten eine Dichte von 14,9 je ha fest, wobei dort, wie auf dem Berliner Friedhof, künstliche Nisthöhlen die Dichte stark beeinflusst haben. Weiter seien noch die Untersuchungen von Garling (1940), Niebuhr (1948) und Schumann (1951) genannt.


kann gesagt werden, dass diese, meist vor 1945 vorgenommenen Untersuchungen recht unterschiedliche Ergebnisse hatten und auch zu unterschiedlichen Schlussfolgerungen führten, die im Rahmen meiner Darstellungen nicht näher diskutiert werden sollen.


Im Winter 1951/52 wurde eine zweite Versuchsfläche von 25 ha Grösse eingerichtet, die ebenfalls im Osten von Frankfurt/Main liegt und Teilgebiet eines 310 ha grossen Waldes ist. Es handelt sich bei dieser Versuchsfläche um ein Querceto-Carbinetum mit unterschiedlichem Untergürt. Eine genaue Beschreibung wurde bereits an anderer Stelle gegeben (Pfeifer und Keil, 1958). Insgesamt wurden 1060 Nisthöhlen (=42,4/ha) der ver-

Abb. 1. Holzbetonnisthöhle für Meisen.

Fig. 1. Concrete nest box for titmice; the concrete has been mixed with sawdust.

Bereits die ersten Ergebnisse auf der Kleinfläche zeigten eine außerordentlich hohe Dichte der vorhandenen Brutpopulation. Im Jahre 1949 konnten schon 22,4 ausgeflogene Höhlen- und 15,2 ausgeflogene Freibrüterbruten ermittelt werden, d.h. also eine Gesamtzahl an ausgeflogenen Bruten von 37,6 je ha. In den nachfolgenden Versuchsjahren erhöhte sich die Zahl der ausgeflogenen Bruten, von gewissen Schwankungen abgesehen, bis auf einen Maximalwert von 70,4 je ha (1958). Im Durchschnitt der 13 Versuchsjuahren betrug die Zahl der ausgeflogenen Bruten 56,5/ha. Durch die getroffenen Kunstmassnahmen konnte also eine Hebung der Höhlen- und Freibrüterpopulation gegenüber dem Jahre 1948 (vor Versuchsbeginn) um fast das 25fache erzielt werden.

**Table 1.—Die Schwankungen in der Dichte der Brutvogelpopulationen in zwei verschiedenen Versuchsgebieten**

Zahl der Bruten = Gesamtzahl der ausgeflogenen Bruten

<table>
<thead>
<tr>
<th>Gebiet</th>
<th>1,25 HA</th>
<th>25 HA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arten</td>
<td>Höhlenbrüter</td>
<td>Frei brüter</td>
</tr>
<tr>
<td>Jahr</td>
<td>Zahl der Bruten</td>
<td>Dichte je ha</td>
</tr>
<tr>
<td>1948</td>
<td>28</td>
<td>22,4</td>
</tr>
<tr>
<td>1950</td>
<td>44</td>
<td>35,2</td>
</tr>
<tr>
<td>1951</td>
<td>47</td>
<td>37,1</td>
</tr>
<tr>
<td>1952</td>
<td>44</td>
<td>35,2</td>
</tr>
<tr>
<td>1953</td>
<td>40</td>
<td>32,0</td>
</tr>
<tr>
<td>1954</td>
<td>34</td>
<td>27,2</td>
</tr>
<tr>
<td>1955</td>
<td>46</td>
<td>36,8</td>
</tr>
<tr>
<td>1956</td>
<td>35</td>
<td>28,0</td>
</tr>
<tr>
<td>1957</td>
<td>44</td>
<td>35,2</td>
</tr>
<tr>
<td>1958</td>
<td>33</td>
<td>26,4</td>
</tr>
<tr>
<td>1959</td>
<td>34</td>
<td>27,2</td>
</tr>
<tr>
<td>1960</td>
<td>29</td>
<td>23,2</td>
</tr>
<tr>
<td>1961</td>
<td>24</td>
<td>19,2</td>
</tr>
</tbody>
</table>

Year | No. of Broods | Density per Ha | No. of Broods | Density per Ha | No. of Broods | Density per Ha | No. of Broods | Density per Ha |
Species | Hole-nesting | Free-nesting | Hole-nesting | Free-nesting | Hole-nesting | Free-nesting |
Plot | 1.25 HECTARES | 25 HECTARES |

No. of Broods = Total number of fledged broods

**Table 1.—Fluctuations in the Density of Breeding-bird Populations on Two Different Test Plots**

Abb. 3. Nisttasche aus Kiefern­zweigen.
Fig. 3. Nest pocket made from branches of pine.

ges im Jahre 1961 dürfte m.E. so gut wie ausschließlich auf die Witterungs­verhältnisse und deren mittel­ und unmittelbare Folgen zurückzuführen sein. Es zeigte sich, dass die Parus­Arten den geringsten Rückgang hatten, während Ficedula hypoleuca, Phoenicurus phoenicurus, Muscicapa striata, Cer­thia brachydactyla und Sitta europaea besonders stark betroffen waren. Die überaus starke Abnahme der Passer-montanus­Population im Jahre 1961 ist
bisher unerklärlich, da durch die getroffenen Verminderungsmassnahmen ein derartig starker Rückgang nicht hätte eintreten dürfen.


fassung, dass das Brutrevier dem zur Ernährung der Jungen benötigten Raum entspricht, in Zweifel und kommt vielmehr zu dem Schluss, dass sich Brut- und Nahrungsrevier keineswegs bei den meisten Vogelarten deckt.


In der Zwischenzeit sind jedoch auch quantitative Untersuchungen über die Ernährungsbiologie eingeleitet worden, über die zu gegebener Zeit berichtet werden wird.


Immer wieder wird die Frage aufgeworfen, ob durch hohe Dichten eine Beeinflussung der Fortpflanzungsraten und damit der Gelegestärke und Mortalität vorhanden ist. Nach den bisherigen Erhebungen konnte ermittelt werden, dass die hohen Populationsdichten auf die Gelegestärke von Parus major und P. caeruleus ohne besonderen Einfluss sind (Pfeifer, 1960) Bei P.

Es zeigte sich, dass die Untersuchungen über Dichte und Dynamik eine ganze Reihe weiterer Probleme mit sich bringt, die hier nur ganz kurz gestreift werden konnten. Leider ist es der Vogelschutzwarte Frankfurt/Main aus personaltechnischen Gründen nicht möglich, alle diese angeschnittenen Fragen entsprechend ihrer Bedeutung zu bearbeiten. So sind noch eine ganze Reihe wichtiger Untersuchungen vollständig unbearbeitet, die jedoch im Interesse der exakten Fortführung dieser komplexen Zusammenhänge einer baldigen Bearbeitung bedürfen.


ZUSAMMENFASSUNG

pfändlich. Neben den beiden Versuchsflächen bei Frankfurt/Main wurden ähnliche Versuche unter anderen Voraussetzungen (Klima, Höhenlage und Biotop) durchgeführt, die auch zu einer Steigerung der Siedlungsdichte der jeweiligen Vogelpopulation führten.

**SUMMARY**

*Density and Dynamics of Breeding Populations in Two German Forest Areas 1949–61*

By providing artificial nesting opportunities (nest boxes, nest pockets, bundles and piles of branches, etc.), it was possible to raise the population density in two wooded districts east of Frankfurt. In one area (1.25 ha) the density was increased on the average 25 times; in the other (25 ha) the increase was 6-fold.

The maximum density in the smaller plot rose to 70.4 fledged broods per hectare (1958); in the larger to 44.9 (1955). Both populations were subject to very considerable fluctuations, which varied according to species. This was especially apparent with *Ficedula hypoleuca* and *Phoenicurus phoenicurus*, which react remarkably quickly to disturbances of any kind (bad weather, nest-site competition from *Passer montanus*). Other species (*Parus major* and *P. caeruleus*) are relatively unaffected. Similar experiments were conducted under different conditions (climate, altitude, biotope) in other areas, and these, too, led to an increase in population.

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Observations on Adelie Penguins (*Pygoscelis adeliae*) at Cape Royds, Antarctica

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The behavior and breeding cycles of Adelie Penguins (*Pygoscelis adeliae*) have recently been studied by Sladen (1958) in the Falkland Island Dependencies, by Sapin-Jaloustre (1960) in Adelie Land, and by Taylor (1962) at Cape Royds in the Ross Dependency. As yet, few observations have been made with marked birds of known age or experience, and few attempts have been made to study population changes in individual colonies over a number of years. This paper describes observations made in the spring of 1961 on a small colony that, 2 years previously, had been studied in some detail by another worker: The activities of 73 banded birds, most of which were known to be experienced breeders, were recorded during the assembly, courtship and nesting, and early-incubation periods.

The Adelie Penguin colony at Cape Royds (77° 30' S, 166° 30' E) is the southernmost penguin colony in Antarctica. Discovered by Scott and Wilson in 1904, it has been visited and described at intervals for over half a century (see summary in Taylor, 1962). Between 1907 and 1956 the size of the colony appears to have remained constant at 1,500 to 2,000 pairs, in spite of heavy losses of adults and eggs suffered during the two expeditions of Shackleton (1907 and 1916). More recently a decline in numbers has become evident. In January 1956, Austin (1957) estimated a population of about 2,000 pairs; in November and December 1958, Caughley (1960) estimated 1,700 pairs; and in 1959-60, Taylor estimated 1,600 pairs. In 1961 the greatest number nesting during the December peak was not more than 1,250 pairs. Since the beginning of I.G.Y. activities in the summer of 1955-56 the colony has frequently been visited by helicopter and sledge parties from ships and from the nearby U.S. and New Zealand bases; human interference may therefore be responsible, at least in part, for the population decline. The University of Canterbury Antarctic Biology Unit has undertaken a 5-year study of the colony, involving little interference, to provide information on which protection and conservation measures may be based.

**POSITION OF THE COLONY IN RELATION TO SEA ICE**

Although only 900 miles from the South Pole, the coast of Ross Island provides breeding grounds for large numbers of birds (Fig. 1). Cape Crozier, site of a well-known colony of Emperor Penguins (*Aptenodytes forsteri*), accommodates also some tens or hundreds of thousands of Adelie Penguins (Harrington, 1960; Caughley, 1960), and further large colonies are found on the western shore of Cape Bird. McCormick Skuas (*Catha-*)
racta maccormicki) breed among and parasitize the Adelie Penguins, and a population of 200–300 breeding pairs of the same species lives nonparasitically along the coast between Cape Royds and Cape Evans (Young, 1963a, 1963b). The success of large numbers of breeding birds in so high a latitude depends on the early seasonal dispersal of ice in the southwestern corner of the Ross Sea. Off Cape Crozier, open water has been recorded as early as

mid-October (Scott, 1905): Observers from the Discovery expedition, visiting the cape in 1902 and again in the following year, found wide expanses of ice-free sea following offshore gales. During a visit on 23–25 October 1961, I found sea ice extending to the horizon, but leads and pools provided several square miles of open water close inshore. The ice shifted constantly, and the open water froze and reopened three times during the 3 days of observation. Much of the ice appeared fresh, and the presence of two large Leopard Seals (Hydrurga leptonyx) in offshore leads suggested that open water, possibly with direct access to the sea beyond the pack ice, had existed for some time. Many penguins, both Adelie and Emperor, were diving and presumably feeding in the pools.

Fig. 1. Ross Island and McMurdo Sound. Solid lines are coast, dotted lines are edge of ice shelf.
Within McMurdo Sound, Murray (in Shackleton, 1909) recorded open water in sight from Cape Royds throughout the winter of 1908. Fast ice extended into the Sound from a line three-quarters of a mile (1.2 km) north of Cape Royds; north of the edge, successive winter gales cleared new ice from the sea within a few hours of its formation. Murray attributed the persistence of open water to a strong south-setting current, which sweeps into McMurdo Sound from the direction of Cape Bird and is deflected westward by an opposing current at Cape Royds. In 1961, the ice edge persisted in a similar position from mid-October (when first seen by members of our party) to mid-December when most of the ice shifted from the Sound. Although the sea froze overnight to a depth of 1 ft (30 cm) on several nights late in October, the new ice was invariably broken within a few hours of its formation. The ice edge was also found in a similar position by Reid in October 1960 (pers. comm.), and reports from Operation Deepfreeze II suggest that an ice edge lay south of Cape Royds during the last week of October 1956. Not all years provide such favorable conditions; in 1959 Taylor reported that unbroken ice extended well to the north of Cape Bird throughout October, and in the summer of 1955–56 ships of Operation Deepfreeze I met the edge of the fast ice off Cape Bird as late as 5 January.

The bird colonies of the Ross Island region are therefore more favorably situated than their latitude would at first suggest. It is possible for the sea ice within a few miles of them to break early in the Antarctic spring (or even to remain open throughout winter), forming polynyas, which allow the birds to feed close to their colonies. Thus, although incoming Adelie Penguins may have to cross many miles of ice on foot during their migration from the pack ice, they are likely, in favorable years, to find open water within a mile of their breeding grounds throughout the whole of their breeding season. Open water in October and November must also be of considerable importance to the Emperor Penguins at Cape Crozier, since their chicks grow rapidly and it is obvious that they require substantial feeding at this period of their life cycle (Stonehouse, 1953).

SIZE OF THE CAPE ROYDS COLONY

Apart from the decline in numbers noted since 1956, the Cape Royds colony appears to have remained fairly constant in size, at least since 1908 (see summary of evidence in Taylor, 1962). The ground immediately surrounding the present breeding area does not show signs of more extensive occupation, although nesting groups within the colony have grown, declined, or shifted during the past half century. Between Cape Barne and the northern extremity of the Cape Royds cliffs, two areas of abandoned colonies are known (map in Debenham, 1923); the presence of others is suspected, and their distribution and age are at present under investigation. Some of the sites, notably those on the cliffs at Cape Barne, appear to have been abandoned fairly recently, and may argue a reduction in numbers nesting in the
Cape Barne and Cape Royds areas during the last 50–100 years. The abandoned colonies compare in size, however, with the present colony; if all the abandoned nesting grounds had been occupied simultaneously, the total population of Adelie Penguins in the area would not, based on present evidence, have exceeded 4,000–6,000 pairs.

Very much larger colonies exist at Cape Bird and Cape Crozier on Ross Island, and also on nearby Beaufort Island; the three together accommodate between 150,000 and 300,000 pairs of breeding birds (Austin, 1957; Caughley, 1960). Their size, and the comparative smallness of past and present colonies within McMurdo Sound, may be due to differences in the feeding areas available from them. Even in a year of favorable ice conditions McMurdo Sound remains frozen south of Cape Royds throughout the first half of the breeding season, leaving only a large polynya, or arm of the sea, available for feeding. Outside the Sound, much greater expanses of open water are available in favorable years; even in seasons of persistent ice, wide leads and cracks are usually found near Beaufort Island from October or November onward, and extensive open water is almost invariably found off the north coast of Ross Island in January and February. The colonies within the Sound might therefore be restricted in size to the numbers of birds that can feed successfully within easy reach of their colony in favorable years.

A similar situation of large and small colonies is found in Marguerite Bay, Western Antarctica (Stonehouse, 1963). Adelie Penguin colonies at Lagotellerie Island and Red Rock Ridge, far back in the bay and some 60 miles from open water in early spring, number only 600–800 pairs each. On the Henkes Islets at the mouth of the bay, a colony numbering tens or hundreds of thousands of pairs occupies more than one of the larger islands, and suitable ground on the neighboring Dion Islets is also colonized. The birds of Lagotellerie Island and Red Rock Ridge feed during December and early January in polynyas which form close to their colonies, and may rely on the dispersal of the sea ice later in the year to provide wider fishing grounds when the demands of their growing chicks are greatest.

ASSEMBLY, COURTSHIP, AND LAYING AT CAPE ROYDS

The method of counting, division of the colony, etc., in these observations followed closely the pattern described by Taylor (1962). The number of birds and number of pairs were counted daily over the whole colony; nests with eggs were counted at 3-day intervals, although more detailed surveys of some of the groups within the colony were undertaken and will be summarized elsewhere.

Particular attention was paid to banded birds, as all but one were known to be breeding adults of at least two seasons' experience. The exception was a bird marked by Taylor as a yearling early in 1960. In 1961 it appeared in the colony on 16 November, and subsequently defended with vigor a site on the edge of one of the larger nest groups. Its behavior was characteristically
male. Attracting a number of temporary partners, it copulated but did not secure a permanent mate and is unlikely to have bred during the 1961–62 season.

The sex of each of the 72 banded experienced breeders was diagnosed by behavior. Birds that defended sites for several days without partners, gave repeated ecstatic displays (Sladen, 1958) early in the season, copulated in the upper position, or took the first long incubation watch were judged, usually on a combination of characters, to be male. Females usually wandered from site to site in the colony, reacted nonaggressively to the calls of neighboring males, took the lower position in copulation, and disappeared shortly after laying.

Assembly in the Colony.—During a short visit to the colony on 21 October, I found no birds and no evidence of current occupation; some 10–20 birds were standing on the sea ice nearby. When continuous observations began on 27 October, 255 birds were present, some already standing in pairs over nest scrapes or piles of stones. By the end of the month over 600 birds were present, about two-thirds of them standing in pairs, and daily counts during the first 10 days of November gave a mean rate of increase of 180 birds per day. On 11 November, 2,564 birds were present; of these, 2,178 were standing in pairs, and over 200 nests already contained eggs. The first eggs were laid on 7 November.

Assembly and the beginning of laying in 1961 differed only in detail from Taylor’s description for 1959; in 1961, daily totals lagged slightly during the first few days but soon caught up, and the first eggs appeared 2–3 days later than in 1959. The first few days of assembly in 1960, observed by Reid (pers. comm.), were again very similar; ice conditions resembled those of 1961, colonization began about 3 days earlier, and daily totals remained about 3 days ahead of those for 1961 until the end of October. Thus, the persistence of sea ice in the Sound in late October 1961 had little effect on the start of the breeding cycle, and colonization in all 3 years began in earnest during the fourth week of October.

After 11 November, daily counts were not by themselves sufficient to show the continuing growth of the colony, for females whose clutches were completed began leaving in steadily increasing numbers and outgoing birds soon outnumbered incoming birds. The numbers of departing females could not be counted directly, and the presence of wandering birds made it difficult to count the number of solitary birds remaining on nests. However, from the 3-day counts of nests with one or two eggs, the rate of departure could be calculated by assuming that the females left, on the average, 3 days after laying the first egg. The assumption was based on a sample of 10 single-egg clutches and 45 clutches of two eggs. Some females left within a day of laying their solitary egg, while others with two eggs left as late as 6 days after laying the first; but 28 out of the 55 females left on the third day after first laying, and a mean of 3.3 days was computed for the sample
as a whole. The number of birds missing from the colony after laying was therefore taken as equal to the number of nests counted 3 days previously, and the number of birds that had entered the colony by a particular day was compounded of the total present on the day plus the total number of "missing" birds. Except at the brief change-over ceremony and during visits of the unoccupied partner to the nest (see below), only one bird is present at a time on the nest during incubation.

![Fig. 2. Growth of the colony in 1961.](image)

The growth of the colony, together with corrected totals to show the number of birds that entered the colony after laying began, is shown in Fig. 2. New birds continued to appear in considerable numbers throughout the third week of November. The influx continued at a reduced rate into early December, although accounting became difficult because of the departure of unknown numbers of birds that had lost eggs or had failed to find partners. I believe they began to depart from about 21 November. By that date slightly more than 3,400 birds had entered the colony altogether, and my impression is that not many (possibly 100 or 200 only) entered during the following week. A further expansion of the colony would be expected during the "reoccupation period" (Sladen, 1958; Taylor, 1962) late in December, when juveniles of the previous year appear and unsuccessful breeders of the
current season return. On 21 November, 2,415 birds were present in the colony, of which 1,054 were incubating alone. The remainder were single or paired, in various stages of courtship and laying.

The movements of banded birds during assembly showed clearly that (a) males tended to arrive at the colony before females, and (b) experienced breeders did not enter the colony particularly early in the season. Table 1 shows the dates of arrival of the 73 marked birds, arranged in groupings of

<table>
<thead>
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<th>Date of Arrival</th>
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<td>1</td>
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<td>4</td>
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<tr>
<td>25–27</td>
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a Cumulative totals.  
b Percentage of the total number of banded birds.  
c Percentage based on 3,600—the greatest number believed to have entered the colony during the assembly period.

3 days. Half of the marked males, but only 5 out of 33 marked females (14 percent), arrived before 3 November: 26 of the marked females (78 percent) arrived after 7 November, compared with only 40 percent of the marked males. Table 1 also shows the percentage of the total number of marked birds that were present in the colony on the third day of each interval, compared with the number of all birds present expressed as a percentage of the estimated peak figure of 3,600. It will be seen that, up to 10 November, the proportion of marked birds lagged, only 59 percent being present when 66 percent of the full colony had arrived. Thereafter the proportion of marked birds increased more rapidly than the intake of birds to the colony as a whole.

A number of Taylor’s banded birds were recovered by Reid early in the assembly period of 1960, i.e. between 23 and 28 October. Of these, 13 were recovered again during the 1961 assembly, 11 of the 13 appearing on or before 3 November and the remaining 2 appearing, respectively, on 6 and 16 November. Thus, a high proportion of birds known to have arrived early in 1960 also arrived early in 1961.

Thirty-three females and 38 males of the marked population were weighed on arriving at the colony, usually during the first 24–48 hours after appearing (Table 2). The mean weight of females was 4.4 kg, that of the males 5.1 kg. These figures are lower than corresponding data derived from Sapin-
Jaloustre (1960), in which the weights of 14 females and 14 males of copulating pairs (i.e. birds that could already have spent several days ashore) averaged, respectively, 4.8 kg and 5.2 kg. At Cape Royds, weight losses during courtship of 22 males and 2 females, measured over intervals of 8–12 days, averaged 73 g per day; the females were weighed before laying, and their losses did not differ significantly from those of the males. Applying this value as a correction, and assuming that the Adelie Land birds had averaged 3 days ashore before being weighed, their calculated weights on arrival would approach 5.0 kg for females and 5.4 kg for males, both substantially higher than the mean weights on arrival of Cape Royds birds.

**Courtship and Nesting.**—Males returning to the colony at the beginning of the assembly period usually headed directly for a particular site and remained attached to it. Females tended to wander, appearing at a number of sites and often with different partners before settling. The importance of the ecstatic call as a male display has been stressed by Sladen (1958) and others. Its function in advertising the presence of an unaccompanied male is clearly seen during the early-season accumulation of birds at the colony.

Among the marked birds whose nest site of 2 years before was recognizable, only 5 females out of 26 returned to their original sites. Sixteen out of 19 males returned to their sites of 2 years before, and the stronger attachment of males to their sites was also shown by pairs in which both birds were marked; of 6 pairs of marked birds in which both members had previously mated with other birds, 4 were settled in 1961 on the site that the male had occupied in 1959. Of the 2 remaining pairs, 1 was established on a site that neither had occupied in 1959, and the second occupied the female’s site of that year.

The Cape Royds colony is divisible into 15 separate groups of nests, ranging in size from less than a dozen to more than 150 nests. Birds that did not settle on their previously recorded site usually settled within the same group of nests as before, although again females showed a greater tendency to wander than males. Seven out of 30 females were found eventually in groups other than those in which they had nested in 1959, while only 1 out of 32 males nested outside his original group. Six of the 8 birds that moved changed from small to larger groups. These figures form an interesting contrast with the observations of Richdale (1957) that in Yellow-eyed Penguins (*Megadyptes antipodes*) males and females are equally apt to shift from one nest site to another.
The early return of the males may help to account for their tendency to settle on sites previously occupied, for their chances of finding the site untenanted by immature or wandering birds are highest at the beginning of the season. Females returning before their partners might settle on their original site for a few hours, but are easily diverted to adjacent sites by the call of lone males, and are rarely seen to defend a particular site in the absence of their partner.

Only three pairs of birds marked as partners in 1959–60 paired with each other again in 1961; all are believed to have occupied the same sites as before. Fourteen banded birds that formed 7 pairs in 1959 paired with other partners (mostly unmarked) in 1961. The males of 4 and the female of 1 of the original 7 pairs retained their old sites; 2 of the old nests were occupied by other birds in 1961. In 4 of the 7 original pairs the male returned more than 7 days before the female in 1961, and was firmly paired by the time his original partner arrived. One female returned to her old partner and nest, was seen in copulation, but later wandered to a site 30 ft (10 m) away and settled with another partner. In the remaining 3 pairs, the partners returned within 1–3 days of each other, but found alternative partners immediately in 2 of the 3 instances; in both cases the male of the original pair retained the nest site. In the third case, male and female returned within a day of each other, but neither spent more than a few minutes at its earlier site and both wandered freely through the colony. Both settled eventually in groups distinct from the group in which they had nested together in 1959.

Males took longer over courtship than females. Table 3 shows length of courtship (i.e. time in days from arrival to appearance of first egg) in 34 males and 31 females of the banded population. The longest delay was experienced by males that returned to the colony during the first 6 days of assembly; both sexes courted more rapidly during the third week of assembly than during the first or second weeks.

The largest number of nests with eggs (1,217) was recorded on 24 No-

<table>
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<tr>
<th>Date of Arrival</th>
<th>NO. of BIRDS STUDIED</th>
<th>MEAN LENGTH OF COURTSHIP (IN DAYS)</th>
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<td>1–3 Nov.</td>
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<td>13–15</td>
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<td>16–18</td>
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<td>1</td>
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<tr>
<td>Totals and means</td>
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<td>31</td>
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</table>
vember and again on 27 November. It is possible that a few more first eggs were laid after these dates. About 25 nests were abandoned or lost to the predation of McCormick Skuas, although predation up to the end of the laying period was much lighter than that recorded by Taylor in 1959. The presence of open water so close to the colony may have helped to divert the skuas away from the nests in 1961; none of the marked birds lost eggs up to the end of the observation period in early December. The total number of nests with eggs probably did not exceed 1,250 in the 1961–62 season. Thus, only 2,500 adults from the total entry of approximately 3,600 succeeded in nesting; nearly one-third of the population did not.

In the 1959–60 season over 1,400 nests with eggs were recorded by Taylor. From his Fig. 5 (1962) it may be calculated that the peak intake of birds was reached about 30 November, some 3,500 having entered the colony by this date. Thus, a similar, perhaps slightly smaller, intake in 1959 produced between 150 and 200 more nests than in 1961, and only about 20 percent of the population failed to breed.

Of the 72 banded experienced breeders, 4 males and 3 females failed to begin incubating before the end of observations and may be counted as non-breeders in the 1961–62 season. The rate of failure to breed among experienced breeders was therefore approximately one-third that of the population as a whole. All birds that failed to breed arrived on or after 9 November, when two-thirds of the breeding birds were already present. The late arrival of the only known third-year bird, and its failure to breed, may suggest that a high proportion of the late arrivers are birds of this category, as postulated by Sladen (1958). However, it is also clear that birds that have bred previously may arrive toward the end of the laying period and, perhaps in consequence, fail to breed in a particular year.

**Eggs and Incubation.**—In 1961, eggs were laid from 7 November onward. Between 9 and 18 November, the rate of laying rose from 26 to 230 eggs per day, falling during the subsequent 9 days to fewer than 4 per day. Very few eggs are likely to have been laid after the end of November. On 27 November, approximately 2,250 eggs (± 50) had been laid in the colony, a mean of 1.85 per nest. At the end of the observation period, 79 percent of the nests held two eggs. Earlier in the season a higher proportion of nests held two eggs; thus, between 12 and 18 November a mean of only 7 percent of completed nests contained a single egg, and many more single-egg clutches were laid late in the season rather than early. The result was perhaps subject to bias in that some clutches may have lost one egg but not both to skuas, but predation was extremely light and I suspect that its influence may be discounted.

Among marked birds, the mean date of first laying for clutches of two was 15 November; the mean of laying in single-egg clutches was 3 days later. No single eggs were laid before 15 November, but in 20 out of 43 clutches of two the first egg was laid before this date.
No naturally occurring clutches of three were found, although nine were induced artificially by removing the first egg within 24 hours of laying. Experiments were tried with groups of 30 nests. In the first group the first egg was removed as stated, in the second group a delay of 24-48 hours was allowed before removal of the egg, and in the third group both eggs were taken after the laying of the second egg. Only in nine nests of the first group were third eggs produced. These experiments were conducted from 14 November onward. It is almost certain that a higher proportion of third eggs would have been laid if the experiments had started earlier in the season, as only half the pairs produced even a second egg in the nests under observation. It seems unlikely, however, that third eggs are produced if the first egg remains in the nest for more than 24 hours; further experiments along these lines are required.

In a fourth group of 15 nests, a single egg was added shortly after the laying of the first. A second egg was laid in 12 of the nests; the presence of the alien egg did not inhibit the laying of a full clutch.

Of 60 recorded intervals between first and second eggs, 6 were of two days, 38 were of three days, and 16 were of four days. Of the 9 recorded intervals between second and third eggs, 1 was of two days and 1 of five days, 4 were of three days, and 3 were of four days. Mean intervals between first and second, and second and third eggs were, respectively, 3.1 and 3.4 days.

Table 4.—Length and Diameter of Eggs (in cm)

<table>
<thead>
<tr>
<th>Egg</th>
<th>No. in Sample</th>
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<td></td>
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<td>3rd</td>
<td>8</td>
<td>6.71*</td>
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</tr>
<tr>
<td>Single</td>
<td>15</td>
<td>6.99</td>
<td>0.30</td>
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</table>

*Significantly smaller than first and second ($P = 0.05$).

Table 4 shows the mean dimensions of first, second, and third eggs, and also of single eggs. Third eggs were significantly narrower and shorter than first or second, but no significant differences of length or diameter were found between first, second, or single eggs. Volumes were calculated from the expression $V = 0.512 \times$ length $\times$ greatest diameter (Stonehouse, 1963). The mean volume of first eggs (107.9 cc: $sd = 10.1$) was significantly greater than that of second eggs (104.3 cc: $sd = 9.7$); single eggs did not differ significantly in volume from first or second in the small sample taken, but the mean volume of third eggs was some 15 percent smaller. Fifteen freshly laid first eggs had a mean weight of 117 g and second eggs in the same nests had a mean weight of 109 g. In 7 out of the 15 nests, the second egg was heavier than the first (cf. Taylor, 1962).

Incubation routine at Cape Royds was found by Taylor to differ markedly
from that described by Sladen at Signy Island, both parents taking shorter watches and a small proportion of females taking the first watch after completion of the clutch. My own observations on marked birds in general confirm Taylor's findings, although incubation watches tended to be even shorter in 1961 than in 1959, possibly because of the closeness of open water throughout courtship and incubation. At 29 nests, Taylor found males taking a first watch with a mean length of 11 days, range 7–18 days, and from his diagram in Fig. 8 (1962) the mean length of the subsequent watch by females appears to have been approximately 9 days. At 35 nests for which accurate data were known in 1961, I recorded a mean first watch of 7.5 days (range 2–14 days), and at 17 of the nests the subsequent watches by females had a mean length of only 1.8 days (range 1–6 days). During their first long watches, seven of the males were visited by their females, which stood by the nests and attempted to take over incubation duties; one male was visited on the seventh and eighth days but did not surrender the eggs until the eleventh day, another was visited three times during an 11-day watch. The early return of the females was almost certainly due to the closeness of the ice edge. Observations ceased shortly after most birds had begun incubating and few data were obtained on subsequent watches, but at ten nests the second watch of the male lasted a mean of 2.3 days (range 1–3 days) and at three nests the second watch of the female lasted a mean of 2 days (range 1–3 days). The pattern of short watches was therefore continued far into the incubation period. A female took the first incubation watch in only 1 out of 63 nests observed; in a second, the female remained on the nest for 4 days after the laying of the second egg while her partner stood by; and in a third, the male left after the laying of the first egg but returned to begin incubation shortly after the second was laid.

The total time spent ashore, between first arrival at the colony and departure after laying or incubation, averaged 21.8 days (range 14–27 days) for 23 males, and 10.0 days (range 6–16 days) for 30 females. Comparable means from 1959 (Taylor's diagram in Fig. 8, data from 26 nests) are slightly longer: males, 23 days; females, 13 days. For seven nests at Signy Island, Sladen gives male and female averages of "at least 40 and 21 days respectively, possibly a few days longer."

**NEST SCRATCHING**

Adelie Penguins of both sexes are well known to carry stones and use them in the construction of their nests. Stone carrying as a pattern of behavior has been described or commented on by almost every contributor to the literature of penguin breeding behavior. Fewer observers have commented on an equally important behavior pattern that appears in the construction of every nest: Nests are usually begun and shaped by short but intense scratching movements of the feet, which are made by birds of either sex and are most marked when both are present at the site.
Nest scratching and its consequences are most apparent in colonies built on surfaces of hard-packed gravel or frozen mud. New arrivals at the colony begin their nests by lying prone and scratching repeatedly at the ground under their abdomen, using the toes of one or the other foot. On frozen ground, the mechanical action and warmth of the body combine to allow the formation of a shallow depression; on impacted gravel, pebbles are dislodged with the same effect. The cavity then forms the focal point of interest to the individual or pair; stones are brought to it, and the nest pile arises over it. Abandoned sites, and those not yet occupied at the start of the season, are often marked by the saucer-like depression which tends to persist from season to season; the depression may be all that remains of a nest, as stones are usually removed or scattered within a few hours of being left by their owner. Experienced breeders probably identify their former sites by the depressions, particularly on beaches or gravel slopes where other landmarks are few or absent.

When partners are building, one usually lies on the site while the other brings material. The prone bird often scratches the site with its hind leg in response to the arrival of its partner, in conjunction with a “bill to axilla” display (Sladen, 1958), or in other situations in which the partners are responding quietly to each others’ presence. In these contexts, the scratching movements are usually deliberate and measured, repeated some 15 or 20 times in 20–30 seconds; they effectively dig into the substratum and later shape a bowl among the stones of the nest pile. At high intensity, they may be vigorous enough to shoot stones several inches from the nest. Such intense movements are seldom seen after the eggs are laid, although small scratching movements persist throughout incubation and are often renewed at the change-over ceremony. The male of one pair of Adelie Penguins at Cape Royds repeatedly dislodged his eggs by violent scratching movements during a period of 2 days between completion of the clutch and departure of the female; after she had left, he settled down quietly to incubate substitute eggs that I provided, but these were dislodged forcibly by excited scratching a week later when the female returned.

Similar nest-scratching movements, made in similar circumstances, have been noted in the Gentoo Penguin (Pygoscelis papua) on South Georgia (Stonehouse, in preparation).

ACKNOWLEDGMENTS

I am grateful to G. A. Knox, who encouraged the work of our expedition, to T. Jacobs, who assisted with some of the field observations, to the New Zealand University Grants Committee for its financial support, and to the Ross Dependency Research Committee and Antarctic Division, D.S.I.R., for making the work possible. The U.S. Navy and U.S.A.R.P. gave most welcome support in the field. I am grateful also to R. H. Taylor, who banded the birds for his own studies in 1959–60 and allowed me generous
access to his work before publication, and to B. Reid, who allowed me to make use of unpublished notes from the 1960–61 season.

SUMMARY
This paper discusses the small colony (southernmost in the world) of Adelie Penguins at Cape Royds, Antarctica. The existence and continued success of the colony is due to favorable ice conditions in McMurdo Sound; in spite of the high latitude (77° S), the sea ice frequently breaks back to Cape Royds early in summer and allows the penguins easy access to open water. The size of the colony may result from the limited feeding area available; a parallel is drawn with similarly situated colonies in Marguerite Bay, Western Antarctica. Observations in October and November 1961 of assembly, courtship, laying, and incubation are described and compared with similar work of other seasons; the activities of marked experienced breeders are described for the first time. It is concluded that persistent ice in spring does not markedly affect the beginning of the breeding cycle or rate of colonization, but may profoundly affect incubation routine. The measurements of 269 eggs are tabulated.

LITERATURE CITED
Ecological Aspects of Irruptive Bird Migration in Northwestern Europe

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The object of this paper is to review recently accumulated data on irruptive bird migration in northwestern Europe and to analyze some of the relationships between this particular kind of bird migration and certain ecological factors, particularly food. A great deal of work on irruptive species has been carried out in Fennoscandia in recent years, and an additional purpose of this contribution is to draw attention to the results. The migration has been closely studied at several places for periods up to 15 or 20 years, and extensive data on annual fluctuations of the seed crop of certain trees are available.

The term *irruption* has often been used in a very loose sense; *invasion* has been used even more loosely (cf. Elton, 1958). Lack (1954:240) opposes the practice of calling any sort of mass occurrence, or any sort of occurrence outside the normal range of a bird species, an irruption or invasion. The term *irruption* has, however, been in long use as referring to a limited number of species, the migratory habits of which have been considered to differ sharply from those of other migratory birds through their irregularity. Various other properties have been thought to be diagnostic for irruptive birds, such as violent population fluctuations in the breeding area, absence of return migration, etc. The idea has been put forward that irruptions, at least of many species, recur with cyclic regularity, or that the disposal of large numbers of birds is the function of the wanderings.

The ecological significance of irruptions has recently become more fully understood, perhaps particularly because of Lack’s (1954) stimulating analysis. An important step has been the realization of the many resemblances between irruptive and *regular* migration (Rudebeck, 1950:49 et seq.), and most authors now agree that no sharp limit can be drawn between irruptive birds and other migratory birds. Several authors have stressed the fact that irruptive birds seem to be more directly influenced by food factors: The fluctuating abundance of some certain kinds of food has a strong effect on the temporal and spatial course of the movements. This difference, however, is qualitative rather than quantitative. Svärdson (1957:328) in an important discussion makes the point that irruptive migration is an adaptation to annual, rather than seasonal, fluctuations in food supply.

Restriction of the term *irruption* seems to be highly desirable. It should be used only in cases where the direct influence of fluctuating food conditions

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1 Report from Falsterbo Bird Station No. 26.

on birds' movements has been demonstrated and these fluctuations are due to variations in productivity of the food organisms.

My recommendation of a stricter use of irruption in no way indicates that I think that birds may be classified as irruptive birds and regular migrants. The direct influence of food on bird movements varies from species to species: In many cases, food scarcity is avoided by an early departure from the breeding grounds, so that food conditions have lost practically all importance as proximate releasers of migration; in many other cases, variations in the food supply exert a mild influence on the migratory movements; in still other cases, the whole annual pattern of movements is governed by the regionally and temporally variable food supply. Irruptive tendencies may thus be more or less expressly present in a species or a population. Yet, the term irruptive bird will sometimes be used in this paper instead of an awkward expression like "bird with pronounced irruptive tendencies in its migratory habits."

RAPTORIAL BIRDS

A number of raptorial birds are usually listed with the irruptive birds, for example Nyctea scandiaca and many other owls, Buteo lagopus, Stercorarius longicaudus, and Lanius excubitor (particularly the North American population of the latter species). To what extent are the movements of these birds dependent on the food supply met with during their postbreeding movements? In the first place, the spring migration of S. longicaudus may theoretically be influenced by the food situation but not the postbreeding movement, for the food of the species during the winter season can scarcely be supposed to bring about irruptive movements. Not even for the spring migration is the influence of food fully clear, for according to Swanberg (1946:18–19) these birds seem to return to previous breeding places every year, although they do not breed if the rodent population is poor. Thus, the migratory habits of S. longicaudus should not be labeled as being irruptive.

The movements of the northern European population of Buteo lagopus have been studied particularly by Schüz (1941–45, 1952), who was only able to obtain rather contradictory evidence as to the degree to which food conditions influence the extent of the movements of these birds. Under no circumstances is the Scandinavian population capable of wintering in the breeding area, so that the first part of the postbreeding movement is in any case performed without regard to food factors. Rosenberg and Curry-Lindahl (1959) seem to be of the opinion that the abundance of rodents exerts some influence on the location of the winter quarters, and in North America the Craigheads (1956) found that the number of birds of prey in a given area was much higher in a winter season with plenty of rodents than in one without. It is well known that the numbers of B. lagopus on passage migration in many districts of northwestern Europe vary from year to year, but the location of their winter quarters requires further study.
Table 1.—Definite Irruptive Migrants, Their Critical Food, and Some Key References

<table>
<thead>
<tr>
<th>Species (Subspecies)</th>
<th>Critical Food</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dendrocopos major</em></td>
<td><em>Picea</em> and <em>Pinus</em></td>
<td>Pynnönen (1939, 1960)</td>
</tr>
<tr>
<td><em>Loxia curvirostra</em></td>
<td><em>Picea</em></td>
<td>Reinikainen (1937)</td>
</tr>
<tr>
<td><em>L. pityopsittacus</em></td>
<td><em>Pinus</em> (and <em>Picea</em>)</td>
<td>Nilsson (1858:539) and later handbooks, Olsson (1960)</td>
</tr>
<tr>
<td><em>L. leucoptera</em></td>
<td><em>Larix</em></td>
<td>(No Fennoscandian food studies)</td>
</tr>
<tr>
<td><em>Pinicola enucleator</em></td>
<td><em>Sorbus</em> (and to some extent <em>Picea</em>)</td>
<td>Faxén (1945), Markgren (1955:174), Markgren and Lundberg (1959:196)</td>
</tr>
<tr>
<td><em>Turdus pilaris</em></td>
<td><em>Sorbus</em></td>
<td>Nilsson (1858:362) and later handbooks</td>
</tr>
<tr>
<td><em>Fringilla montifringilla</em></td>
<td><em>Fagus</em></td>
<td>Nilsson (1858:506) and later handbooks, Granvik (1916)</td>
</tr>
<tr>
<td><em>Nucifraga c. caryocatactes</em></td>
<td><em>Corylus</em></td>
<td>Swanberg (1951, 1959)</td>
</tr>
<tr>
<td><em>N. c. macrorhynchus</em></td>
<td><em>Pinus cembra</em></td>
<td>Formosof (1933)</td>
</tr>
<tr>
<td><em>Parus major</em></td>
<td><em>Fagus</em></td>
<td>Ulfstrand (1962:27), Cramp et al. (1960)</td>
</tr>
<tr>
<td><em>P. caeruleus</em></td>
<td><em>Fagus</em></td>
<td>Ulfstrand (1962:30–32)</td>
</tr>
<tr>
<td><em>P. ater</em></td>
<td><em>Pinus</em></td>
<td>Haftorn (1956:6–8)</td>
</tr>
<tr>
<td><em>Bombycilla garrulus</em></td>
<td><em>Sorbus</em></td>
<td>Nilsson (1958:241) and later handbooks, Hansson and Wallin (1958:234–235)</td>
</tr>
</tbody>
</table>

HERBIVOROUS SPECIES

Definitely Irruptive Migrants.—Table 1 lists those cases where critical food factors behind the irruptive tendencies have been established beyond reasonable doubt. However, not even in these species should the degree of food specialization be overrated. They may occur in numbers during months in districts where the critical food, the one about which the irruptions are centered, does not exist. Hansson and Wallin (1958) list a great number of vegetable products utilized as food by migrating flocks of *Bombycilla garrulus*. *Parus major* and *P. caeruleus* certainly are not monophagous birds (Ulfstrand, 1962), and irrupting *Loxia curvirostra* have been known to interrupt a movement for months to exploit an outbreak of *Operophthera brumata* larvae (Carlsson, 1962:10). *Loxia leucoptera* has several times successfully nested in Sweden (Sveriges Ornitolögiska Förening, 1958), although *Larix* trees are scarce and restricted to parks and plantations; and *Nucifraga caryocatactes macrorhynchus* has bred once, subsisting during the previous winter largely on food supplied by man (Lundberg, 1955).

In some species, food conditions within the breeding areas exert their influence on the migratory movements, so that the birds may remain more or less stationary during years with a rich food supply. Such is probably the case in *Pinicola enucleator*, *Bombycilla garrulus*, *Nucifraga caryocatactes* (both subspecies), *Dendrocopos major*, and *Parus ater*. This statement does
not imply that all individuals of a given population remain stationary, even if the food supply is abundant. Siivonen (1941) points out that a proportion of the *Bombycilla garrulus* population moves irrespectively of the food situation. Holm (1957) states that *Pinicola enucleator* departs for a brief period in midwinter from northernmost Fennoscandia, and such is probably the situation in most species. In other species the critical food factor does not operate in the breeding areas, but the birds have to travel a longer or shorter distance before irruptive tendencies are noticeable. Such is the case in *Fringilla montifringilla, Turdus pilaris, Parus major,* and *P. caeruleus.*

The only vegetarian irruptive species that are dependent on the critical food factor during both the winter and breeding seasons belong to the genus *Loxia.* In this connection, attention is drawn to Olsson’s (1960) estimate that a clutch of *L. pityopsittacus* devours about 70,000 *Pinus* seeds during the nesting period. The role of seeds during the breeding season is rather unclear in *Carduelis spinus* and *C. flammea.*

All the other species listed in Table 1 live on lower animals or on a mixed diet during the breeding season, and their young are fed mainly or wholly on insects. Thus, during the breeding season they are independent of the critical food factor. The statement by Svärdson (1957:320), therefore, that the irruptive birds “search for” a new breeding area during their movements is too wide a generalization; except perhaps for some of the rodent-eating raptore species and for the *Loxia* species, the irruptive birds “search for” a wintering area with satisfactory food abundance. It is quite a different thing that they often remain in the area and breed, given certain circumstances.

**Questionably Irruptive Migrants.**—In Table 2 a number of species are listed which are more or less generally suspected of exhibiting irruptive tendencies in their migration habits but for which the critical food factor has not been convincingly demonstrated. To that list, in point of fact, several species might be added.

<table>
<thead>
<tr>
<th>Species (Subspecies)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sitta europaea asiatica</em></td>
<td>Svärdson (1955)</td>
</tr>
<tr>
<td><em>Aegithalos caudatus</em></td>
<td>Svärdson (1935), Tischler (1941:281), Ulfstrand (1962:93 et seq.)</td>
</tr>
<tr>
<td><em>Pyrrhula pyrrhula</em></td>
<td>Rudebeck (1950:50), Svärdson (1957:327)</td>
</tr>
<tr>
<td><em>Chloris chloris</em></td>
<td>Rudebeck (1950:50)</td>
</tr>
<tr>
<td><em>Emberiza citrinella</em></td>
<td>Rudebeck (1950:50)</td>
</tr>
<tr>
<td><em>Carduelis spinus</em></td>
<td>Svärdson (1957:317 et seq.)</td>
</tr>
<tr>
<td><em>C. flammea</em></td>
<td>Svärdson (1957:320 et seq.), Lennerstedt and Ulfstrand (1959)</td>
</tr>
</tbody>
</table>
There seems to be little doubt that *Carduelis spinus* and *C. flammaea* have irruptive migration habits. For the latter species, *Betula* and *Alinsus* seeds make up by far the largest proportion of the winter food, and these seeds are known or likely to occur in fluctuating abundance (cf. Table 3). However, the species also takes a great many seeds of herbs. In the former species, the situation is very complicated. In his important analysis, Svärdson (1957) tries to correlate the passage of the species at Ottenby on the island of Öland in the Baltic with *Betula* seed abundance (p.317), but in another connection points to the importance of *Picea* seeds for the birds (p.319). A glance in some Scandinavian handbooks reveals that the relative importance of different seeds for *C. spinus* is poorly known. Nilsson (1858:489) mentions *Betula, Pinus, Picea*, and *Alinsus* in that order; Svärdson and Durango

### Table 3.—Chief Movements of Species with More or Less Obvious Irruptive Migration Habits (Marked by X) in 1942-44* and 1949-61; with Fructification Indices of Picea and Betula (Whole Sweden), Quercus (Southern Third of Sweden), and Fagus (Southernmost Provinces Only)*

<table>
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<tbody>
<tr>
<td><strong>Dendrocopos major</strong></td>
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<tr>
<td><strong>Nucifraga caryocatactes sp.</strong></td>
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<tr>
<td><strong>N. c. caryocatactes</strong></td>
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<tr>
<td><strong>N. c. macrorhynchus</strong></td>
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<tr>
<td><strong>Garrodus glandarius</strong></td>
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<tr>
<td><strong>Parus major</strong></td>
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<tr>
<td><strong>P. caeruleus</strong></td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>-</td>
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<tr>
<td><strong>P. ater</strong></td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>-</td>
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</tr>
<tr>
<td><strong>Aegithalos caudatus</strong></td>
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<tr>
<td><strong>Carduelis spinus</strong></td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>x</td>
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<tr>
<td><strong>Loxia curvirostra</strong></td>
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<tr>
<td><strong>Pyrrhula pyrrhula</strong></td>
<td>-</td>
<td>x</td>
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</tr>
<tr>
<td><strong>Picea</strong></td>
<td>3.1</td>
<td>0.5 1.6</td>
<td>0.8 1.3 1.6 1.3 1.5 3.7</td>
<td><strong>0.4</strong> 2.1</td>
<td><strong>0.8</strong> 2.0 1.4 1.8</td>
<td>1.2</td>
<td></td>
<td></td>
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<tr>
<td><strong>Betula</strong></td>
<td>3.1</td>
<td>1.4 2.5</td>
<td>1.4 2.5 2.4 2.0 2.1 2.9</td>
<td><strong>1.2</strong> 2.8</td>
<td><strong>1.6</strong> 2.7 2.1</td>
<td>2.9 2.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Quercus</strong></td>
<td>1.5</td>
<td>0.9 2.1</td>
<td>1.3 1.9 1.5 1.7 1.2 2.6</td>
<td><strong>1.0</strong> 1.3</td>
<td><strong>0.9</strong> 1.2</td>
<td>1.6 2.0</td>
<td>1.4</td>
<td></td>
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<tr>
<td><strong>Fagus</strong></td>
<td>2.5</td>
<td>0.5 3.0</td>
<td>0.1 1.6 1.3 1.6 1.0 3.4</td>
<td><strong>0.2</strong> 3.7</td>
<td><strong>0.0</strong> 1.2</td>
<td><strong>0.3</strong> 3.3</td>
<td>0.7</td>
<td></td>
</tr>
</tbody>
</table>

* Rudebeck (1950).
* At Falsterbo, southern Sweden; taken from annual reports of Falsterbo Bird Station, published serially in *Vär Fågelvärld*, and from unpublished material in the archives of the bird station. Movements of *Pinicola enucleator* scarcely ever reach this place. *Turdus pilaris*, *Bombycilla garrulus*, and in part also *Carduelis flammea* usually occur so late in the season that they are not recorded. The figures for *Loxia curvirostra* are somewhat uncertain, for part of the movements occur so early in the season that the birds are not recorded. *L. pityopsittacus* and *L. leucoptera* are extremely rare in southernmost Sweden.
* The figures are averages from a great number of indices, estimated by professional foresters, and published by Tirén (1942-44, 1949-50) and Fall (1951-61).
* The two cases of *Aegithalos caudatus* involve relatively large-scale movements, but the status of this species as an irruptive bird in the sense of this paper is open to strong doubt.
* In the most extensive *Fagus* districts the crop was better than indicated by this figure, which was lowered by indices from some peripheral districts with a poor crop.

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*Indices:*

- **0** = practically no crop
- **1** = very poor crop
- **2** = rather poor crop
- **3** = rich crop
- **4** = extremely rich crop

The figures are averages from a great number of indices, estimated by professional foresters, and published by Tirén (1942-44, 1949-50) and Fall (1951-61).
(1950:182) list *Picea* and *Alnus*; and Poulsen (1959:133) enumerates *Picea*, *Pinus*, and *Betula*. The standard works by Niethammer (1937:55) and Witherby et al. (1948:62) both state that *C. spinus* takes both coniferous and deciduous seeds. Hence, the correlation between irruptive movements of this species and its food factors is very complex, and that may explain why Svärdson (1957) found one of the highest totals for passing *C. spinus* during a year with the highest "Betula seed index." These uncertainties have caused me to include *C. spinus* in Table 2 rather than in Table 1.

*Garrulus glandarius* is another species that almost certainly has a strong irruptive component in its migrations, but both Putzig (1938) and Berndt and Dancker (1960) are of the opposite opinion. However, according to my judgment, the evidence produced by these authors is not convincing. Putzig (p.203) says that the great movement through East Prussia in 1936 was contemporaneous with a heavy crop of *Fagus* and *Quercus* seeds, but points out that no information was available from the area in which the movement had its origin, namely Poland. In any case, the fact that the birds neglected an area of rich food supply is of great interest, but it certainly does not prove that food is without significance for the movements. In 1955, when the largest *Garrulus* movement in recent years took place, the *Quercus* acorn crop in southern Sweden was extremely poor, several forestry districts reporting "no crop" (Fall, 1955–61). Berndt and Dancker (1960) argue that the species must be independent of this source of food, since a considerable population lives north of the northern limit of *Quercus*. However, even if this northerly population is independent of *Quercus* acorns, the more southerly and denser populations probably are very dependent on this food. Until further studies on the ecology of this species have been made, it seems, however, better to place *Garrulus* in Table 2.

*Aegithalos caudatus* is stated to be exclusively insectivorous, and therefore it seems unlikely that its movements are irruptive in the sense of this paper.

**FACTORS OTHER THAN FOOD**

Even if we restrict ourselves to the species listed in Table 1, food is obviously not the only factor influencing the movements. It has already been mentioned that certain populations have to travel a considerable distance before they enter the area in which the critical food exists. During the first part of their journey, they apparently are stimulated by the same factors as all other birds. Svärdson (1957) stresses the fact that the movements of several irruptive birds start very early in the season, before food shortage has become apparent. However, for *Nucifraga c. macrorhynchus*, *Loxia curvirostra*, and *Dendrocopos major*, Formozov (1960:228) points out that the new crop of seeds constitutes the chief food beginning in June or July. It seems very likely that the population density as such may act as a proxi-
mate stimulus for releasing the movements under certain circumstances. Kluijver (1951) has demonstrated this factor in *Parus major*, and Kalela (1954:7) points out that in some species the movements start at the season when the young gain independence and disperse to occupy their own territories.

Meteorological factors also play an obvious role. Low temperatures may start movements even in midwinter in *Pinicola enucleator* (Grenquist, 1947; Markgren, 1955:175–176), and midwinter movements, probably released by cold weather, have also been recorded for *Turdus pilaris* (Mathiasson, 1960:115). Svärdson (1953:185) found that temperature drops in autumn release migration in *Carduelis flammea*, *Turdus pilaris*, and *Loxia*, as well as in more or less all other species of migrants. Climatic fluctuations have been suggested by Malmberg (1949) to play an important role in the reduced frequency and extent of the irruptive movements of *Pinicola enucleator* in the twentieth century.

As mentioned above, Putzig (1938) recorded large numbers of *Garrulus glandarius* passing through areas of abundant food supply, and the poor correlation between low *Picea* seed crop and high figures of departing *Loxia curvirostra*, *Parus ater*, and *Dendrocopos major* at Falsterbo, southwesternmost Sweden, indicates that the birds may under certain conditions pass through extensive areas of rich food supply (cf. Table 3 for the years 1953 and 1956). This provides further confirmation of the fact that food is not all-dominant but that other factors also play a role.

**ANNUAL FLUCTUATIONS IN THE SEED CROP OF CERTAIN TREES**

In Table 3 the annual variations in the seed crop of *Picea*, *Betula*, *Quercus*, and *Fagus* in Sweden are set forth. It is unfortunate that we do not possess corresponding data from *Alnus*, *Sorbus aucuparia*, *Corylus avellana*, and other plant species of significance for certain bird irruptions.

A weakness of the data in Table 3 is that the figures are based upon field estimates (by professional foresters) of the cone frequency and not on measurement of the number of filled seeds. However, Sarvias (1957) has shown that, in general, the rule holds that the higher the number of cones, the higher the proportion of filled seeds. Thus, the data are certainly adequate for the present purposes.

A glance at the figures in Table 3 tells us that a certain amount of seed is nearly always produced in all the trees. Particularly in *Betula* and *Quercus* the fluctuations are of only moderate extent. In the former, however, the fluctuations are partly smoothed out due to the fact that the figure given is an average for the whole country. If attention is restricted to a single sample area or to a number of adjacent areas, sharper fluctuations can be found. *Picea* shows stronger fluctuations, and *Fagus* has in a few years reached an average index of only slightly above zero. It should, however, be kept in mind that smoothing out of the figures occurs least in *Fagus*,...
for this tree occurs only in the southern third of Sweden and is frequent only in the three southernmost provinces, so that the average is based only on about 10 sample districts (as contrasted to about 90 for *Picea* and *Betula* and about 25 for *Quercus*).

Striking local differences are exhibited by these phenomena. It is not unusual for two adjacent districts in the same year to report a “good crop” and “very poor crop,” respectively. Thus, only very rarely are all the *Picea* forests of Sweden empty or nearly empty of seed crops in 1 year. Because of the local differences, it is not necessarily inexpedient for the birds to return to approximately the same breeding place in 2 consecutive years. Even if the same tree and probably the same woods do not carry a rich crop in both years, the birds have a considerable chance of finding a fairly rich area in the vicinity.

**THE “PENDULUM” THEORY**

Svärdson (1957) is of the opinion that the movement patterns of the more extreme irruptive birds are totally different from those found in other northwest European birds. He assumes that these birds start their postbreeding movements in alternate directions in different years. In short, his idea is that the birds move west in 1 year, breed, move back toward the east, breed again, and so forth. According to this “pendulum” theory, Scandinavia would receive large quantities of birds from the east in some years, while corresponding quantities would depart from the area toward the east in other years. Westbound movements are much easier to observe, according to Svärdson, because of the influence of the guiding-line systems of western Europe.

In my opinion, however, this theory has a great weakness, viz. that the evidence for eastbound movements of irruptive species from Scandinavia is virtually nonexistent. Extensive studies of visible migration have in the last 20 years or so been conducted in Sweden at two places: Ottenby on the island of Öland, off the Swedish southeast coast, and Falsterbo, situated in the extreme southwestern corner of the province of Skåne (Scania) and of Scandinavia. Data from these places have been published in *Vår Fågelvärld* (seriatim) in the form of annual activity reports; see also Rudebeck (1950) for Falsterbo and Svärdson (1953) for Ottenby. It has been repeatedly demonstrated that birds flying in a southeasterly direction are proportionately more numerous at Ottenby, those in a southwesterly direction at Falsterbo. It is, therefore, highly significant that large numbers of irruptive birds have practically never been recorded at Ottenby. Recently, extensive observations have been made at another place in southeastern Sweden, at the sound between the island of Öland and the mainland. No irruptive species have been recorded in numbers (Edberg, 1960, 1961). Finally, some less regular studies have been made at the extreme southeastern corner of the Swedish mainland in the province of Blekinge, and Carlsson (1962)
reports fairly high numbers of *Carduelis flammea* and certain other birds mentioned in Tables 1 and 2. The high number of *C. flammea* recorded during the autumn of 1958 agrees well with the finding by Lennerstedt and Ulfstrand (1959) that the midwinter population was much denser in southeastern than in southwestern Sweden. Further observations at this place seem highly desirable, but so far no proof of southeastbound movements has been obtained. Linkola (1960) states that a low number of *Pinicola enucleator* flocks moved toward the southeast at Signilskär, Åland, in 1956. However, his data on the movements of *Parus* spp. at the same locality indicate that the migratory pattern is very peculiar there. Many tits were seen flying east and southeast, but ringing recoveries showed that the direction of the movement was south-southwest and west-southwest (Linkola, 1961).

Observations from the northeastern part of Sweden, at the northernmost part of the Bothnian bay, would be of extremely great value in the present context. However, regular observations of visible migration have not been made in that region. In a discussion between P. Linkola and G. Markgren (Linkola, 1960), the reactions of irruptive migrants and particularly of *Pinicola enucleator* at encountering the open sea were debated. Markgren, in spite of many years’ field work on the Bothnian coast, was able to cite only an isolated case of birds departing out over the sea and that was in the spring. There remains the possibility that movements of, say, *Pinicola, Bombycilla*, and *Loxia* spp. take place north of the Bothnian bay. This route, however, is unthinkable in species with less northerly distribution, such as *Parus ater, Dendrocopos major, Carduelis spinus*, and, of course, *Nucifraga c. caryocatactes* (for distribution, see Sveriges Ornitologiska Förening, 1958).

The conclusion drawn from this discussion is that east–west movements are not a general feature in Fennoscandian irruptive birds, not even in the species inhabiting the coniferous forests (the taiga), and that their existence has not been proved in any single case. The support for eastbound irruptive movements, presented by Svärdson (1957), consists of (1) a few observations of traveling *Loxia* and (2) the observation that the Scandinavian breeding population of *Bombycilla garrulus* had dropped sharply from one year to the next without any departure over southern Sweden having been noted.

**SPRING MOVEMENTS**

Many irruptive migrants occur in much smaller numbers in spring than in autumn in southern Sweden. The numerous local breeding populations of, for example, *Parus major* and *P. caeruleus*, contribute to rendering the spring passage inconspicuous. Such birds as *Dendrocopos major, Nucifraga caryocatactes*, and *Bombycilla garrulus*, on the other hand, are unlikely to be overlooked for such reasons. Low numbers in the spring may be due to a heavy winter mortality, but there is also the possibility that many birds
return by a different route. A certain confirmation of this idea is found in Tischler’s (1941) data concerning the passage through East Prussia where, for example, Bombycilla garrulus is obviously not scarce in spring. Return movements are often remarkably late, as reported for Garrulus glandarius by Berndt and Dancker (1960) and for Bombycilla by Tischler (1941).

PATTERNS OF MOVEMENT AND THE ECOLOGICAL BACKGROUND

The following statements seem to be based on satisfactory evidence:

1) There is no evidence for eastbound movements of irruptive birds from Scandinavia.

2) The density of the breeding population of Bombycilla garrulus, Loxia curvirostra, Dendrocopos major, and probably several other species in Scandinavia is very variable and generally low after an irruptive movement (Svärdson, 1957, and sources quoted by him).

3) The wintering range of irruptive birds is very variable, the breeding range much less so. Even the most extremely irruptive birds rarely or never breed south and west of certain limits.

4) Population-density variations cannot be explained by changes in productivity or by accumulated production of a stationary population. In point of fact, among all the species listed in Table 1 only Parus major and P. caeruleus have particularly large clutches. The sudden increases in population density in northern Sweden which undoubtedly do occur must therefore be caused by immigration. Thus, the population dynamics of these birds are quite different from those of the small rodents (Lemmus, Clethrionomys spp., etc.) in which the population fluctuations depend on changes in productivity and mortality and not on long-distance movements.

5) Among all the vegetarian irruptive birds, the three species of the genus Loxia differ from the rest in their extreme food specialization and—still more important—their dependency on the critical food factor also during the breeding season.

Many authors have assumed that irruptive movements have a fairly wide angle of spreading, particularly in their initial stages, and Svärdson (1957) states that they have a more distinctly westerly course (as opposed to a southwesterly) than most other migrants in the northwestern Palearctic. This seems to be true. In Scandinavia and western Europe, the westerly direction is changed to a more southerly one, which at least largely depends on the influence of macrotopography. Such a change in primary direction occurs in many other species, sometimes due to the effect of guiding-line systems, sometimes to other factors.

The extent of travel and the position of the winter quarters vary strongly. Thus, in some years great flocks of Bombycilla garrulus and Turdus pilaris winter even in the northern part of Sweden, in other years practically all the birds have left Scandinavia by midwinter. In some years vast quantities of Fringilla montifringilla, Parus major, and P. caeruleus spend the winter in
the south Swedish Fagus woods, in other years the former is almost absent and the density of the two latter very much lower. The Swedish population of Nucifraga c. caryocalactes is usually completely stationary, but sometimes the birds move hundreds of kilometers to the southwest.

It follows that in some years such birds as Bombycilla garrulus, Turdus pilaris, and Dendrocopos major find suitable winter quarters and remain within the normal breeding area of the respective population, even if far from the previous breeding localities or the birthplaces of the individuals. In other years, on the other hand, large numbers of birds winter 20° or 30° south or southwest of the breeding range. The sudden increases in the breeding population of, for example, Bombycilla garrulus in Sweden no doubt are due to the fact that the birds remain and breed in the wintering area. Birds that have traveled far to the south, on the other hand, obviously have to perform a prebreeding movement.

With regard to the preceding discussion, I conclude that the "pendulum" pattern becomes an unnecessary hypothesis. It seems to be possible to explain the movements of irruptive birds without demanding special navigational or other faculties on the part of the participating birds. Let us assume that a given population in a given year occupies a breeding range with an easterly center, for example in the taiga of the eastern part of the European U.S.S.R. After completion of their breeding, the birds start moving westward like most other northwest Palearctic birds. When they reach an area with a rich supply of the critical food, the movement is brought to a standstill. If such a suitable wintering area is found within the normal breeding area of the species, for example in northern Fennoscandia, the birds remain and start a new breeding cycle in the following spring. Next autumn, if the critical food is scarce, a new movement is started toward the west; the course later becomes more or less southerly because of the large guiding lines of western Europe, and the winter quarters are situated in western Europe. In the following spring, the birds find themselves far south of normal breeding latitudes. Then a prebreeding movement is released, probably by the same general stimuli as in other migratory birds, and an eastbound or north-eastbound movement is performed. It may be that the return movement keeps a rather strictly easterly course: Spring and autumn primary directions are very often opposite to each other, and the Baltic Sea might contribute to leading the birds eastward via north-central Europe rather than via Scandinavia.

In this pattern no extraordinary abilities are demanded of the birds, for it is only a modification of the general pattern among northwest Palearctic birds. In point of fact, it demands less than is known to exist in the "ordinary" migrants, for the birds may lack or have only poorly developed homing ability (Ortstreue). On the other hand, this pattern of more or less circular movements would confer distinct advantages to the birds. Thus, the amount of time spent traveling is reduced because of the lack of prebreeding move-
ments in most years and to the abbreviation of the postbreeding movements, in comparison with birds having a fixed wintering range. And yet the birds are able to spend most winters in areas with a rich supply of critical food.

Several populations are probably able to survive within the taiga zone for a number of years in succession, and departure from this area becomes necessary only at irregular intervals. No regular periodicity has been demonstrated in the species discussed in this paper (cf. Lack, 1954).

The circular pattern outlined above certainly does not exist in all the species listed in Table 1. Every species has many ecological characteristics of its own, and adaptive changes are unlikely to produce identical ecological patterns in different species. Irruptive-migration habits are, of course, acted upon by selection, and it is according to expectation that we find all transitions from extreme dependence on annually fluctuating food supplies, such as the seeds of several trees in the North Temperate Zone, to nearly complete independence of this kind of factor. Most extreme are the food specializations of the *Loxia* species. These may have approached the “pendulum” pattern, as suggested by Svärdson (1957), although this is not proved. Less extreme is the ecology of, for example, *Dendrocopos major*, *Parus ater*, *Bombbycilla garrulus*, and *Pinicola enucleator*, which are dependent on a limited variety of vegetable foods in winter and autumn but which subsist on other foods for the rest of the year. In these birds, the circular pattern seems to have reached a higher or lower degree of development. With regard to the rudimentary *Ortstreue* of all these species, their movements are called nomadic by Kalela (1949). Some evolutionary consequences of nomadic habits are briefly discussed by Salomonsen (1955:19) and Svärdson (1957).

A different pattern is present in a number of species with rather strictly fixed breeding ranges but variable winter quarters. These birds are obviously much more similar to the nonirruptive migrants. They always perform two annual movements. The border line between this group and the nonirruptive birds is very diffuse, and many birds show irritive tendencies insofar as they sometimes discontinue their migration in the presence of particularly rich food sources. A gradual transition between stationary and migratory habits has been demonstrated in recent years, and it seems that the same gradual series is present between irritive movements, directly and strongly influenced by the food situation, and nonirruptive movements, the course and extent of which are governed by factors other than food. The ultimate factor behind both kinds of movements is the fluctuating food supply in the Temperate Zone.

**SUMMARY**

A restriction of the term *irruption* is advocated. Closer examination of the migratory habits of certain raptorial birds is necessary before their status as possible irritive migrants may be established. A list of undoubted irritive
migrants is presented (Table 1) and discussed. Many types of evidence exist that not even in these species is food the exclusive factor governing the movements. In several irruptive species the postbreeding movement starts irrespective of food conditions, although the latter influence the timing and extent of the movements.

Some questionable cases of irruptive migration are discussed, and population density and meteorological factors as releasers of movements in irruptive migrants are briefly touched upon.

Annual and regional fluctuations in the seed crop of certain trees are reviewed on the basis of a large body of data from Sweden (Table 3) and are correlated with movements observed at Falsterbo bird station in southernmost Sweden. Some cases where agreement was lacking between poor crop and heavy migration are discussed. Svärdson's "pendulum" theory is criticized chiefly on the ground that there is practically no evidence for east-bound postbreeding movements in Scandinavia. An alternative pattern in irruptive movements is suggested. Irruptive migration is considered as an adaptation to reducing the movements as far as possible, and it is put forward that in more fully developed cases irruptive migrants have a multi-annual migratory cycle. The considerable differences between different irruptive species are stressed, and the flexibility of the pattern is pointed out as a possible advantage with regard to the variable winter conditions within cold temperate regions.

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Ecological Factors Affecting Distribution of a Nesting Royal Albatross Population

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The only known breeding ground for the large Southern Royal Albatross (*Diomedea e. epomophora*), aside from a few pairs nesting on the Auckland Islands, is Campbell Island, located about 400 miles south of New Zealand in latitude 52°30' S.

Campbell Island is 4,000 miles from the coasts of South America where we know now, through banding, that the young albatrosses spend several years before they are ready to nest for the first time, and which the adults frequent between their alternate breeding years. The island consists of about 42 square miles of rough country, a much dissected volcanic cone with a rugged coastline. It measures about 10 by 10 miles and is deeply dissected from east to west by the 6-mile-long Perseverance Harbour (Fig. 1). The highest point is Mt. Honey (1,867 ft).

**VEGETATION**

The type of vegetation on Campbell Island is of paramount importance for the nesting albatrosses. The climax plant formation of the ridges and
slopes above the scrub line is tussock, the dominant plant being *Poa litorosa*. The scrub line—there are no trees on Campbell Island—is somewhere between 400 and 600 ft above sea level, and the slopes up to this altitude are covered with a dense scrub consisting of *Dracophyllum scoparium* and *D. longifolium*. This scrub in places provides suitable nesting sites for colonies of Yellow-eyed Penguins (*Megadyptes antipodes*) but is of no importance to the albatrosses.

![Fig. 2. Three young albatrosses on gam, St. Col Ridge, with Mt. Lyall in the background. 15 January 1958.](image)

Above the scrub, on the windblown ridges, spurs, and plateaus, tussock with a few other species interspersed reigns supreme. This is the nesting habitat of the Royal Albatrosses, also the resting and display grounds (Fig. 2), as well as the landing and takeoff areas for these heavy, long-winged birds which are dependent upon updrift winds for takeoff. This tussock formation formerly had a larger variety of species, *Poa foliosa* and *Danthonia antarctica* being abundant, together with large and beautiful flowers such as *Pleurophyllum speciosum* and *P. hookeri*. The radical change in the tussock formation has been caused through the introduction of sheep in 1896. By 1903 the number of these animals had increased to about 4,500. The scrub was burned in order to make easier the movements of sheep as well as shepherds. Sheep were by 1903 found on only half of the island, and Cockayne (1903) noted that they were particularly fond of eating *Danthonia*, both species of *Pleurophyllum*, and other of the large flowering plants.
Sheep did not eat *Chrysobactron rossii*, a plant that spread among the dying tussock, which the sheep ate right down to its base. *Chrysobactron* spread from the gullies, and today covers many acres of the slopes (Fig. 3), but the albatrosses do not nest in or in any other way utilize these dense, wet stands of pure *Chrysobactron*. By 1907—11 years after their introduction—Laing (1909) reported that there were about 8,000 sheep on the island. Grazing of sheep, in addition to such indirect results of sheep farming as burning, fenc-

*Fig. 3. Dense stands of Chrysobactron rossii, in such places as above covering acres, exclude the nesting of albatrosses; they result from burning and from the overgrazing of tussock by sheep. Slopes of Mt. Dumas, 8 January 1958.*

...ing, and the many other activities of the shepherds on the island, modified its vegetation. It can be suggested that grazing has opened up the dense tussock stands and thus made the island more suitable as a nesting area for albatrosses, but there is no denial of the fact that the island’s flora has undergone radical changes; nor can it be denied that the combined effects of sheep, burning, spread of *Chrysobactron*, and erosion have resulted in the whole or partial exclusion of nesting albatrosses from areas where they formerly nested; the southern slopes of Mt. Honey are outstanding examples of this condition (Fig. 4).

Sheep farming was given up in 1927 and, although an attempt was made to remove the sheep, a thousand or more were left behind. Sorensen (1951), who spent 4½ years on Campbell Island over the period 1941–47, reckoned that there were about 2,000 by 1947. When I visited Campbell Island dur-
ing January–February 1958, there were still many sheep left in spite of constant killing by meteorological station personnel for food, and flocks were seen in most parts of the island. There possibly were between 1,000 and 2,000 sheep on the island at that time. A recommendation that the sheep be removed has been subsequently agreed to in principle by the government departments involved.

The upper ridges of Campbell Island are still clothed in tussock, although there are many bare patches, slips, and areas covered with *Chrysobactron*. On the ridges and spurs and in the tussock-covered gullies, the Royal Alba-

![Fig. 4. Unstable and damaged vegetation on southern slopes of Mt. Honey where sheep are common. The tussock is largely gone; *Chrysobactron* has taken over, while large scars of erosion have exposed the black peat. Albatrosses still nest here, but available nest sites are few. 8 February 1958.](image)

trosses build their sizable nests, so practically all of their nests are found above 400 ft in elevation. As this level coincides with the lower layer of fog, mist, and clouds so frequently covering the ridges, the incubating albatrosses and later their single young spend much of their time sitting in a misty, moist, and cold world.

In addition to the tussock-covered ridges, another habitat type provides nesting areas for the albatrosses, the upland peat bogs. These are found in several places, a typical example being the flat plateau east of Moubray Hill. The wind here is severe, and albatross nests not placed in small gullies out of the wind are usually sheltered behind the numerous stunted *Dracophyllum* bushes (Fig. 5). Especially on the Faye Ridge in the northernmost part of the island, the main stronghold of the albatrosses, the peat bog has been partly destroyed by grazing sheep, and large barren areas of black peat are visible.

Royal Albatrosses do not land on or near their nest as do most birds. However elegant and efficient they appear in their rightful element, the
roaring winds above the waves, on land they are awkward creatures. Nests are placed in shelter from the fierce westerly winds, and albatrosses often have long distances to waddle to the nest from their landing and takeoff area on or near a ridge; in several instances this distance was several hundred yards. Approaching its nest, the albatross makes its way in and out among the tussock, but where many birds nest in fairly close proximity, they may develop much-used "highways" leading up slopes and ridges. Another re-

Fig. 5. The upper peat-bog formation on the flat east of Moubray Hill characterized by solid stands of young and stunted Dracophyllum bushes behind which the albatrosses find sheltered nesting sites. Moubray Hill, 16 January 1958.

quirement of the albatross colony is the loafing, resting, and general "hang-out" areas of the older age-groups of young birds, not yet breeding but visiting the island for extended periods. Up to several hundred birds are found in some of these congregation areas.

Campbell Island is thus a place for nesting only. The birds spend little time there when they do not have to. Males and females fairly evenly share both incubation and the 5-week chick-guard period following hatching; and if not incubating the egg or brooding the small chick, the adult bird is away. Only at changeover are the two mates seen together at the nest, sometimes for a few minutes, sometimes up to half an hour. The only contact the nesting albatrosses have with the island is therefore the grounds where they perform their courtship displays, the landing and takeoff site, the ground between it and the nest, and the nest and its immediate surroundings. Those
areas have to be relatively clear of dense vegetation or partly sheltered behind protective vegetation but with easy access. Campbell Island’s wind-blown tussock ridges and slopes with their net of sheltered gullies provide the needed shelter and accessibility for the albatrosses.

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**CLIMATE**

The climate of Campbell Island is characterized by a striking uniformity of temperature conditions throughout the year (Fig. 6), an almost constant high wind, very high humidity, frequent drizzles and rain, almost constant fog and cloudiness on the ridges, and—as one would expect—a low number of sunshine hours (Table 1).

Absolutely essential for the albatrosses is an almost permanent strong wind, enabling them to land and take off. Adult albatrosses that I weighed
ranged between 15 and 21 lb. With such body weight, long and narrow wings, and slow wingbeat, albatrosses need the aid of strong air currents to lift and carry them. They are extremely efficient gliders but not really good fliers; nor are they capable of bursts of speed. On the very rare calm days experienced on the island, all albatrosses are "grounded," incapable of taking off except, in rare instances when forced, by running down slopes, they launch themselves over a vertical bluff. On such calm days, catching of albatrosses for banding is easy.

### Table 1—Some Weather Records for Campbell Island, 1941-57

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean No. of Rain Days(^b)</th>
<th>Maximum Daily Rainfall(^c)</th>
<th>Duration Rainfall (hours)(^d)</th>
<th>Mean % Relative Humidity</th>
<th>Mean No. Sunshine Hours</th>
<th>Mean Wind (m.p.h.)(^e)</th>
<th>Maximum Wind (m.p.h.)(^f)</th>
<th>Mean Days of Gale(^g)</th>
</tr>
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<tbody>
<tr>
<td>Jan.</td>
<td>26</td>
<td>1.20</td>
<td>99</td>
<td>85</td>
<td>93</td>
<td>26</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Feb.</td>
<td>24</td>
<td>2.63</td>
<td>80</td>
<td>85</td>
<td>80</td>
<td>33</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Mar.</td>
<td>28</td>
<td>1.54</td>
<td>109</td>
<td>87</td>
<td>61</td>
<td>36</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Apr.</td>
<td>27</td>
<td>2.12</td>
<td>103</td>
<td>88</td>
<td>36</td>
<td>26</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>May</td>
<td>28</td>
<td>2.08</td>
<td>139</td>
<td>89</td>
<td>21</td>
<td>32</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
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<td>1.70</td>
<td>115</td>
<td>88</td>
<td>12</td>
<td>34</td>
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<td>July</td>
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<td>88</td>
<td>15</td>
<td>30</td>
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<td>88</td>
<td>27</td>
<td>34</td>
<td>41</td>
<td>7</td>
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<td>Sept.</td>
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<td>102</td>
<td>85</td>
<td>54</td>
<td>31</td>
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<tr>
<td>Oct.</td>
<td>28</td>
<td>1.65</td>
<td>102</td>
<td>84</td>
<td>67</td>
<td>28</td>
<td>40</td>
<td>6</td>
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<tr>
<td>Nov.</td>
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<td>1.50</td>
<td>110</td>
<td>82</td>
<td>89</td>
<td>31</td>
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<td>5</td>
</tr>
<tr>
<td>Dec.</td>
<td>26</td>
<td>2.41</td>
<td>91</td>
<td>82</td>
<td>99</td>
<td>32</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>Year</td>
<td>325</td>
<td>2.63</td>
<td>1,281</td>
<td>86</td>
<td>652</td>
<td>31</td>
<td>65</td>
<td>71</td>
</tr>
</tbody>
</table>

\(^a\) Wind records from St. Col Peak (984 ft above sea level); remaining records from Tucker Cove (70 ft above sea level).

\(^b\) 0.01 inch or more per day.

\(^c\) In inches.

\(^d\) At rate of 0.04 inch per hour or more.

\(^e\) Measured over 24 hours and mean for month; 1950 only.

\(^f\) Measured over 24 hours on 9 May, 4 June, 16 July, 3 August, 20 September, 2 October, and 5 November 1948.

\(^g\) Gale = 40 m.p.h. and over.

In regard to winds, Campbell Island is ideal for the albatrosses. On no fewer than 71 days of the average year winds of gale force are blowing. Calm days, i.e. days with a wind velocity less than 4 m.p.h., make up only 1 percent of the year. The mean wind velocity for the year is 30.9 m.p.h. Winds are mainly from a westerly quarter (Fig. 7).

The constant winds have many and varied effects on the flora and fauna of the island; one of their prime effects—aggravated by their high saline content—is undoubtedly that they exclude growth of trees. Even the Dracophyllum scrub is very stunted and bent where it is exposed to the wind. Alone on the windswept hills, the tussocks sway and bend in the roaring gales, but they stay; and on the rare calm days they unfold their fountain-shaped leaves in an even ring. The albatrosses usually go to the top of a flat ridge, run into the wind, and are in the air after running up to maybe 10 yd or more—depending upon the strength of the wind. On several occa-
sions I have seen albatrosses taking off straight into the air from where they stood, but only when strong gales were blowing. I have also watched unsuccessful takeoffs; the albatrosses ran into the wind, became airborne for 5-10 yd, still with their feet dangling below them, but were forced to land again due to insufficient updrift.

Another effect of the prevailing strong winds is the placement of nests. All nests are placed on the leeward slopes of ridges, in protected corries and gullies, behind stunted scrub, and on partly protected plateaus (Westerskov, 1959). The vegetation is very short on exposed slopes and provides no shelter for the albatrosses. The incubating bird, sleeping or resting on the nest, head into the wind, is rarely if ever exposed to the full force of the wind.

In spite of its southern location, very cold temperatures are never experienced. The surrounding sea, with a very uniform surface temperature ranging between 42° and 49°F., has a modifying effect, keeping the air masses passing over the island at a very uniform temperature. On only 44 days in the year has ground frost been recorded. Mean daily temperature for the year is 44.2°F.

Readings of 100 percent relative humidity are not rare. The high relative
humidity—together with the strong wind—makes the air feel uncomfortably cold. Such high air humidity is a convenient medium in which to incubate albatross eggs; and furthermore, most nests are so placed and built that the nest itself is wet, sometimes almost oozing with moisture. Consequently, albatross eggs are exposed to and probably require a very high humidity for sound embryonic development and successful hatching. The young albatrosses are brooded and guarded by their parents for 5–6 weeks after hatching, after which follows a period of about 30 weeks when the chick is left unguarded at the nest, being fed only from time to time by the returning parents. This postguard period falls from late March to early November, the coldest part of the year; the whole winter season falls within it, and it is understandable that the chicks are warmly clothed in a thick, fluffy down which is gradually replaced by an equally warm juvenile plumage, identical with that of the adult birds. The down in particular is greasy and thus capable of shedding the rain as well as preventing the constant mist and fog from penetrating to the skin. The fatness of the young birds, resulting from their rich food, also adds protection against the cold.

The precipitation on Campbell Island is 57 inches (1,425 mm) a year and comes in the form of a persistent, drizzling, never-ending rain. There are never violent downpours; the daily maximum recorded was 2.63 inches in February.

While rain is an almost daily occurrence, it also snows and hails in every month of the year, snowing on an average 41 days, mainly during May to October, and hailing on an average 63 days annually. During the winter months, June–August, snow lies on the ground for about 11 days. An annual average gives hail on 3–8 days of each month.

The peaty soil, which is the only type of soil on Campbell Island, usually is capable of absorbing the rain, and it is rare to see pools of water, except where the closely underlying rock makes drainage poor. The high humidity and frequent and liberal rain showers create a suitable climate for optimum growth of the tussock. Where the vegetation is undisturbed by man and sheep, the gradual penetration of the rainwater through the plants to the littered ground results in a gradual absorption of the water; but where sheep have created tracks in the turf or have eaten out the tussock wholly or in part, rainwater reaches the bare ground directly and small-scale erosion begins. It is fortunate, however, that the peaty turf lends itself so poorly to erosion. During days with exceptionally heavy and persistent rain, I saw on several occasions a little standing water in the trench ("moat") around albatross nests. As many days are wet days, the ground surrounding the nest as well as the nest material is often wet, and on such days the bills of the sitting albatrosses are brown and dirty with the stain of the peat from the nest improvement being carried out by the sitting bird.

Sunshine is rare. The number of sunshine hours on the ridges where the albatrosses nest is even lower than the records given in Table 1 for Tucker
Cove, near sea level. The albatross chick, moored for months on the misty ridges, is prevented by fog and rain and low clouds from receiving sunshine of any importance, and thus is deprived of the supply of vitamin D, activated from sunrays by many birds. The diet of albatrosses and their young consists primarily of fish and squid, which contain an abundant supply of vitamin D, especially needed for bone development of growing chicks.

DISTRIBUTION

Interrelated as they are, climate and the distribution of vegetation determine to a very large extent the distribution and number of albatross nests on Campbell Island. The Southern Royal Albatross is not a colonial-nesting bird, like gulls and terns; but forced by limitation of optimum sites, nests are found in certain areas in fairly close proximity. The shortest distance I have found between nests was 4 yd, but even in areas with many nests, they are usually 20–30 yd apart or more. A few pairs will nest quite a distance (some hundred yards) from other albatrosses.

During my stay on Campbell Island in 1958, I attempted to count and map the number of occupied nests and their distribution (Fig. 8) on the island, which for convenience was divided into eight districts.

1) Mt. Faye Area.—The northernmost part of the island consists of the Faye Ridge, which is the main nesting area for the Royal Albatross. On this broad spur, rising into the inconspicuous Mt. Faye (1,155 ft), a total of 465 occupied nests were counted. Much damage has been caused here by sheep; no less than 68 sheep were counted in the valley below Mt. Faye. Highest concentration of albatross nests was 12 occupied nests in an area of about an acre. The nests were mainly in small sheltered spots on both sides of the ridge, although mainly on the leeward. The ridge proper with its side gullies was calculated to cover approximately 750 acres, meaning a nest density of about 62 nests per 100 acres.

2) Mt. Fizeau Area.—South of the Faye Ridge is a high ridge running west–east from Mt. Azimuth and Mt. Fizeau. There are no albatross nests on the exposed northern and western slopes, but farther east on the ridge there were good concentrations. In all, 544 occupied nests were found, located between 700 and 1,100 ft above sea level. On the eastern slope of Mt. Azimuth, nests were found up to an altitude of 1,300 ft.

3) Mt. Lyall Area.—The Lyall Ridge runs west–east, and north of Perseverance Harbour. Its northern and southern slopes are both steep and exposed and shelter only few albatross nests, but on the flat ridge and plateau farther east, many nests were found, totaling 321 for the area.

4) Moubray Hill Area.—This eastern extension of the Lyall Ridge, terminating in Moubray Hill (808 ft), where a few pairs of Wandering Albatrosses (Diomedea e. exulans) nest, is a fairly low plateau, windblown and partly
Fig. 8. Distribution of Royal Albatross nests on Campbell Island. Each dot denotes an occupied nest, 1957-58 breeding season. Contours are 100-ft contours.

eroded and with many waterlogged, peaty areas. In sheltered corries and behind protecting scrub a total of 233 nests of the Royal Albatross were located.

5) St. Col Ridge Area.—Linking the northern and southern halves of the dissected island is the Col Ridge. The seaward side is steep and battered by wind and erosion, but the eastern slopes are more gentle and tussock-

covered. As Dracophyllum scrub grows from the valley bottom high on the slopes, nest sites are confined to the upper parts, above the scrub. A total of 98 nests were found.

6) Mt. Paris Area.—The western peninsula, thrusting into the fierce westerlies, is crowned by Mt. Paris (1,526 ft) and Yvon Villarceau Peak (1,100 ft), rising directly from the sea. This part of the island is inhospitable, and only small colonies of Royal Albatrosses cluster on sheltered east-facing slopes and the protected plateau farther below. In all, 99 nests were located throughout this area.

7) Mt. Dumas Area.—Southwest of the inner arm of Perseverance Harbour the impressive peak of Mt. Dumas shelters a system of basins, providing nest sites for albatrosses. In altitudes between 500 and 1,100
ft above sea level, scattered colonies were found, a total of 137 nests being located.

8) **Mt. Honey Area.**—South of Perseverance Harbour, Mt. Honey (1,867 ft) rises, its gently sloping peak providing sheltered basins and protected flat ridges to the east and south. In many of the gullies and basins, good nest sites for albatrosses were found. Total number of occupied nests located was 381. Much damage to the vegetation has been wrought by sheep, which are still plentiful in this area.

The total number of occupied nests that I found on Campbell Island in 1958 was 2,278. Nests have unquestionably been overlooked in such difficult terrain where the nesting albatrosses prefer the corries and other small depressions for their nest sites. It would appear that approximately 2,300 pairs of Royal Albatrosses nested on Campbell Island during the 1957–58 breeding season.

**TOTAL POPULATION**

With approximately 2,300 pairs of Royal Albatrosses nesting on Campbell Island in any one breeding season, one may conclude that—based on the assumption that the breeding population is a constant one—the total number of adult Southern Royal Albatrosses of breeding age is about 4,600 pairs, or slightly less. The detailed studies by Sorensen (1950) and Richdale (1950, 1952) have clearly shown that Royal Albatrosses breed in alternate years only, and the length of their complete breeding cycle is some 12–14 months, thus preventing annual reproduction. As only nine pairs of Royal Albatrosses were found nesting on the Auckland Islands in 1962–63 (Brian Bell, pers. comm.), this number can be absorbed into the one above, so that the figure given is in effect the approximate total world population of breeding Southern Royal Albatrosses. The preservation of Campbell Island in as natural a state as possible is therefore of prime importance to safeguard the welfare and future of this unique and beautiful bird.

In order to assess the total world population of the Southern Royal Albatross, including the year-classes of nonbreeding young birds, we must be in possession of certain basic biological facts.

**Breeding Age and Sex Ratio.**—Only little information is available about the age when the albatrosses first breed. Richdale (1950, 1952) studied the Northern Royal Albatross on Taiaroa Head (near Dunedin) between 1936 and 1952. After 1952, intensive work on this small colony, including continued banding and observation, was taken over by a field officer, S. Sharpe of the Department of Internal Affairs; under my supervision for most of this period, he has collected much useful information. The return of birds banded as young in this colony has shown that Royal Albatrosses on the average commence breeding when 9 years old; some females have returned and bred while 8 years old, males when 9 and 11 years old.

The sex ratio in the albatross population is but little known. Sexing
of 40 sitting albatrosses by external characteristics (Westerskov, 1960) showed that 23 were females, 17 males. In the breeding population, however, a 50:50 sex ratio is necessary not only because both sexes share fairly evenly in incubation, brooding, and chick-feeding duties, but also because divided parental care is a simple necessity for the successful incubation and raising of a young albatross.

**Breeding in Alternate Years.**—The fact that breeding takes place only every other year is evident from a brief review of the complete breeding cycle and from field observations of banded birds.

Pairs of Royal Albatrosses return to Campbell Island in October; courtship display and nest building go on throughout October and November; egg laying takes place from late November to early December; hatching—after an incubation period of 79 days—occurs from late February to early March; and the young birds leave the nests in October and November. Sorensen (1950) found a late chick unable to fly as late as 6 December.

The breeding seasons of the two biennial breeding populations overlap at both ends: There are still some almost fully grown fledglings left from the previous season’s breeding population when the new breeders come to the island to commence their courtship displays in October, and before their offspring have left in the following year, the alternate breeding population has returned.

**Clutch Size.**—The Royal Albatross lays only one egg in a season. I checked the contents of 390 nests on Campbell Island and found only one egg per nest. Our experience on Taiaroa Head shows that Royal Albatrosses do not lay another egg in the same season if the first egg is destroyed. Such a female, however, will return to nest the following season, and thus becomes out of phase with the usual members of her breeding cohort.

**Egg and Chick Mortality.**—The albatrosses have few, if any, enemies on Campbell Island when they are left undisturbed by man. Southern Skuas (*Stercorarius skua lÖnbergi*) swoop down and steal the egg if the sitting albatross has been forced from its nest by man. Under the somewhat unnatural conditions at Taiaroa Head, of 48 albatross eggs laid between 1951 and 1959, 7 were lost; and of 41 chicks hatched, 19 were lost, giving a survival percentage of 46 from egg to leaving stage. Such relatively poor survival is undoubtedly a result of man, directly and indirectly. One egg was stolen by man, 5 chicks died as a result of human interference, 2 were killed by cat, 6 killed by dog, and 2 chicks were killed by ferret—this in spite of vigilant watching by conservation officers. Such man-induced mortality would not occur on Campbell Island.

On Campbell Island I was able to obtain data about the fate of 101 occupied nests. Colonies near our camp were selected and thanks to the good cooperation of one of the meteorological station staff, Eric Clague, these nests, which he and I first visited in January and February 1958, were
revisited by him in July and October of that year. Of 101 eggs, 6 were lost; of the chicks, 13 were lost, and it could not be determined whether an additional 7 disappeared as eggs or chicks. Thus, 75 chicks were successfully reared and left the island: approximately a 75 percent survival from egg to flying stage.

**Total World Population.**—Based on these collected facts—number of breeding pairs, breeding interval, mean first breeding age, sex ratio, clutch size, and egg and chick mortality—it is possible to construct life tables and calculate the approximate total world population of the Southern Royal Albatross. For advice with the following statistical calculations, I am grateful to P. Whittle, Manchester University, formerly of Applied Mathematics Laboratory in the Department of Scientific and Industrial Research at Wellington.

The basic biological facts used in these calculations are: (1) a breeding population in any one year of 2,300 pairs, (2) each pair breeds every other year, (3) birds start breeding at 9 years of age, (4) equal number of males and females in population, (5) only one egg is laid in each breeding cycle, and (6) combined egg and chick mortality amounts to about 25 percent of the eggs laid. Furthermore, it is assumed that: (1) after the first year of life, mortality is constant, and (2) the population maintains itself at a more or less constant size.

If \( a \) is the proportion of birds that survive to the stage when they can leave the nest, and \( b \) is the proportion of birds that survive a given year (adult mortality is assumed here to be independent of age once the bird has left the nest), then the proportion surviving to at least the \( j \)th year will be:

\[
ab^{j-1}
\]

since a bird \( j \) years old will have spent roughly \( j - 1 \) years away from the nest. The expected number of eggs from a particular female bird (this expectation being taken from the time when the bird is itself a newly laid egg) is:

\[
a(b^8 + b^{10} + b^{12} + b^{14} + \ldots) = \frac{ab^8}{1 - b^2}.
\]

If the total population size is not changing, then this figure must be 2 because on the average a pair will just replace itself.

As egg and chick mortality is 25 percent, \( a = 0.75 \). Supposing, as above, that the expected number of offspring is 2, then we must have:

\[
\frac{(0.75)b^8}{1 - b^2} = 2.
\]

This equation for \( b \) has a solution \( b = 0.909 \), indicating an annual mortality for birds that have left the nest of \( 100(1 - 0.909) = 9.1 \) percent.

The total number of eggs laid in a year is known to be 2,300, from which is inferred that at any time the expected number of birds in the \( j \)th year of
life is \(2,300a^{j-1}\), so that the total number of living birds that have left the nest is:

\[
2,300a(1 + b + b^2 + \ldots) = \frac{2,300a}{1 - b}.
\]

With a combined egg and chick mortality amounting to 25 percent, the total population is calculated to be 18,960 birds.

A life table (Table 2) has been calculated for a considerable period, but presumably the failure of the assumption of constant mortality will invalidate the latter part of the table.

**Table 2.—Life Table for Southern Royal Albatross, Campbell Island, Based on a Combined Egg and Chick Mortality Amounting to 25 Percent and Other Facts as Discussed in Text**

<table>
<thead>
<tr>
<th>Age in Years</th>
<th>Number of Birds</th>
<th>% of Total Population</th>
<th>% Surviving to Given Age</th>
<th>Age in Years</th>
<th>Number of Birds</th>
<th>% of Total Population</th>
<th>% Surviving to Given Age</th>
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<td>9.1</td>
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</tbody>
</table>

\(^a\) Eggs.

A number of interesting facts on the life equation, age composition, and total numbers of the population of Southern Royal Albatrosses emerge from this material.

It appears that the total population of Southern Royal Albatrosses, i.e. young in nest and all juvenile (nonbreeding) and adult birds, consists of about 19,000 birds. The proportion of nonbreeding albatrosses, i.e. birds from 1 to 8 years of age, is 53 percent, while 47 percent of the birds that have left the nest survive to maturity and breed, i.e. reach the age of 9 years or more.
Both the findings of Richdale (1950:64) and our own data procured from Taiaroa Head since 1951 indicate that young Royal Albatrosses are away from their breeding ground for approximately 5 years; this means that approximately 38 percent of the total albatross population (= ca. 7,200 birds) are away, roaming the South Pacific and the waters along both the Pacific and Atlantic coasts of South America. Consequently, the number of not-yet-breeding albatrosses—the ones seen displaying on the “gams” on Campbell Island—should amount to a little less than 3,000 birds. It was my impression that the number of such unattached birds was somewhat lower—indicating that only a proportion of these young birds was present—although several hundred such birds were seen on several preferred resting grounds. The unattached birds present, based on my notes, probably numbered about 1,500–2,000. In addition to the segment of the not-yet-breeding year-classes, non-breeding adults are also away from Campbell Island.

When the first eight nonbreeding age-groups are subtracted from the calculated total population, it appears that a total of about 2,210 pairs of breeding albatrosses lay every other year, together with some renesting birds from the previous year, making a total of some 2,300 pairs nesting in any 1 year. The proportion of the population actively engaged in breeding at any one time is about 24 percent.

The annual mortality of the albatrosses—after the nest period—is approximately 9 percent. One may conclude that Royal Albatrosses are very long-lived, probably among the most long-lived birds in the world, and theoretically (Table 2) may reach the age of 80 years. It is significant that many albatrosses survive for a considerable time: 9 percent to ages of 25 years or more.

SUMMARY

In 1957–58, about 2,300 pairs of Diomedea e. epomophora nested on Campbell Island, 52°30’ S, approximately 450 miles south of Dunedin, New Zealand. Strong winds, which are essential for the birds to take off, averaged 30.9 m.p.h. for the year. Young birds are well adapted to the persistent rains that occur on about 325 days of the year, and nesting success was 75 percent. Tussock (Danthonia, Poa) has been greatly modified on the 42-sq-mile island since sheep were introduced in 1896, and nesting places for albatrosses have been restricted by Chrysobactron rossii, which has spread as the result of overgrazing. On the assumption that the 75 percent nesting success found in 1957–58 is typical and that the young attain an adult mortality rate once they leave the nest, it is estimated that the annual adult mortality rate is 9 percent and that the total population of this subspecies is about 19,000 birds, almost half of which are nonbreeders less than 8 years of age.

LITERATURE CITED

Populationsuntersuchungen am Weissen Storch (Ciconia ciconia)
in SW-Deutschland

Gerhardt Zink
Vogelwarte Radolfzell, 7761 Schloss Möggingen, Deutschland


Abbildung 2 und 3 zeigen die Verteilung der Brutpaare in Baden-Württemberg in vier verschiedenen Jahren. 1948 war ein Jahr mit ungewöhnlich


Gerhardt Zink: Populationsuntersuchungen am Weissen Storch

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Die Kreise (O) der Abb. 2 und 3 bezeichnen Storchpaare, die keine erfolgreiche Brut machten. Darunter sind sowohl Paare, die Eier oder Junge verloren haben, wie auch solche, die zwar längere Zeit ein Nest besetzt hielten, aber keinen Versuch zur Brut machten. Ringkontrollen weisen darauf hin, dass in diesen Fällen meist mindestens einer der beiden Partner zu jung für eine erfolgreiche Brut ist. Diese nichtbrütenden Paare finden sich meist in Nestern am Rande der Verbreitung oder in Nestern, die schon längere Zeit nicht mehr besetzt waren und deshalb vermutlich weniger günstig gelegen sind. 1961 waren 18 von 21 nichtbrütenden Paaren in solchen "Randnestern.” Diese Vögel brüten in den folgenden Jahren nur selten im gleichen Nest. Fast immer siedeln sie für ihre erste Brut um in günstigere Lebensräume. Das liegt wahrscheinlich daran, dass die Nicht-Brüter noch nicht ebenso ernsthaft um die Nistplätze kämpfen wie die älteren Störche, und dass sie deshalb nur dort sesshaft werden können, wo die Konkurrenz weniger stark ist. Für ihre erste Brut setzen sie sich dann aber auch in den günstigeren und daher mehr umworbenen Lebensräumen durch.

Das sind wenige Beispiele aus einer Arbeit, die für einen längeren Zeitraum geplant ist und durch die Verbindung von Bestandsaufnahmen mit der Ringkontrolle des Brutbestands noch weitere wertvolle Ergebnisse zu liefern verspricht.

SUMMARY

Population Studies on the White Stork (Ciconia ciconia) in Southwestern Germany

Investigations have been carried out in two ways: census work in a wide area and observations of banded birds in the same area, all breeding storks having been checked each year. About one-third of the breeding population of 1962 was banded. Maps and diagrams show the population changes over a period of 14 years in two different areas, not along political boundaries as
in previous papers but conforming to two different habitat groupings. One is the center of distribution in southwestern Germany along the Rhine Valley, showing fluctuations about its mean with no significant decline; the other, in more hilly or dry country at the edge of the stork’s distribution, shows heavy losses, many areas being abandoned entirely.

Sight records of banded birds explain the difference between these two groups. In the first group (in Zone A) about 70 percent of the storks settle for their first breeding within 50 km of their place of birth. In the second group (in Zone B) the average distance is 86.5 km, only 1 out of 6 being closer than 50 km and remaining in the same zone. Therefore, most birds of the second group emigrate to more favorable areas, whereas birds of the first group usually remain within their zone. Emigration from this group may also occur but is almost always to more distant favorable zones rather than to Zone B.

Evidence is presented that some subadult storks occupy nests but do not breed. These birds are frequently found at the edge of the geographical range of the species or in otherwise relatively unfavorable sites. These non-breeding birds move to more favorable sites where they breed as adults. An explanation may be that the non-breeding birds are not as strongly motivated to acquire favorable nest sites as are the adult birds, and therefore they are unable to compete successfully for the better sites.

LITERATUR


Population Systematics in Bird Conservation

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Population systematics as characterized by Mayr (1959) is the classification of species in terms of their component populations which tend to differ from one another in different parts of their range. This involves the determination of morphological, physiological, and behavioral differences between populations within species and the correlation of these with the isolating and selection factors in the environment that produce and maintain them.

Bird conservation is defined in the present discussion as the process of managing populations of all species of birds to obtain optimum numbers and distribution for maximum enjoyment, utilization, and conformance with economic requirements of human populations. With the rapid increase of human populations, this obviously is becoming an increasingly more complicated problem.

PURPOSE

The purpose of this paper is to call to the attention of the conservationist the potential usefulness in wildlife management of a knowledge of the ecological, physiological, and behavioral characteristics that may be associated with morphological variations of population segments within species.

Although recognizing that geographical isolation facilitates the establishment of new heritable characteristics in a population, there is much evidence that adaptation to environment through natural selection of genetically produced variations is the chief process by which biologically different population segments of species are formed (Huxley, 1938; Thorpe, 1945; Mayr, 1951; Miller, 1956). Furthermore, physiological and behavioral characteristics are frequently linked with the morphological variations (Mayr, 1951; Ross, 1962). Therefore, critical study of morphological variations within species at the subspecific level or below may give clues to the physiological and behavioral as well as morphological characteristics that are being selected by the environment. This knowledge in turn may indicate what the most critical factors in the environment are that are selecting the observed characteristics and which at the same time may be controlling the size and distribution of the population. Wildlife-conservation programs are particularly concerned with such factors and thus should utilize clues that may be discovered through the study of racial or ecotypical variants within species and apply them to the study of population management.

EVIDENCE FOR ADAPTATION TO ENVIRONMENT

The so-called Bergmann's, Allen's and Gloger's rules governing the relationship of climate to size and color variations of warm-blooded animals are

well known. Mayr (1956) has recently reviewed and elaborated on these. Hamilton (1961) has further developed the concept of the adaptive significance of trends in size of birds in relation to climate.

Plant ecologists for a long time have recognized the importance of the combined climatic factors of temperature and moisture in controlling the distribution of plants of particular life form, such as coniferous forest, deciduous forest, grassland, and desert scrub. Animal ecologists are in general agreement that the distribution of animal species conforms, to a large extent, to the limits of those climax plant aggregations that characterize the areas of different combinations of climatic factors (Clements and Shelford, 1939; Pitelka, 1941; Kendeigh, 1961). In addition, the infraspecific (racial) variation of animals also tends to conform to the limits of these major ecological subdivisions.

Pitelka (1941) has commented that the species showing variations between climax areas are not necessarily those confined to the climax habitat. They may occupy the climax habitat in one area and a seral habitat in another. For example, one race of the Ovenbird (Seiurus aurocapillus) occupies deciduous forest of both climax and seral stages in the eastern part of North America and another race occupies only the deciduous seral stages of mountain coniferous-forest climax in the West. Pitelka further pointed out that geographic variation occurs chiefly in those species, such as Ruffed Grouse (Bonasa umbellus) Sharp-tailed Grouse (Pediocetes phasianellus), Downy Woodpecker (Dendrocopos pubescens), Song Sparrow (Melospiza melodia), and Screech Owl (Otus asio), ranging broadly over areas with several climax types. Miller (1956) noted these same correlations in analyzing the ecological distribution of birds in California. He further commented that, although the races of vertebrates are not precisely like those ecotypes of plants that tend to occur wherever a particular ecological situation is present, they do resemble plant ecotypes in that they have evolved distinctive characters adapted to ecological conditions, but the adjustment seems to be related to a considerable range of such conditions. These conclusions are based on the relationships of named subspecies and their ecological distribution. A more critical study of morphological differences in populations correlated with areas characterized by different ecological climax would probably reveal greater agreement than has been demonstrated so far.

If we compare specimens representative of the different major ecological climax areas of North America, based on climax vegetation, we find that Ruffed Grouse from the dripping, mossy, dark-barked rain forest of the Olympic Peninsula in the northwestern United States are dark mahogany brown, whereas those from the dry, light-barked aspen growths of the Rocky Mountains in Wyoming are pale gray. This same general color difference, correlated with the same life areas, is repeated in a number of other species, such as the Blue Grouse (Dendragapus obscurus), Song Sparrow, Fox Sparrow (Passerella iliaca), and Red-shafted Flicker (Colaptes cafer), even
though they have quite different habits and habitats. Grinnell (1910) noted this same difference in birds from the humid coast of Alaska and interior situations. Thus, it appears that this sort of correlation occurs in a definite geographical pattern involving species of diverse ancestry and habits, and suggests a factor or combination of factors in the environment of that area which select the same characteristics in different species for perpetuation in that population. Examination of specimens representing these same species from ecologically intermediate (not necessarily geographically intermediate) climax areas discloses intermediate color characters that are correlated with the degree of difference in the environment.

Furthermore, there is frequently a convergence of characters in populations of birds of the same species in relatively similar environments on opposite sides of the North American continent, which are separated from each other by much more distinctly different-appearing populations exposed to the quite different environments of the interior regions. A few examples are Black-capped Chickadees (*Parus atricapillus*), Ruffed Grouse, Robins (*Turdus migratorius*), Song Sparrows, Gray Jays (*Perisoreus canadensis*), Horned Larks (*Eremophila alpestris*), and Meadowlarks (*Sturnella magna* and *S. neglecta*).

One of the most convincing lines of evidence for the importance of ecological factors in guiding morphological variations is that, in geographic areas of the greatest ecological diversity, morphological variation is also greatest. This may be the case even though there are no more physiographic barriers to contribute to disruption of gene flow in that area than in others of greater ecological and morphological uniformity.

Marked morphological differences can occur in relatively short distances if sharp differences in environment occur. Examples are: differences between the appearance of Bobwhite Quail (*Colinus virginianus*) on the Wabash River bottomland and those of the surrounding uplands in Illinois, noted by Robert Ridgway (1895); the case of Song Sparrows of marsh and upland habitats in the San Francisco Bay, California, area (Marshall, 1948a, 1948b); variation in the Song Sparrow in mountain and desert associations in southwestern Utah (Marshall and Behle, 1942); color differences in Crested Larks (*Galerida cristata*) living on soils of different colors in Egypt (Moreau, 1930); apparent protective coloration of birds on desert soils in Arabia, discussed by Meinertzhagen (1950); a similar situation in Horned Larks on different-colored soils in North America, described by Behle (1942); and differences in Rock Partridges (*Alectoris graeca*) noted by Watson (1962) at different altitudes in the mountains of southern Turkey.

Friedmann (1946) has called attention to the multitude of instances of convergence in morphological, ecological, and behavioral characteristics of representatives of different taxonomic groups of birds occupying similar niches, but in different continents. Some examples cited were the resemblance of the American meadowlarks (*Sturnella*) and the African pipits
(Macronyx), some African species of weaver-birds (Ploceidae) and some American troupials (Icteridae), some South American tanagers (Tanageridae) and some North American finches (Fringillidae). These cases of parallelism of unrelated species that fill similar ecological niches are strong evidence of the potency of environment through natural selection in molding the morphology and behavior of birds. A study of the characteristics that these species have in common would suggest which ones are of importance to their survival.

There has been very little experimental work with birds to find out how certain population characteristics are produced through natural selection or their survival value. Avian taxonomists have been engrossed in describing the differences and naming the recognizable populations. Avian ecologists have been involved with studying the species composition and interrelationship of biotic communities, and in measuring environmental factors. The study of the relationship between these disciplines in the dynamics of speciation in birds has barely begun.

A few cases where higher vertebrates have been viewed experimentally from the ecotypical standpoint might be mentioned. Sumner (1925) and Blair (1950) found correlation between color of various species of deer mice (Peromyscus) and the hue of the soil on which they lived. Blair went further and found a correlation between the frequency of genes giving color to animals most closely resembling the soil color and the actual distribution of the mice. A recent study of great significance in this field is that of Bowers (1960), which demonstrated a correlation between the variation in color in Wrentits (Chamaea fasciata) and their environment. These little birds apparently exhibit very definitive ecotypical variations. The shade of brown in their plumage varies with the general tone of the background in their habitat from the dark-stemmed, close-growing chaparral of the more humid Pacific Coast to the light-stemmed, more open brush of the more arid interior valleys of California. However, we are still left with the unanswered question of why this correlation exists. A unique experiment to show the relative frequency of capture by owls of deer mice placed on backgrounds contrasting with the mouse’s pelage color in varying degrees was performed by Dice (1947). The experiment suggested that predation may be a significant mechanism producing natural selection for color in the higher vertebrates. There is need for a great deal of controlled experimental work on this and other possible selection factors.

PROCESS OF POPULATION CHANGE

The significance of habitat in the evolution of birds has been discussed by a number of authors, including Stresemann (1943), Thorpe (1945), Mayr (1947), and Miller (1942, 1955, and 1956). The first small adaptive changes probably come about mainly through exploration and extension of ranges of species into appropriate unoccupied niches in new areas of different
ecological types. Presumably this is by young individuals that have not nested before and become attached to specific sites, and which, therefore, are thought to be the pioneers in range extension. Extension of range is a complicated ecological process involving not only adaptation to the physical environment, but competition with other species occupying related ecological niches in the new environment. Stresemann (1943), Thorpe (1945), Gause (1947), Mayr (1951), and Miller (1955, 1956) believe that most distinct populations are started by individuals that are able to adjust themselves (nongenetically) to new conditions when colonizing a new region. Once such a population comes to occupy a new environment, a new set of selective factors will operate to reconstruct this population genetically.

Miller (1955) analyzed the rather considerable amount of data on the population dynamics and infraspecific variations in Song Sparrows. He concluded that random or chance fixation of genes was responsible for the initial variations noted in populations, and that in some distinct-appearing island populations this is the only obvious cause of the difference. In the continental populations, however, he noted what appeared to be ecologically controlled variations superimposed on the random variation. He favored the idea that natural selection is aided and accelerated by the availability of a local group of Song Sparrows possessing a considerable proportion of beneficial genetic traits acquired partly by chance, rather than by the occasional individual with slightly favorable characteristics which must be selected from a large population of less well-endowed individuals.

Although agreeing that genetic change after extension of range is the general situation, Mayr (1951) qualifies this by stating that in all cases of explosive range expansion, such as have occurred in the Serin Finch (*Serinus serinus*) and the Ringed Turtle Dove (*Streptopelia decaocto* [= *risoria*]), there is reason to believe that this expansion followed a genetic alteration of the peripheral populations, as postulated by Aldrich (1946). Actually, evidence is lacking as to which of these sequences is most frequently the case. However, it would seem that successful adaptation of a bird species to a new environment may be like the development of tolerance of insect species to an insecticide. A few mutants that can survive in a different environment eventually arrive there, and a new, adapted population develops from them.

Salomonsen (1955) calls attention to the different ways environment may act as a force of natural selection, depending on how populations are isolated from one another. He points out particularly that adaptive characteristics of migrant species must be in harmony with both winter and summer quarters. In some, winter conditions seem to be more important as selective forces, and in others the breeding-ground conditions. In some species, populations tend to mingle on the wintering grounds, as in the case of Savannah Sparrows (*Passerculus sandwichensis*) (Norris and Hight, 1957), and others tend to be separated. The interesting cases of leap-frog migration cited for Fox Sparrows by Swarth (1920) and for Yellow Wagtails (*Motacilla flava*) by
Stresemann (1943), in which the more northern breeding population winters farther south than the more southern breeding group, are examples of the latter.

**RELATIONSHIP OF MORPHOLOGICAL, PHYSIOLOGICAL, AND BEHAVIORAL CHARACTERISTICS**

Extremely pertinent to the thesis presented in this paper is the fact that physiological and behavioral differences frequently accompany morphological variation. It is not necessarily the morphological character that is adaptive but rather the underlying gene. The same gene may produce not only the visible conditions but also all sorts of invisible physiological processes which may have very pronounced selective properties (Mayr, 1951). Rigid artificial selection for long-leggedness in chickens was found in one instance to result in reduced rate of reproduction because of genetic linkage of these two characteristics (Ross, 1962). This suggests that reduced rate of reproduction in small populations of certain wild bird species may result from genetic linkage with some factor that is being subjected to intense natural selection. Innumerable cases of such character linkage have been discovered in the exhaustive genetic experiments with the insect group *Drosophila*.

There are many examples of morphologically distinct variants of bird species that also have distinct physiological or behavioral characteristics. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific Coast of North America have a sedentary population (*nuttalli*) in the San Francisco Bay region and a migratory one (*pugetensis*) nesting from northern California north to southern British Columbia (American Ornithologists' Union, 1957). In Canada Geese (*Branta canadensis*), different breeding populations have differentiated spectacularly in size, color, voice, nesting sites, nest structure, and migration season. Movement of these populations has resulted in bringing two very different forms into close proximity on the Yukon Delta, Alaska, and southern Baffin Island, but apparently without interbreeding in either case (Sutton, 1932; Soper, 1946; Aldrich, 1946; Mayr, 1951.)

Ecotypical differences in populations may be entirely in physiology or in habits, without morphological manifestation. Lack (1947) shows a correlation between (a) the number of eggs laid by individual birds of the same species and (b) the climate. Larger clutches are laid in the cooler, more northern parts of the range. Brooks (1940) and Kendeigh (1945) describe differences in nesting habitat chosen by different populations of certain species of New World warblers with no detected morphological variation. However, it should be noted that the observers did not mention any study of specimens to determine whether or not morphological differences existed. Slight differences in color, size, or proportions correlated with ecological distribution can be easily overlooked. For many years this was the case in the eastern populations of the Traill's Flycatcher (*Empidonax traillii*). This
species had been noted by field ornithologists to have different songs and types of nests long before the discovery that these habits, as well as prairie and boreal forest distribution, were correlated with slight morphological differences (Aldrich, 1951, 1953; Snyder, 1953; Stein, 1958).

In another instance of this sort, Bullough (1942) explained the differences in the physiological cycles of the resident British population and the migratory continental population of the European Starling (*Sturnus vulgaris*). The difference in the reproductive cycles of these two populations was considered to be the basis for all the other differences in habits and morphology. The continental Starlings reach a peak of gonad development much later than the British birds. The white tips to the feathers wear off on the underparts of British individuals sooner than the continental ones because of abrasion from entering winter roosting cavities, which are not used by continental birds. The beaks of British Starlings turn yellow in the autumn and not until February in continental examples. Thus, all differences between these two geographically distinct populations were thought to be either physiological, behavioral, or due to mechanical wear. However, even with this well-studied species which had been thought to show physiological differences in two populations without morphological manifestations, there is evidence that a slight color difference between them might have been overlooked in the earlier observations, since Meinertzhagen (1947) has mentioned a more purplish color of the heads of British Starlings.

**SIGNIFICANCE TO CONSERVATION**

What is the significance of all this to conservation? Knowledge of the process of natural selection of adaptive characteristics in the process of speciation is important in understanding the factors that control occurrence or abundance of a species. If a factor is critical enough to bring about evolutionary change within species through natural selection, it would seem likely that it can be critical also in controlling the distribution and abundance of that species. Having been molded by such exacting environmental forces into a special form adapted to a particular ecological situation, it is reasonable to suppose that such an adapted population segment might not thrive in a distinctly different environment as long as it possesses these modifications (Aldrich, 1946). This has been demonstrated in the case of attempted Bobwhite and Turkey (*Meleagris gallopavo*) transplanting in Georgia and Texas, respectively, and in the case of innumerable foreign bird species introduced unsuccessfully into North America. This concept should be considered in research designed to locate any species and particularly subspecies and ecotypes of game birds for transplanting into new territory or areas of former occurrence. The principle should always be to find species and their populations that are preadapted to the particular ecological niche to be filled. Whenever introductions occur, specimens should be preserved as a permanent record of the morphological characteristics of the stock that was
introduced so that these may be correlated with the records of success or failure and thus will be of use in the future.

Examples of putting this principle into practice in wildlife management may be cited. The U.S. Fish and Wildlife Service is attempting to develop new breeding populations of Canada Geese on its wildlife refuges where the species does not nest at present. To do this, it is trying to use birds of the same subspecies that formerly nested in the area or those with habitat most similar to the area to be stocked. Also this Service is cooperating with the International Association of Game, Fish and Conservation Commissioners and with many states in a program of selecting geographical races of foreign game birds that are preadapted to presently unfilled ecological niches in the United States. Certain state game farms are going even farther and crossing races of these game birds in hopes of obtaining genetic types that will be better adapted than already existing stock. This is experimentation in the dynamics of speciation, attempting to find a shortcut to the long processes of evolution through natural causes. Nature works on such problems strictly by trial and error, but has the virtue of persistence. Man, through population-systematics studies, may be able to improve on nature's method by facilitating the arrival of the stock most likely to succeed at the right place for establishment.

There is much need for additional experimental breeding of different species, geographic races, and ecotypes of birds of special interest from the conservation standpoint. This should involve the study under controlled conditions of behavioral and physiological differences that are correlated with morphological differences, also of environmental factors that may be limiting to distribution or function in selection of new characters. Great strides have been made in producing desired characteristics of plumage, size, shape, egg laying, and temperament in domestic birds through artificial selection in captive breeding. A similar approach with captive wild stock offers a great challenge. Captive rearing of two races of the Sandhill Crane (*Grus canadensis*) being conducted currently by the U.S. Fish and Wildlife Service, as well as many private avicultural ventures, provide opportunities to obtain this sort of information.

The conservation of migratory birds is particularly complicated by the difficulty of determining the migratory movements of the various segments of the population within each species. Much has been learned of the migrations of some of these population units through banding representative individuals. In certain circumstances where banding is not feasible, another possible approach is the identification and recording of representatives of these populations when found away from their breeding area. Identification would be by the distinctive characteristics of size and color which we may learn to recognize as representative of a particular geographical or ecological region. Aldrich and Burleigh (unpubl. MS.) demonstrated that the abundant Lesser and rare Greater Sandhill cranes (*Grus c. canadensis* and *G. c.*
tabida) have different migration patterns, permitting hunting of the former without endangering the latter. By collecting large series of specimens, Kalmbach (pers. comm.) determined that Red-winged Blackbirds (*Agelaius phoeniceus*), causing damage to rice crops in southwestern Louisiana during the ripening period, were the resident coastal group, whereas blackbirds that caused damage to shocked grain in the fall were mostly migrants of northern groups. By identifying subspecies of Mourning Doves (*Zenaida macroura*) in hunters’ bags in southern Florida, Aldrich (1952) determined that these birds had come almost entirely from breeding areas in the United States rather than the West Indies, as had been supposed. This discovery resulted in modification of hunting regulations. Norris and Hight (1957) identified races of Savannah Sparrows caught in mist nets in ecological studies near Savannah, Georgia, as coming from several widely separated sections of North America. It has been conceived by some that such studies may be useful in geographical delineation of activity of certain viruses carried by birds.

In addition to recognizable morphological differences as indicators of distinct populations, we have evidence that identification of serological differences may be a rewarding approach to population systematics, and one that might become an important tool in wildlife management. Although not yet demonstrated with bird populations, Fujino (1962) found differences in blood types of certain populations of Antarctic whales, and Ridgway (1962) and Sindermann (1962) were able to detect serological differences in populations of fish species of commercial significance.

Preservation or creation of habitat suitable for the support of a desired species is one of the recognized methods of birds conservation. Obviously, differences in habitat requirements of different population segments of a species would be vital information to such a management program. Since variations in environment are important factors in the process of population differentiation, study of the way species vary morphologically through natural selection by the environment may give clues to the existence of physiological and behavioral differences in these population segments that will lead to a better understanding of habitat requirements. This would be of value in important programs of land acquisition for habitat preservation.

**PROCEDURES**

In the course of future studies of this sort we are confronted with correcting inadequate methods of indicating differences in populations which might be of significance in their management. Sibley (1954) described very well the inadequacy of trinomial nomenclature for indicating variation in infraspecific populations. This has been of growing concern to students of population systematics, and no adequate solution has been found. The general practice has been to use the formal trinomial for obviously different populations with at least 75 percent of the individuals of one distinct from
99+ percent of all others (Amadon, 1949), and merely to refer to variations within this population, including character clines of Huxley (1938), in a descriptive way. The lack of uniformity in formal description and naming of subspecies, so poignantly described by McAtee (1941), is definitely a drawback to using present nomenclature for designating the sort of meaningful adaptive differences of interest in the present paper. To be useful for management purposes, it will be necessary to work out units that group individuals with morphological differences, no matter how slight, that are correlated with ecological distribution or other factors of importance in species management. As Sibley (1954) and others have pointed out, it is undesirable to clutter up the standard trinomial nomenclature further by attempting to give each of these variants a formal name. Furthermore, it would be too cumbersome for use in management. It would be preferable to use a series of numbers or short descriptive phrases to indicate the units of interest.

In consideration of the foregoing, it seems reasonable to presume that a thorough study and classification of morphological variations through analysis of present specimen collections which can be associated with exact habitat conditions will suggest many patterns of ecotypical variation. Judicious collecting of additional specimens accompanied by precise data on environment will be necessary in most cases to establish definitely these relationships. We need more study of the correlation of variations with environment to learn which are adaptive and thus give clues as to the critical factors in the environment that control survival and distribution. When critical morphological studies are correlated with ecological, physiological, and behavioral information on the various ecotype populations, good basic biological knowledge of the species of great practical value to the wildlife manager will be at hand. Although quite different in approach from the Linnaean typological sort of systematics, neo-Darwinean population systematics still depends upon the museum study specimen as a basis for much of the necessary morphological information. Thus can research in population systematics in natural-history museums contribute in the future to basic information necessary for sound procedures in bird conservation.

**SUMMARY**

Population systematics classifies species in terms of population isolates, thus stressing the differences between populations within species. Adaptation to environment through natural selection of genetically produced variations is the chief process by which biologically different populations are formed. Visually distinct populations tend to be limited to the areas of distinct ecological climaxes. Marked morphological differences can occur in relatively short distances if there are sharp differences in environment. Genetic change in populations may involve extension of range of a species into new environment. Migratory populations must be adapted to both winter and summer ranges to survive. Adaptive physiological and behavioral differences fre-
quently accompany morphological variation. Knowledge of adaptive variation in physiology, behavior, and morphology of populations aids selecting appropriate stock for introduction. Recognition of morphological and serological characteristics of populations is useful in following their movements. Population systematics needs a system of designating populations without dependence on the straitjacketed and cumbersome standard systems of trinomial scientific nomenclature. Study and classification of morphological variations of populations within species correlated with physiological and behavioral differences will give information of value to bird conservation.

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A Review of Oceanic Studies of the Biology of Seabirds

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During the last few years much progress has been made in the study of the natural history of seabirds when they come ashore to breed, but there have been fewer additions to our knowledge of events during the larger part of their lives which they spend at sea. There are a number of obvious reasons for this. It is difficult to study birds at sea, especially when they disperse widely into inaccessible areas outside the breeding season. Marine biologists, who probably enjoy the best opportunities to study and interpret events at sea, are occupied with other groups and have little time for birds, while experienced ornithologists rarely spend much time at sea. Professional sailors, who spend much time at sea and could make important contributions to the simpler branches of marine biology such as marine ornithology, rarely know how to make effective use of their exceptional opportunities for observation. There is little contact between these three groups of people, or between ornithologists studying the same species in different countries, although many seabirds have a worldwide distribution. As a consequence, rather little is known about the behavior of most birds at sea.

During the course of a survey of the birds of the Cape Verde Islands in 1951, I became interested in the rich avifauna of the little-known area of upwelling off West Africa, and later, for purposes of comparison, in the similar areas of upwelling on the other side of Africa off southern Arabia and in the comparable parts of the Southern Hemisphere (Bourne, 1955, 1957). While collecting information about these regions, I met the Chairman of the Royal Naval Bird Watching Society, Captain G. S. Tuck, R.N., who was good enough to allow me first to extract information from notes of seabirds regularly collected by members of the Society, and later to experiment with the organization of annual reports of these observations (Bourne, 1960a; Bourne and Radford, 1961). It became clear from this work that, while the main outlines of the natural history, behavior, and distribution of most species of seabirds are now well-known, there is still a great need for more detailed information about many aspects of the biology of seabirds away from the breeding stations.

The notes on seabirds collected by an increasing number of members of the Royal Naval Bird Watching Society are being added to a collection deposited for public reference and eventually a full systematic analysis in the Bird Room at the British Museum (Natural History). It is the purpose of this review to summarize the results of some past work on the biology of seabirds at sea, and to define ways in which such studies could be developed on a larger scale in the future.

The sea appears to be the oldest and, if we exclude the atmosphere, is still the largest and simplest habitat available to animals in the world, occupying some five-sevenths of its surface. Owing to the simple character of seawater as a medium of dispersal, the fauna of the sea still remains comparatively simple in nature despite its great antiquity, wide distribution, and the extreme abundance of individual animals. It includes only about 250 species of seabirds, as opposed to a number of thousand on the smaller area of dry land. These are listed with brief descriptions and the essential details of their life histories and distributions in the only comprehensive short guide to all seabirds yet available, Alexander’s *Birds of the Ocean* (1928, 2nd ed. 1955). His vernacular nomenclature is used for most species throughout the remainder of this paper, and his scientific names are given in the appendix.

**Character of the Marine Environment as a Medium for the Study of Bird Biology**

The principles of oceanography and marine zoogeography are summarized by Sverdrup, Johnson, and Fleming (1942) and Ekman (1953) and their application to marine ornithology is fully discussed by Murphy (1936) and Hutchinson (1950), but it may be worth trying to review them briefly again as a basis for discussion here. All life in the surface layers of the ocean depends ultimately for its existence on the presence of a combination of dissolved nutrient salts, especially nitrates and phosphates, derived mainly from the deeper layers of the ocean, and dissolved carbon dioxide and oxygen coming partly from the atmosphere. These are synthesized into more complex organic compounds by phytoplankton, using the energy provided by sunlight. A series of larger animals, including seabirds, eat either the phytoplankton or each other, and the nutrient salts eventually return to the depths of the ocean when the last animal in this food chain dies and sinks beneath the surface layers of water. This cycle provides one of the best opportunities available for the investigation of the way in which inorganic materials and energy from the sun are converted into birds, if we approach it in the right way.

The amount of living matter present in the surface layers of the ocean thus depends on the availability of both nutrient salts and sunlight. Nutrient salts are most abundant in areas where there is much mixing between the surface and deeper layers of the ocean, notably where convection currents develop around ice, in areas with strong winds and rough weather, where there is turbulence in ocean currents along irregular coastlines and around islands, and where either winds blowing the surface water away from a coast or diverging currents cause upwelling at sea. Sunlight is available throughout the year in the tropics, so that marine productivity is mainly limited by the availability of nutrient salts, and therefore by the distribution of upwelling at sea, which seasonally shifts with the change in the prevailing winds.
and currents. In higher latitudes, however, daylength becomes increasingly longer in the summer than in the winter, so that both the marine productivity and the amount of daylight during which diurnal seabirds can feed are limited by the availability of sunlight in winter. Hence, while high latitudes provide a very favorable habitat for marine animals in summer, most of them must either hibernate or migrate in winter, and it is incidentally a matter of some interest exactly what the highly specialized plankton-feeding birds of high latitudes, such as the Ivory Gull and Snow Petrel, do in the winter.

The surface waters of the oceans, like the air of the atmosphere, do not vary uniformly in temperature and chemical composition from place to place. Owing to the action of the prevailing winds of different areas, they become segregated into distinct water masses of relatively uniform temperature and composition which may meet each other at well-defined boundaries analogous to the “fronts” between air masses of the meteorologists and which are usually referred to as “convergences.” The main vertical circulation of the waters of the oceans tends to occur along the boundaries of water masses off the continental coasts and along the convergences between different water masses at sea. In areas where upwelling predominates, there is a high marine productivity associated with the development of a rich and varied marine fauna, including large seabird colonies.

The circulation of the oceans is indicated diagrammatically for open and closed seas in Fig. 1. In the open ocean far from land, the surface-water masses tend to become arranged in a series of distinct circumpolar zones as a result of the influence of the circumpolar zones of planetary winds blowing in different directions. The different zones meet with much turbulence at convergences in the regions lying between opposed belts of winds, and most sinking and upwelling occur here. Four distinct zones of surface water separated by three convergences normally develop between the poles and the equator. There has been some confusion over the nomenclature applied to these zones because oceanographers appear to use the terms “Boreal” and “Subantarctic” for regions equivalent to the whole temperate zones of geog-

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Fig. 1. Zones of winds and surface waters. The ideal distribution of winds and surface waters in the open ocean is shown on the left, and the situation in an ocean surrounded by land at the same latitudes on the right.

Continuous arrows = winds and surface currents. Heavy stippling = land masses. Light stippling = areas of sinking water. Broken arrows = deep currents. Bold lines = regions of upwelling.
raphers on land. Many names have been applied to the central convergence, but the following seems to be a reasonable compromise:

Near the poles occurs a polar (Arctic or Antarctic) zone with east winds and surface currents and much floating ice in high latitudes. There are polar (Arctic or Antarctic) convergences with much turbulence at about 55° latitude. There is a subpolar or temperate (Subarctic or Subantarctic, Boreal or Antiboreal) zone with strong westerly winds and surface currents between roughly 55° and 35° latitude. There is a temperate (subpolar, subtropical, Subarctic, Subantarctic, Boreal, Antiboreal) convergence with more turbulence at about 35° latitude. A wide subtropical zone of surface water with easterly winds and surface currents occurs between about 35° and 10° latitude. Finally, there is normally a single tropical front in the atmosphere, but two tropical convergences normally bound a westerly equatorial counter-current in the seas near the equator, while the rest of the central tropics are occupied by warm stagnant tropical surface water with weak or variable winds and currents.

In land-locked oceans where the surface water is unable to circulate freely around the world before the circumpolar belts of planetary winds in the way just described, it starts to circulate around anticyclones which appear in the centers of these oceans in middle latitudes. Owing to the persistence of the belts of planetary winds and as a result of the coriolis force arising from the rotation of the earth, the direction of circulation tends to be clockwise in the Northern Hemisphere and anticlockwise in the South. The wind also tends to drift the surface water offshore in the east and pile it up against the shore in the west in the subtropical parts of closed oceans, and drift it offshore in the west and pile it up in the east in the temperate parts of these oceans. Upwelling occurs where the surface water is drifted away from the coast, and sinking occurs where it is drifted toward it.

In addition, where water is piled up against the coast, some also flows out of the area on the surface. Some passes on around the central anticyclone, and some flows back in a counter-current. Where water piles up in the west in the tropics it flows back east in a counter-current in the area of calms and westerly monsoon winds near the equator, until it becomes saline and dense through evaporation and sinks beneath the lighter upwelling water in the east. Where water piles up in the east in temperate seas, it flows back west through the polar oceans until it becomes dense through cooling and sinks beneath lighter upwelling water in the west. In these oceans the richest seabird communities occur over areas of upwelling where the winds blow offshore and convergences form along the boundaries of counter-currents. This takes place in the west in high latitudes, and in the east in lower ones, and not in the centers of the oceans. These areas are roughly equivalent to the convergences of the open ocean.

In most areas the prevailing winds and zones of surface water tend to shift north and south with the seasons. A reversal of the direction of the
Fig. 2. The effect of the monsoon on the circulation of the Arabian Sea. Early in the year the northeasterly monsoon drifts the surface water southwest, and seabirds tend to congregate in the northeast, while later the southwesterly monsoon causes a reversal of the surface currents and seabirds congregate farther south. Breeding also reaches its maximum in the Maldives and Laccadives during the northeasterly monsoon, and the Seychelles with the southwesterly monsoon. Heavy black lines indicate where seabirds congregate over areas of upwelling.

winds and surface currents also occurs with the seasons in the monsoon area around the southern border of the Old World, as shown in Fig. 2.

**DISTRIBUTION OF SEABIRD COMMUNITIES**

It has been recognized by sailors for a very long period, and by ornithologists at least since the time of Gould (1865) and Hutton (1865), that seabirds tend to have a zonal type of distribution in particular latitudes. Murphy (1936) and numerous subsequent authors have shown that their distribution usually appears to coincide with that of particular zones of surface water. There have been detailed studies of the birds of a number of different areas, including surveys of the birds of the North Atlantic by Hagerup (1926), Wynne-Edwards (1935), Rankin and Duffey (1948), and Moore (1951), the tropical and South Atlantic by Bierman and Voous (1950) and van Oordt and Krujlt (1953, 1955), the South Atlantic by Dab-bene (1921–26), the southern ocean by Roberts (1940a), Holgersen (1945, 1957), Routh (1949), Bierman and Voous (1950), and van Oordt and Krujlt (1953, 1955), the southern Indian Ocean by Paulian (1953), the South Pacific by Fleming (1950), the tropical Pacific by Macdonald and Lawford (1954), and the North Pacific by Kuroda (1960a) and Wilhoft (1961). However, few authors have attempted to compare the distribution of seabird communities in different parts of the oceans as a whole. The relationship between the analogous bird communities of different oceans and the Northern and Southern hemispheres in particular has been neglected, to the extent that it has only recently been recognized that the fulmars of the Northern and Southern hemispheres or the Manx Shearwaters of the Atlantic and North and South Pacific may be closely related (Voous, 1949; Murphy,
It may therefore be useful to try to distinguish some general associations of bird species that appear to be characteristic of the appropriate parts of all oceans.

**Polar Communities.**—These are found on the cold side of the polar convergences above about 55° latitude in both hemispheres. They include associations of species exploiting the highly productive convection currents around floating ice in high latitudes, described by Hagerup (1926) and Routh (1949) among others, and the area of upwelling along the polar convergences. The main species are penguins, Southern Skuas, terns, and petrels in the south, the Northern Fulmar, auks, skuas, gulls, and terns in the north. The particularly rich avifauna of petrels and penguins found along the Antarctic Convergence and the cool-current areas off Argentina, and eastern New Zealand, Australia, and South Africa in the south seems directly comparable to the rich seabird communities of the borders of the Labrador Current in the Atlantic and the Kurile Current in the Pacific in the north. There are some remarkable examples of convergence in unrelated species in these areas, as with the Snow Petrel and Ivory Gull, the penguins and Great Auk, and the diving petrels and smaller auks.

**Subpolar Communities.**—These are found between the polar and subtropical convergences in both hemispheres. The greatest marine productivity appears to occur in the immediate vicinity of the convergences and where there is upwelling on the lee coasts of the continents and around islands, but there is still a high marine productivity due to the development of strong winds and turbulent currents at sea. This is therefore the area where large concentrations of strong-flying birds are found at sea, including albatrosses, fulmars, shearwaters, gadfly petrels, storm-petrels, and Great Skuas in both hemispheres, with penguins, diving petrels, and prions in the south, and Kittiwakes and auks in the north. Cormorants, gannets, skuas, gulls, and terns are also found around the coast in both hemispheres. The rich seabird associations breeding on the subantarctic islands and feeding at sea along the subtropical convergence in the Southern Hemisphere (Holgersen, 1945) seem directly comparable to the rich seabird associations of the central archipelagoes in the North Atlantic (Bourne, 1955, 1957) and North Pacific (Richardson, 1957), both associations sometimes sharing the same species.

**Subtropical Communities.**—These are found between the subtropical convergences and the large areas of calms, variable winds, and monsoons in the central tropics, many apparently subtropical species feeding far into the tropics along the convergences which form along the borders of the equatorial counter-currents. The richest seabird associations now occur over the areas of upwelling along the west sides of the continental coasts off Peru (Murphy, 1936), California (Palmer, 1962), West Australia (Serventy, 1952), west and southwest Africa (Moreau, 1950), and in the monsoon area off the south coast of Arabia (Meinertzhagen, 1954). The dominant species are gulls, terns, phalaropes, cormorants, boobies, pelicans, shearwaters, and storm-petrels. Petrels and Sooty Terns also occur at sea along the convergences and the gadfly petrels and tropic-birds at sea in the center of the zone.

**Tropical Communities.**—These occur mainly offshore, where there is upwelling around islands, and along the borders of local currents in the central tropics. Very few birds apart from occasional tropic-birds occur at sea away from land. The terns and Pelecaniformes seem particularly characteristic of this area, especially the Red-footed Booby, Yellow-billed Tropic-bird, Sooty and Noddy terns, and frigate-birds, with other more local species. Areas of upwelling at sea also appear to support numerous gadfly and storm-petrels, but it seems doubtful whether they can be considered to be truly tropical because the upwelling water is much cooler than that of the rest of the area.

Individual species and groups of species clearly have much more restricted ranges within this general classification of habitats, particularly successful groups often having broken up into a series of closely related species characteristic of either different zones or parts of zones of surface water within the same ocean, or equivalent zones of surface water in different oceans. In some cases several closely allied species also feed together in the same area, usually taking food of different sizes, so that a very complicated mosaic of
distributions may be found in the more complex groups, such as the penguins, auks, shearwaters, gadfly petrels, or storm-petrels. Unfortunately, it is still impossible in many cases to define the range and food of closely related species in relation to each other with sufficient accuracy to see if they overlap. In many cases they are clearly often complementary, as with the Great and Cory’s shearwaters in the North Atlantic (Rankin and Duffey, 1948) or the Black and Markham’s storm-petrels off South America (Murphy, 1936). Even when the distribution of a species is well known, it is still usually impossible to determine exactly what controls it. For this purpose, much more information is needed concerning the birds’ biology at sea, especially comparative information concerning behavior and the diet of closely related species, such as was presented for the southern fulmars by Voous (1949).

THE STRUCTURE OF TWO COMPARABLE SEABIRD COMMUNITIES

The study of the ecology of seabirds has been approached in many different ways. By 1865, Gould and Hutton already seem to have appreciated that most species have a well-defined distribution in particular latitudinal zones at sea. The fact that each species plays a different role in the marine community does not seem to have been appreciated for another fifty years, when Nichols (1914) and Murphy (1914a) simultaneously pointed out how the petrels have differentiated into a series of different species of different sizes feeding in different ways. Hagerup (1926) then pointed out that most species in the marine community appear to be food specialists of one sort or another. Jesperson (1930) and Hentschel (1933) demonstrated how, regardless of the different roles played by different species in the marine community, the number of birds of all sorts present in different parts of the open sea tends to be directly proportional to the density of the plankton. Wynne-Edwards (1935) then defined distinct associations of seabirds occupying distinct inshore, offshore, and pelagic ranges in the same zone of surface water in the North Atlantic, while Murphy (1936) demonstrated that different but frequently closely allied species tended to replace each other in similar ecological situations over different zones of surface water around South America. The relationship that exists between a number of allied species occurring together in one habitat in the South and their representatives in the Northern Hemisphere has finally been demonstrated by Voous (1949) in his study of the northern and southern fulmars.

While Hutton (1865), among others, had started to provide accounts of the breeding biology of some southern seabirds a hundred years ago, systematic studies of breeding behavior only seem to have been started in America shortly before the First World War (Chapman, 1908; Watson, 1908; Gross, 1912). These led almost inevitably to investigations of the powers of orientation of seabirds (Watson and Lashley, 1915). These studies were interrupted by the war, but were resumed in Britain by Lockley from 1930 (1942). The breeding aspect of these studies has since been developed in
the Southern Hemisphere first by Falla (1934, 1937), then by Richdale (1949, 1950, 1953, 1957) in New Zealand and Serventy (summarized, 1962) in Australia in numerous papers, and finally by Coulson and his associates in Britain (Coulson and White, 1960), the personnel of the Falkland Islands Dependencies Survey in the Antarctic, the British Ornithologists’ Union Centenary Expedition to Ascension (Ibis vol. 103b), and numerous other workers. The orientation aspect of these studies has been developed by Griffin (1955) in North America and by Matthews (1955) in Britain, among other investigators.

At the same time, Thomson (1924, 1939, 1943) in Britain and the Austins (e.g. O. L. Austin, 1928; O. L. Austin, Jr., 1929, 1953) in numerous papers from America were investigating the movements and life cycles of migratory seabirds by marking, while Lockley (1953) attempted to correlate the movements of the Manx Shearwater off the northwestern coast of Europe with the seasonal movements of its main food supply, the pilchard (*Clupea pilchardus*). Fisher and Waterston (1941) set out to estimate the numbers of fulmars in the British Isles, and Fisher and Vevvers (1943) the number of Northern Gannets in the world. Roberts (1940b) attempted a complete study of both the breeding behavior of Wilson’s Storm-petrel in the Antarctic and its dispersal at sea outside the breeding season, a technique which has since been used for the Great Shearwater of the Atlantic by Rowan (1952) and the Slender-billed Shearwater of the Pacific by Serventy (1962).

Information on the biology of the seabirds of the North Atlantic has been reviewed by Fisher and Lockley (1954), and that available on the functional morphology, distribution, and breeding seasons of the petrels in a series of papers by Kuroda (1954, 1957, 1960b).

A vast amount of work has been carried out on the biology of individual species over the last half century, and detailed accounts of the seabird communities of South American waters and the North Atlantic have been provided by Murphy (1936) and Fisher and Lockley (1954). However, little attempt has been made to assess either the relation to each other of different species in particular seabird communities, or the importance of seabirds in the animal community of the oceans as a whole, apart from the attempt by Hutchinson (1950) to assess the amount of nutrient salts removed from the oceans by seabirds as guano. The next stage in the development of the study of seabird biology should involve an attempt to assess the role of each species in a seabird community more precisely, and then, by estimating the total numbers and food requirements of different species, eventually to discover the importance of seabirds in the economy of the oceans as a whole. Unfortunately, little information is yet available to serve as a basis for such an analysis in most areas, and it is part of the object of this paper to appeal for the more systematic collection of such information. Meanwhile much may be learned by judicious comparisons of the situation in different areas so far as it is already known.
I will therefore attempt an analysis of two seabird communities which have developed in similar ecological situations in two oceans and which appear to have been isolated from each other for a very long period. In this attempt, I wish to identify similarities and differences, the reasons for them, and the opportunities that they offer for the further investigation of seabird ecology. The distinctive communities of the two areas of upwelling water lying off the west coast of Africa described by Swinburne (1886), Bannerman (1914, 1930-51), Bierman and Vouws (1950), Lockley (1952), Bourne (1955), and de Naurois (1959, 1960) and off the south coast of Arabia described by Alexander (1931), Archer and Godman (1937), Jung (1941), Phillips (1947, 1955), Meinertzhagen (1954), Jouanin (1957), and Bourne (1960b) seem highly suited for this purpose.

Off both west Africa and south Arabia upwelling occurs because the prevailing wind drifts the surface water offshore, the distribution of surface-water currents and water temperatures in the British Admiralty and other charts suggesting that the main area of upwelling moves north in summer and south in winter with the tradewinds off west Africa, as I have suggested elsewhere (Bourne, 1955), but northeast in winter and southwest in summer with the development of the northeast and southwest monsoons in the Indian Ocean (Fig. 2). Numerous reports show that there is a very high plankton production in the areas of upwelling, and that many marine animals including fish, whales, and seabirds congregate there. The density of these animals then declines progressively downwind away from the area of upwelling toward the centers of the North Atlantic and the Arabian Sea. Different seabirds appear to fill the following roles in these two areas:

**Phalaropopidae.**—It has been shown by Meinertzhagen (1925) that the phalaropes winter at sea in the area of upwelling water in low latitudes, and Stanford (1953) and W. F. J. and M. F. Mörzer Bruijns (1957) have shown how Grey Phalaropes winter in the area of maximum plankton concentration off west Africa and are replaced by Red-necked Phalaropes in the Indian Ocean. Red-necked Phalaropes have also been reported off west Africa by Tâning (1933) and Grey Phalaropes in the Arabian Sea by Meinertzhagen (1954) but they seem to be uncommon there, although D. M. Neale informs me that he has seen a few Grey Phalaropes with much larger numbers of Red-neckeds off the coast of Somaliland. The precise ecological relationship between the two species in their winter quarters is not at all clear, but Mr. Neale suggests that the Grey Phalaropes occurred farther out at sea. They seem to be particularly characteristic of the trade-wind zones in the Atlantic and Pacific, whereas the Red-necked Phalaropes seem to be more characteristic of the monsoon areas in the Arabian Sea and north of the East Indies. The two species apparently feed directly on the zooplankton over the center of the areas of upwelling at sea; since this is comparatively easily sampled and identified, their ecology in winter quarters offers outstanding possibilities for the investigation of the abundance of birds in relation to their food supply.

**Hydrobatidae.**—After the phalaropes the storm-petrels appear to feed at the lowest level in the marine food chains, differing from them mainly in collecting their food in flight and not while swimming, although the precise nature of their food supply does not seem to have been worked out. There appear to be few or none in the Arabian Sea when phalaropes are commonest there in the northern winter, but they become very common when the phalaropes migrate north in the northern summer. Three species appear to have complementary ranges in successive zones offshore, Wilson's Storm-petrel occurring in large numbers offshore, the White-faced Storm-petrel in smaller numbers
farther offshore (Junge, 1941), while Captain W. F. J. Mörzer Bruïns confirms Phillips' (1947) report that a species of Fregetta occurs in the middle of the monsoon zone of the central Arabian Sea. Lt. Cdr. G. S. Willis has produced a sketch of a bird seen there, and Lt. N. Bailey measurements of a bird that came on board there that agree with the Black-bellied Storm-petrel (Fregetta tropica).

The same three southern migrants enter the Atlantic, but whereas Wilson's Storm-petrel is common throughout the offshore zone off west Africa in summer and appears to be the dominant storm-petrel there then, the typical race of the White-faced Storm-petrel and both the White-bellied and Black-bellied storm-petrels, which have all been collected in the Ascension area, stop short at the equator, apparently being replaced by endemic races of the White-faced Storm-petrel and the Madeiran Storm-petrel out at sea farther north. When Wilson's Storm-petrel migrates south in the northern winter, it is replaced as the common storm-petrel off west Africa by the British Storm-petrel close to the shore (Wolff, 1950) and Leach's Storm-petrel in much the same area out at sea (Murphy, 1915, 1918).

It is not clear to what extent the phalaropes and storm-petrels take different foods or occupy different ranges, but it is extremely conspicuous how, for example, Wilson's Storm-petrel and the phalaropes replace each other on a very large scale as the dominant small plankton feeders in the Gulf of Aden and how Wilson's and Leach's storm-petrels replace each other in the tropical Atlantic at different seasons. It seems possible that these birds have become adapted to take the same food in much the same area at different times of year.

Sternidae.—Terns appear to take rather larger foods than the Hydrobatidae, including many small fish. Very large numbers occur in both areas, and precisely which species are resident, which migrants winter in the area, and which are passage migrants is not clear. Some of them, notably the Little and Black terns, appear to feed close to the shore, while others, such as the wintering Common Terns off west Africa, the endemic White-cheeked Tern in the Arabian Sea, and the Bridled Tern in both areas, appear to feed in large flocks over areas of upwelling offshore as well. The Sooty Tern appears to replace the others in large flocks far out at sea, presumably feeding mainly over convergences along the borders of ocean currents, but there seems to be little evidence for the nature of the food supply that supports vast colonies on remote islands in the central tropics. There are some conspicuous examples of ecological replacement by allied species in the two tern communities, notably the replacement of the Crested, Lesser Crested, and White-cheeked terns of the Arabian Sea by Royal and migrant Sandwich and Common terns off west Africa.

Laridae and Stercorariidae.—The main resident gulls are the Slender-billed in both areas, the White-eyed Gull in the north and the Aden Gull in the south in the Arabian Sea area, and the Herring Gull in the north and the Grey-headed Gull in the south in west Africa. The Slender-billed Gull seems to feed mainly in shallow water; the others feed along the shore and out to sea, being joined by numbers of migrants, especially Black-headed and Lesser Black-backed gulls in both areas in winter. The Lesser Black-backed Gull seems most prone to feed out to sea, where it overlaps with Pomarine Skuas wintering over the areas of upwelling offshore. Arctic Skuas also occur in both areas, but mainly at the season of migration, while west Africa receives stray Great Skuas and Kittiwakes from the north, and the Arabian Sea straw Great Skuas from the south. Sabine's Gull has recently been shown to pass through west African waters on migration (Mayaud, 1961), but it apparently passes on to winter off south Africa.

There is usually only one resident gull along the shore in any area. The species change from place to place, possibly with changes in the character of the shore as a breeding place, although until very recently (de Naurois, 1959, 1960) there seem to be few critical accounts of where the seabirds breed as well as where they feed. It is not completely clear how the skuas feed out at sea; they certainly appear to parasitize terns at times, but they apparently sometimes occur alone as well, especially where they are commonest off west Africa.

Procellariidae.—Petrels are represented in the area by the two most widespread groups, the shearwaters, taking mainly fish and some cephalopods, and the gadfly petrels, apparently feeding mainly on cephalopods. Three shearwaters of different sizes are present in both areas. In west Africa these include a sedentary Little Shearwater from the assimilis
end of the *Puffinus assimilis-lherminieri* assemblage which seems to feed mainly offshore, although it is seldom reported at sea, the medium-sized Manx Shearwater feeding mainly offshore in the north only, and the large Cory’s Shearwater which is extremely widespread at sea. Off Arabia it includes a sedentary Little Shearwater from the *therminieri* end of the assemblage which occurs abundantly offshore, concentrating in the approaches to the Red Sea and Persian Gulf in the winter and spring and dispersing farther out at sea in summer, the medium-sized Wedge-tailed Shearwater which is widespread at sea, and the Flesh-footed Shearwater which is again common offshore. The two larger shearwaters are transequatorial migrants in both areas; whereas they breed in the north and molt in the south in the Atlantic (Palmer, 1962), they apparently molt in the north and breed in the south in the Indian Ocean (Junge, 1941; Jouanin, 1957; Bourne, 1960b).

I have already pointed out how the bills of the different species of shearwater vary in size with the incidence of interspecific competition for food in the Atlantic area (Bourne, 1955, 1957); a marked difference in bill form is also found among the three species occurring in the Arabian Sea, the Little Shearwater having a slender bill, the Wedge-tailed (which may feed largely out at sea away from the other two) an intermediate one, and the Flesh-footed a very large one.

The same phenomenon of variation in size with the incidence of interspecific competition for food is also found in the gadfly petrels of the two areas, which all appear to feed far out at sea on cephalopods. Where two species, Bulwer’s Petrel and the Soft-plumaged Petrel, occur together in the Atlantic they differ markedly in size. The single species occurring in the Arabian Sea, Jouanin’s Petrel, is almost intermediate between them in size (Jouanin, 1957), although an X-ray of its skull confirms that it has a lightly ossified skull of the type peculiar to Bulwer’s Petrel, and is different from other large gadfly petrels such as the Mascarene Petrel.

**Pelecaniformes**.—Resident cormorants fish in large numbers along the shore in both areas, the species being the Common Cormorant off west Africa and the endemic Socotra Cormorant in the Arabian Sea. Brown Boobies fish inshore from the air mainly in the Red Sea and Gulf of Aden in the east, and in the Cape Verde Islands and Gulf of Guinea in the west, and are replaced by resident Blue-faced Boobies in the Arabian Sea and migrant gannets off west Africa. A small population of the Magnificent Frigate-bird breeds in the same area as the Brown Boobies off west Africa and may or may not parasitize them; the Greater Frigate-bird has been collected twice in the vicinity of the Gulf of Aden, although it is not yet clear that it breeds there. Different races of the Red-billed Tropic-bird feed on fish and cephalopods from the air far out at sea in both areas.

Although these sea areas do not appear to have been in communication for a very long period, a similar seabird community of the order of thirty species has developed in each of them (Table 1), involving an adaptive radiation of different forms capable of exploiting all elements in the oceanic food chains from the smaller zooplankton up to the larger fish and cephalopods. The gulls and terns forage mainly from the air near the shore, the phalaropes, cormorants, and diving shearwaters in large groups on the water where the marine productivity is high and the food supply good in the areas of upwelling offshore, while the remaining species disperse more widely and forage from the air where the food supply is less good so that they must search wider areas farther offshore. Most groups are represented by a comparatively small number of species and most species have a conspicuously different range or feeding routine. Where several closely related species are present in the same area, as with the phalaropes, shearwaters, or gadfly petrels, they may vary markedly in size, bill shape, or range, according to the incidence of interspecific competition for food.
Table 1.—Comparison of the Structure of Two Subtropical Seabird Communities

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<th>WEST AFRICA</th>
<th>REPRESENTATIVE SPECIES</th>
<th>SOUTH AFRICA</th>
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<tr>
<td>Range Offshore</td>
<td>Western/Eastern</td>
<td>Status²</td>
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**General Information:***
- **N** = Northern migrant.
- **R** = Resident.
- **S** = Southern migrant.
- * = Breeds in area.
- Arrows indicate increasing distance away from coastline.

**West Africa**

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<th>Representative Species</th>
<th>Status²</th>
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<td>xxxxxxxxxx x R Red-billed Tropic-bird</td>
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*The precise status of a number of groups, such as the terns and larger petrels of the Indian Ocean, is still obscure; a number of other species, such as Sabine’s Gull and the Arctic Skua, occur regularly as passage migrants; and others, such as the Kittiwake and Great Skua, as strays.
This variation in size according to the incidence of competition for food emphasizes another point: The size of any animal is likely to be closely adapted for the size of food items available to it. Thus, the individuals of species taking small food items tend to be small, those of species taking larger food items are larger. Their manner of foraging is also adapted to the habits and density of their food; where it is abundant, seabirds forage in flocks on the water, most flocks probably congregating over focal concentrations of food; where it is more dispersed, they disperse in the air. Different groups clearly have different feeding techniques used either for catching different foods, or surprising the same foods in different ways. The methods of dispersal and feeding of seabirds have clearly not been studied sufficiently.

If the two seabird communities are compared together on a larger scale, it is found that, while nearly half the species are the same in the two areas (although the subspecies is often different), and similar representative species can be distinguished in both areas in most other cases, there are also three additional storm-petrels and an additional gadfly petrel off west Africa. There are also different proportions of migrant forms in the two areas. Thus, while there are comparatively few endemic forms, no endemic species, and migrants appear to form a proportionately large part of the population off west Africa, there is a much higher proportion of endemics off southern Arabia, including some five endemic species—Jouanin’s Petrel, the Socotra Cormorant, the White-eyed and Aden gulls, and the White-cheeked Tern. This may be partly because the west African seabird community is of relatively recent origin and has developed as a result of changes in the oceanic circulation following the changes in the geography of the North Atlantic in the late Tertiary and its climate during the Pleistocene (Ekman, 1953). It may also be because it is still in free communication with other oceanic areas with similar climatic regimes in all directions except the east, while the Arabian Sea has been isolated for a longer period in all directions except the south and has an unusual type of climate.

The presence of more open water to the north must certainly explain the different proportion of migrants in the two communities. While both areas receive comparable numbers of migrants, mainly petrels from the south, two of the storm-petrels not going so far north in the Atlantic as in the Indian Ocean, the three commonest terns, the Black Tern, Common Tern, and Sandwich Tern, the offshore sulid, and the cormorant are either migrants or widely distributed to the north in the Atlantic, and are replaced by apparent residents in the Indian Ocean. There also seem to be more skuas off west Africa, while two migratory storm-petrels visit the area in the winter when the group is almost entirely absent from the Indian Ocean.

The appearance of a higher proportion of migrants in the area of high marine productivity in the subtropics, which is in closer communication with seas to the north, also emphasizes the fact that, while most areas of high marine productivity in the tropics are quite capable of supporting large sea-
bird communities if access to other areas is difficult, as with isolated islands, most birds must be at a competitive advantage there if they can find somewhere else to breed with a better food supply. Thus, many mainland coasts in the tropics appear to be populated almost entirely by migrants, which pass their period of immaturity there away from the stiff competition for food in the breeding areas, but, after reaching maturity, eventually migrate into higher latitudes to breed during the summer when food is abundant. This will presumably explain why, while the Arabian Sea is populated by Blue-faced Boobies, the exactly comparable area off west Africa, which is in fairly close contact with areas containing populations of this species to the west and south, is populated by the young of gannets breeding far to the north (Thomson, 1939).

OPPORTUNITIES FOR THE INVESTIGATION OF SEABIRD BIOLOGY

A consideration of the past work on seabird biology and our present knowledge of the structure and distribution of seabird communities suggest that the following fields might prove rewarding on fuller investigation.

1) **Evolution.**—Marine zoogeographers such as Ekman (1953) have conspicuously neglected to include birds in their deliberations on the grounds that their powers of flight enable them to behave differently from other animals, while marine ornithologists such as Murphy (1952) and Kuroda (1954) have tended to restrict their attentions to limited groups. In consequence, the question of the manner of origin of the marine avifauna as a whole has only been studied by Williams (1952), who unfortunately only appears to have a general knowledge of the subject. Since the manner of origin of different groups of seabirds is a fundamental consideration in studying all aspects of their subsequent development, it surely deserves more study.

2) **Structural Adaptations for the Marine Environment.**—The different major groups of seabirds appear to have developed some very different morphological adaptations for the exploitation of the marine environment in different ways very early in their history. Some use flapping and some soaring flight, some feed from the air and some on the water, from the surface or by diving. The main adaptive trends of this type seem to have developed very early in the history of seabirds, and some of the differences between different groups are very obvious, while others, such as the difference between the aerial and aquatic shearwaters investigated by Mayaud (1932) and Kuroda (1954 onward), have been widely overlooked. This subject deserves more study, both from the anatomical aspect following the approach used by Storer (1960) in his studies of diving birds, and by critical study of the behavior of living birds, as in the case of the studies of specialized aspects of the flight of the Northern Fulmar by Erickson (1955) and Penny- cudick (1960), and the manner of flight of the petrels and albatrosses in general by Nichols (1946).
The recent discovery that seabirds regulate their salt balance by excretion via the nasal gland (Fänge, Schmidt-Nielsen, and Osaki, 1958; Doyle, 1960) explains the function of one puzzling organ possessed by seabirds, and also why it has proved so difficult to keep seabirds in captivity in the past, leaving the way open for investigations of the behavior of captive birds such as those of the Frings (1960) with albatrosses. It seems likely that seabirds may possess other special organs which deserve closer study, such as the highly developed olfactory apparatus of the petrels, which has received little attention since it was described by Wood-Jones in 1937. Such a large organ must serve some useful function, possibly to locate food, although it may be significant that the members of this order (who normally visit their nests in darkness) have a strong odor themselves, so that they may also locate their nests or each other by smell.

3) The Nature of the Relationship between Closely Related Forms.— While the larger groups of seabirds seem to have developed different types of adaptation to the marine environment, the more successful ones appear subsequently to have split up into large numbers of closely related species occupying different zones of surface water, the same zone of surface water in different oceans, or taking different foods. The basic differences between these closely related forms require study from different aspects, including the precise differences between their distributions, markings, behavior, food, and structure. Examples are the studies of the evolution of the prions and small gadfly petrels by Fleming (1941) and Falla (1942), of the Wedgetailed and Manx shearwaters by Murphy (1951, 1952), and the larger gadfly petrels and storm-petrels by Murphy and Pennoyer (1952) and Murphy and Snyder (1952); of the distribution of the albatrosses by Dixon (1933) and Wilson’s Storm-petrel by Roberts (1940b); of the molts of the petrels by Loomis (1918) and the plumages of the gulls by Dwight (1925); of the migrations and breeding seasons of the petrels by Kuroda (1957, 1960b); and the behavior of the gulls by Moynihan (1959).

4) Food.—It should be possible to calculate the productivity of the sea from the movement of water through the oceans and the density of nutrient salts and the plankton on the one hand, and its relation to the number of seabirds in different areas on the other. So far this calculation has only been tried in a very general way by Jesperson (1930) and Hutchinson (1950). It should also be possible to estimate the numbers of particular species of seabirds, by counting them at the breeding stations as was done by Fisher and Ververs (1943) or by relating their numbers to the available food supply, in the way attempted for the Manx Shearwater by Lockley (1953), much more closely than has yet been done. There is clearly a need for more direct observation of where and how birds feed at sea, and aircraft could prove to be particularly useful for studying the movements and feeding places of large, conspicuous birds like gannets. More detailed study of food fed to young, vomitus, and stomach contents could be useful in some areas, and might inci-
dentally yield results that would be interesting to marine biologists as well as ornithologists.

5) Markings.—The distribution and character of seabird markings deserves more study, particularly in relation to the incidence of different types of markings in different groups, and their function in life. It seems likely that bird markings serve at least two functions, concealment from predators and prey, and communication with other individuals and species, as in the case of the gadfly petrel wing markings illustrated by Murphy and Pennoyer (1952). The different functions of bird markings need to be identified and their effect studied in the natural environment.

6) Voice and Display.—This subject is now the object of increasing study at breeding stations. Types of social organization and communication at sea also require to be studied and evaluated.

7) Life and Annual Cycles.—Most seabirds go through long and complex life cycles, and the annual cycle may vary with increasing age. The investigation of seabird breeding biology has been reduced to a routine, but there is a great need for more study of some other aspects of the life or annual cycle, including events in the period immediately after fledging, and behavior and survival in the immature period and outside the breeding season. Many species also appear to go through a complex sequence of behavior when they are first prospecting breeding sites which presumably determine where they will breed ever after, and this requires more study. Seabirds also seem likely objects for the study of the effects of advanced senility in birds, since they have so few predators.

8) The Timing of Events in the Life and Annual Cycle.—Owing to the irregular distribution of regions with a good food supply and suitable isolated breeding stations at sea, seabirds commonly show very variable annual cycles, concentrating in different areas to feed, and molt, and breed at different stages in the life and annual cycle. Thus, immature birds commonly congregate in “nurseries” away from the breeding places during the first few breeding seasons, and go into molt earlier than adults. Later, adults may congregate in different parts of the range to molt and breed, carrying out either function at very variable times according to the distribution of available food supplies and breeding stations in different latitudes. Much more accurate information is needed about breeding distribution and seasons in many parts of the world, about molting seasons and ranges in most parts, and the distribution of birds of different age groups during these periods in practically all areas. This involves more accurate discrimination of birds of different age-groups, if necessary by marking, and of different stages in molting and breeding cycles than is often current practice.

9) The Effects of Disturbances in Atmospheric and Oceanic Circulations.—The effect of storms in displacing seabirds from their normal range is well known (Murphy and Vogt, 1933; Boyd, 1954), but the full consequences of these events on the birds that remain at sea have hardly been studied. The
effect on birds of changes in the distribution of ocean currents are also well
known (Murphy, 1936; Hutchinson, 1950). Hardly studied at all are the
possible effects of more temporary and local fluctuations in the oceanic cir-
culation, and in particular eddies traveling along oceanic currents, in causing
birds to leave their normal range. The young of a number of species of sea-
birds also appear to show differences in their survival rate from year to year,
which presumably reflect the results of more long-term fluctuations in con-
ditions at sea. Both short- and long-term fluctuations require more study.

CONCLUSION

Marine ornithology had a bad start, when the detailed field notes made
by Solander, Forster, and other naturalists during Cook's expeditions at the
end of the eighteenth century were never published at the time, and the birds
they encountered only became known through garbled accounts of their
drawings and specimens that were published by Latham (1781–85; see also
Mathews, 1912; Lysaght, 1959). In consequence, the confusion that arose
when many different expeditions from various countries brought back small
numbers of specimens of seabirds from many parts of the world throughout
the nineteenth century has only been resolved by the work of the compilers
of the Catalogue of Birds in the British Museum, Gregory Mathews in his
Birds of Australia (1910–25), Dr. Murphy at the American Museum of
Natural History, and others in very recent times.

The situation has been made worse by the fact that seabirds are often dif-
ficult to collect or identify while alive at sea. As a result, work on their biol-
ogy at sea has had to wait upon the development of good binoculars and
field guides in the last fifty years. Thus, while Gould (1865) provided the
first detailed account of the southern species in the Birds of Australia nearly
a hundred years ago and Hutton (1865) clearly distinguished some of the
main problems of zoogeography and adaptation to a marine environment at
that time, and valuable work was done especially on the anatomy of seabirds
in the latter part of the nineteenth century, the first really important work
on seabirds seems to have been started just before the First World War.

It is difficult now to appreciate the problems encountered by the first
people to work at sea. Thus, when Vanhöffen (1901, 1905) and Jesperson
(1930) carried out their pioneer work on seabird distribution from oceanic
survey vessels, they had no reliable field guides to enable them to identify
species. When Edward Wilson (1907) went to the Antarctic with Scott's
expeditions he had to compile his own field guide, now at the Edward Grey
Institute, Oxford, which adds to the achievement represented by his excel-
 lent field notes. Dr. Murphy (1914a) must have encountered similar prob-
lems during his first voyage to South Georgia, and he seems to have been
the person who really started the tradition of accumulating careful observa-
tions during successive parts of a voyage at sea which have served as a basis
for most subsequent work on distributions at sea.
The first good observations were just starting to be made at sea when they were interrupted by the First World War. There was a hiatus afterward during which several people, notably W. B. Alexander (1928) and Dabbene (1921–26) started to collect records of seabird distribution in a more detailed way, and then the modern era of seabird study really began with the publication in 1928 of the first comprehensive field guide to any group of birds, Alexander’s *Birds of the Ocean*, based partly on his own wide experience with birds at sea in the south combined with advice from Dr. Murphy. Since that time there has been published an increasing torrent of records of voyages in different parts of the oceans and studies of particular areas or aspects of seabird biology, but few studies of seabird biology on a really large scale.

The biology of seabirds is not a subject that can be studied fully by people of any one nationality or in any one area, since many species are dispersed over a large part of the world. Some areas and species are now well known, while other areas and species are still virtually unknown; thus, two petrels are still only known from single specimens collected in the last century, while nobody seems to have any clear idea of the distribution of seabirds at sea in large areas in the tropical Pacific or in the immediate vicinity of many of the marine convergences. A number of interesting hypotheses regarding the natural history of seabirds have now been formulated by different authors, and numerous different techniques of investigating their biology have been applied in a small way. It is now time that they were applied internationally on a much larger scale throughout the oceans to complete the picture.

Individual ornithologists are clearly never going to have time to do this, while nobody in the world has the space to publish really detailed records from all parts of the oceans. Clearly, if we are ever going to obtain really detailed records of seabird distribution and natural history, they will have to be collected by the only people who spend much time at sea, professional oceanographers and sailors, and accumulated in places where they are easily available for detailed analysis in bulk. Since this type of observer is unlikely to have much experience with marine ornithology, and this type of record is extremely difficult to analyze on a large scale if it is not recorded in a methodical way, this requires the development and application on a large scale of simple systematic methods of recording information, the obvious method being the use of questionnaires as developed for its members by the Royal Naval Bird Watching Society.

In addition, while this method of collecting notes in a regular way still yields much information of immediate interest in little-known areas, in the better-known areas the notes only start to become valuable when really large series are available. This requires the organization of depositories for the information where it can be accumulated until it becomes useful. It would be extremely valuable if a journal could be organized in the style of *Audubon*
Field Notes where raw information from all parts of the oceans could be placed on record in a systematic way. Failing this, it would be useful if people who collect information about seabirds could always make a point of either publishing it in a form that will make it possible to extract the basic data for incorporation into subsequent more detailed analyses using larger series of data, or preferably saving the space that is often at present wasted by the publication of comparatively trivial notes in full by filing all original raw data in some place where it will be easily accessible to future workers.

It would be useful if all such material, like other information of a comparable nature such as census, molt, and breeding data, and especially ringing recoveries, could be filed in some central establishment under international auspices. However, while this seems impracticable at present, it is always possible that it may become practicable in the future, and when this happens it would be very convenient if really useful quantities of fundamental data were already available in different parts of the world and if these data could be photocopied and assembled in the central institution. Meanwhile, there is an immediate need for the wide development of methods of systematically recording data about seabirds, and the safe accumulation of these data in public places where they will be available to future workers. After this has been done, it will be time to start trying to organize means and especially funds for combining the data and arranging for detailed analysis on an international scale.

SUMMARY

The distribution of seabirds appears to be controlled by the manner of circulation of the water in the oceans, and especially the amount and character of the food available in the surface water in different areas. Comparable seabird communities have therefore tended to develop in comparable parts of different oceans in the main climatic zones of both hemispheres of the world. However, while the general pattern of distribution of most seabirds at sea is now well known, the detailed distribution and ecology of the birds at sea is often still far from clear. It seems likely that this is only going to be elucidated by the collection of systematic observations of the distribution and behavior of birds at sea on a far larger scale than has yet been possible, and by comparison of this information with other information on marine biology. If this approach is developed with sufficient thoroughness, it offers outstanding opportunities for the investigation of the relationship between the character and abundance of bird species and the food available in their environment.

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———. 1915. The Atlantic range of Leach’s Petrel (Oceanodroma leucorhoa [Vieillot]). Auk 32:170–173.


Scientific Names of Birds Mentioned in the Text

The scientific names are taken from Alexander's *Birds of the Ocean* (second edition, 1955), while vernacular names have been modified to a variable extent.

<table>
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APPENDIX
Audubon's Shearwater P. iherminieri
Wilson's Storm-petrel Oceanites oceanicus
White-faced Storm-p. Pelagodroma marina
White-bellied Storm-p. Fregetta grallaria
Black-bellied Storm-p. F. tropica
British Storm-p. Hydrobates pelagicus
Madeiran Storm-p. Oceanodroma castro
Leach's Storm-p. O. leucourhoa
Black Storm-p. O. melanias
Markham's Storm-p. O. markhami
Northern Gannet Morus bassanus
Blue-faced Booby Sula dactylatra
Red-footed Booby S. sula
Brown Booby S. leucogaster
Greater Frigate-bird Fregata minor
Magnificent Frigate-bird F. magnificens
Common Cormorant Phalacrocorax carbo
Socotra Cormorant Phal. nigrogularis
Red-billed Tropic-bird Phaethon aethereus
Yellow-billed Tropic-bird Ph. lepturus
Great Skua Catharacta skua
Southern Skua C. maccormicki
Pomarine Skua Stercorarius pomarinus
Arctic Skua S. parasiticus
Ivory Gull Pagophila eburnea
Kittiwake Rissa tridactyla
Herring Gull Larus argentatus
Lesser Black-backed Gull L. fuscus
Slender-billed Gull L. genei
Aden Gull L. hemprichi
White-eyed Gull L. leucophthalmus
Grey-headed Gull L. cirrocephalus
Black-headed Gull L. ridibundus
Sabine's Gull Chlidonias nigra
Black Tern C. nigra
Common Tern Sterna hirundo
White-cheeked Tern S. repressa
Roseate Tern S. dougallii
Bridled Tern S. anaethetus
Sooty Tern S. fuscata
Little Tern S. albifrons
Royal Tern Thalasseus maximus
Crested Tern T. bergii
Lesser Crested Tern T. bengalensis
Sandwich Tern T. sandvicensis
Noddy Tern Anous stolidus
Grey Phalarope Phalaropus fulicarius
Red-necked Phalarope Lobipes lobatus
Great Auk Alca impennis
Autumnal Distribution of Young Mallards Banded at Kindersley, Saskatchewan

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This paper deals with some aspects of the seasonal and geographical distribution of the recoveries of Mallards (Anas platyrhynchos) banded as flightless young at Kindersley, Saskatchewan. It is based only on direct—first-year—recoveries and only on those direct recoveries of birds reported as shot by hunters during the hunting season—from early September in Canada to 15 January in the southern United States. It does not deal with birds found dead, trapped and released, or recovered in any manner other than by shooting.

Kindersley is located near the northwest corner of the treeless grasslands of Saskatchewan, 200 miles (322 km) northwest of Regina. From 1952 through 1959, 16,601 young Mallards between the ages of 3 and 8 weeks were banded to determine local movements in connection with damage caused by this species to cereal crops, subsequent movements during the hunting season, homing, and survival. Practically all of the banding was carried out west of Kindersley in various parts of a 2,900 square-mile (7,510 sq km) block bounded by the lines of 51° and 52° N and 109° and 110° W (Alberta-Saskatchewan boundary). This paper is based on data for the 4 years for which there were more than 150 direct recoveries each: 184 in 1955, 197 in 1956, 384 in 1957, and 339 in 1958.

Crews of two men and one or two dogs caught 8,650 of the 13,264 young Mallards banded from 1955 through 1958. Approximately 85 percent of the birds banded by these crews were caught and retrieved by dogs. The remaining birds were herded into traps set on land by crews of 5–7 men. Between 100 and 150 water areas, varying in size from a fraction of an acre to almost 4 square miles, were worked each year through June, July, and August. Details of these techniques may be found in Gollop (1956a, 1956b) and in Jensen (1956).

In 1955, 52 percent of the young Mallards were fitted with plastic neck bands for individual identification. These did not affect the recovery rate (Gollop, 1956a). Comparisons of direction and distance of recoveries with non-neck-banded birds for this and previous years indicate no significant differences owing to neck bands.

Although most of the personnel used in the banding phase of this project were employed by the Canadian Wildlife Service, other agencies contributed generously at various times. The author wishes to acknowledge assistance from the U.S. Bureau of Sport Fisheries and Wildlife, from the Saskatchewan Wildlife Branch, Department of Natural Resources, from Ducks Unlimited.

(Canada), and from private citizens at Kindersley. I also wish to thank the more than a thousand hunters who voluntarily reported recovery data to the U.S. Fish and Wildlife Service Banding Office which, in turn, kindly forwarded the information to me.

The following is a summary of information on hunters and hunting regulations during these years. The number of duck hunters in Alberta and Saskatchewan was probably less than 100,000. In the Pacific, Central, and Mississippi flyways of the United States the total number of active hunters alternated between 1.8 and 1.7 million (Crissey, 1957, 1958, 1959). (The Atlantic Flyway and Mexico are omitted here because of the few recoveries from these areas.) The legal daily kill in Alberta remained at 10, in the Mississippi Flyway at 4, and in the Central Flyway at 5. In Saskatchewan the daily limit dropped from 15 to 11 after the first 3 years and in the Pacific Flyway from 6 in the first 2 years to 5 in the last 2. In the northern parts of Saskatchewan and Alberta, hunting seasons opened on 1 or 2 September; in the south, on 6 or 7 September, except in 1956 when this date was 12 September. In all years Mallards left the Canadian prairies in November before hunting seasons legally closed. The earliest U.S. hunting seasons opened in October and the latest closed on 15 January. Season lengths remained at 70 days in the Mississippi Flyway, went from 65 to 75 in the Central, and from 80 to 95 in the Pacific. These variations apparently had no effect on the results reported below.

**GEOGRAPHICAL DISTRIBUTION**

The geographical distribution of 1,104 direct recoveries by province and state is presented in Fig. 1. In this figure, the distribution is shown diagrammatically, i.e. the dots indicating percentage are more or less centrally located in each state and province and are not located at the actual points of recovery. Thirty-five percent of the recoveries were from Canada. In individual years this has varied from 27 to 40 percent. The remainder of the hunting-season reports were from the United States, except for one from Mexico.

In Canada 36 percent of the kill was reported from within 10 miles (16 km) of the banding areas; 70 percent was within 50 miles (80 km). The remaining 30 percent of the Canadian reports were divided equally between Saskatchewan and Alberta, with more recoveries coming from north of the banding sites than south of them.

In the United States 91 percent of the reported harvest was southeast of Kindersley: 50 percent was from the Mississippi Flyway, 40 percent from the Central Flyway, and less than 1 percent from the Atlantic Flyway. Nine percent of the recoveries were from the Southwest in the Pacific Flyway. Almost two-thirds of the United States reports were from eight states—Montana, South Dakota, Nebraska, Iowa, Missouri, Arkansas, Louisiana, and Texas. The other third came from 25 states, including one or two reports
which were scattered among South and North Carolina, Florida, Michigan, and Nevada.

The reported kill within 50 miles of the banding sites was 24.6 percent of the continental total and represented the highest kill per unit area. The remainder of the Canadian kill (10.6 percent of the total) equaled the Arkansas kill (10.7 percent), but was much lower on a unit-area basis.

The average percentage distribution for the 4 years by direction, time, and distance from the banding area is presented in Fig. 2. There are five major divisions in this figure: the first includes reports indicating recoveries within 10 miles (16 km) of the banding sites, regardless of direction. The remaining four divisions are for reports beyond 10 miles to the northeast, to the southeast, to the southwest, and to the northwest. Whether a bird was shot 200 miles (322 km) north and 10 miles (16 km) west, or 200 miles west and 10 miles north of the banding area, the record appears in the northwest quadrant. For each direction the divisions are 10-day periods and 100-mile (161 km) zones (90 miles in the case of those zones adjacent to the 10-mile-or-less zone).

The boundaries of the period and area in which hunting was legal at some time from the 1955-56 through the 1958-59 season are also shown (Fig. 2). Since hunting dates often changed from year to year, this is a composite boundary showing the extreme dates for each zone. To the northeast this boundary delimits legal hunting in the southern and northern sections of Saskatchewan; to the southeast it includes southern Saskatchewan and the Central and Mississippi flyway seasons. (Recoveries in the Atlantic Flyway are designated by an abbreviation of the state name.) To the northwest, only southern and northern Alberta seasons have been outlined, although some records northwest of the banding sites were from Saskatchewan. The boundary to the southwest includes southern Alberta and the Pacific Flyway states, with the Montana hunting season appearing in both the southeast and southwest areas.

Direction of Movements.—Reports of recoveries north of the banding sites average 16 percent and reached a maximum of 22 percent in 1957. (Percentages in this section were calculated after deletion of recoveries in the 10-mile zone.) In 1957, also, the recoveries from northwest of the banding area were double the average of the other 3 years. However, this above-average northwest movement was not reflected in a subsequent increased reported kill to the southwest. It was followed by above-average kills in Montana and South Dakota and, as a result, 1957 was the only year in which Central Flyway reports outnumbered those from the Mississippi Flyway. On the other hand, this northwest increase was apparently at the expense of reported harvest within 10 miles of the banding sites and, to a lesser extent, to the southeast.

Northwest movement usually involved more birds and greater distances

(Text continued on page 860)
J. B. Gollop: Autumnal Distribution of Saskatchewan Mallards

Average percentage distribution of recoveries presented in Fig. 1 by direction, 10-day period and 100-mile zone.

- = 1%  o = 0.33%
X = less than 0.16%  x = one record

Boundary of area open to hunting, composite 1955-1958, maximum limits.
1094 Usable records.

FIG. 1
1955 to 1958 incl.

DATE
Fig. 1 1955-1958 incl.

Average percentage distribution of recoveries presented in Fig. 1 by direction, 10-day period and 100-mile zone.
than reports from the northeast. However, in 1955 the number of recoveries from the northeast was double that from the northwest.

Recoveries south of the banding sites averaged 72 percent to the southeast (Saskatchewan, Central and Mississippi flyways) and 12 percent to the southwest (Alberta and the Pacific Flyway).

Distance of Recoveries.—When plotted by distance, the reports showed a major peak within 50 miles of the banding sites, a minor peak between 1,000 and 1,100 miles, and a higher minor peak between 1,400 and 1,500 miles. However, this statement demonstrates a problem involved in basing statements on averages or totals. Both of the minor peaks were significantly affected by 1955 data: The 1,400-mile peak was not a peak in any 1 year; it was exceeded by the 1,500-mile peak in 3 years, but the 1955 contribution was so low that the average was pulled down. The 1,000-mile peak was higher than the 1,400-mile peak in 1955.

Considering zones of low kill, the 300–400-mile and the 200–300-mile zones (southward) alternated for light reporting rates, and the 1,300–1,400-mile zone was lower than adjacent zones in 3 of 4 years (1958 excepted).

SEASONAL DISTRIBUTION

On the average, reported recoveries through the autumn and early winter were fewest in early September, built up to a peak in mid-November, and fell off gradually to 15 January.

In considering periods of low kill, there was little deviation from the gradual buildup and decline each year. However, the period 21–30 October was significantly lower than the periods immediately before and after it in 3 of the 4 years (1957 excepted).

Young Mallards were shot within 10 miles of the water areas on which they were banded almost every week through September, October, and into November each year until practically all ducks had left the district.

There were differences in the seasonal rate of kill between years, and there was a direct correlation between the kill during the first half of the season and the kill in the north. This can be seen in Table 1 (where unusable dates are eliminated).

<table>
<thead>
<tr>
<th>Hunting Season</th>
<th>No. of Usable Recoveries</th>
<th>Percent by Nov. 10</th>
<th>Percent within 800 Miles</th>
<th>Percent within 1,200 Miles</th>
</tr>
</thead>
<tbody>
<tr>
<td>1955–56</td>
<td>184</td>
<td>60</td>
<td>60</td>
<td>83</td>
</tr>
<tr>
<td>1957–58</td>
<td>374</td>
<td>50</td>
<td>58</td>
<td>72</td>
</tr>
<tr>
<td>1958–59</td>
<td>339</td>
<td>43</td>
<td>46</td>
<td>62</td>
</tr>
<tr>
<td>1956–57</td>
<td>197</td>
<td>31</td>
<td>38</td>
<td>56</td>
</tr>
</tbody>
</table>

This distinction is more striking between 1955 and 1956 when only the Central and Mississippi flyways are considered, the percentages in these years being as follows:
There were no recoveries from Wisconsin and Michigan. The four recoveries farthest from the banding sites—in the Atlantic Flyway—were made in years of a "late" harvest, 1958 and 1956.

The monthly distribution of recoveries is summarized in Table 2. Thirty-day periods were used to correspond with the data in Fig. 2; this means that

<table>
<thead>
<tr>
<th>Recovery Period</th>
<th>Percent of Total Reports</th>
<th>Legal Hunting Season*</th>
<th>Extreme Miles (km) from Kindersley</th>
<th>Majority of reports</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept. 1–Sept. 30</td>
<td>9</td>
<td>0–400 (0–644)</td>
<td>Canada</td>
<td>0–150 (0–241)</td>
</tr>
<tr>
<td>Oct. 1–Oct. 30</td>
<td>23</td>
<td>0–1,600 (0–2,574)</td>
<td>Canada and 23 states</td>
<td>0–1,280 (0–2,060)</td>
</tr>
<tr>
<td>Nov. 30–Dec. 29</td>
<td>19</td>
<td>0–1,900 (0–3,057)</td>
<td>Canada and 31 states</td>
<td>0–1,880 (0–3,025)</td>
</tr>
<tr>
<td>Dec. 30–Jan. 15</td>
<td>7</td>
<td>400–1,900 (644–3,057)</td>
<td>15 states</td>
<td>510–1,790 (821–2,880)</td>
</tr>
</tbody>
</table>

*Canada: Saskatchewan and Alberta only; U.S.A.: all 31 states of Pacific, Central, and Mississippi flyways; Atlantic Flyway omitted.

calendar months are not strictly adhered to. If hunting was legal on only 1 of the 30 days in a state, it was listed as having an open season in that period.

Although these young Mallards could have been shot in Canada up to 400 miles (644 km) from the banding sites in September, more than half of them were still within 10 miles (16 km) and none were more than 150 miles (241 km) away.

In October, the hunting season opened in the northern and central states of the three western flyways, up to 1,600 miles (2,574 km) from Kindersley. Still closed were Arkansas, Louisiana, Kentucky, Tennessee, Alabama, Mississippi, Texas, and New Mexico. However, almost two-thirds of the re-
recoveries were made within 100 miles (161 km) of the Kindersley district, and no bird was reported within 300 miles of the most distant point where hunting was legal. Of the recoveries less than 100 miles away, more were north of the banding sites than south of them and more were in Alberta than in Saskatchewan.

During at least part of November, hunting was legal within 1,900 miles (3,057 km) of Kindersley, i.e. in all 31 states of the Pacific, Central, and Mississippi flyways and in Saskatchewan and Alberta. The scarcity of Canadian records (10 percent of the period’s total) reflects what experience had shown: that most Mallards moved out of the Canadian prairies by mid-November. These three 10-day periods were individually the highest for the entire season—17 percent for 10–19 November, 14 percent for 31 October to 9 November, and 11 percent for 20–29 November. Young Mallards were shot as far away as hunting was legal and almost two-thirds were shot between 700 (1,126 km) and 1,700 miles (2,735 km) away, mostly to the southeast.

In 1956, these Mallards were banded within 60 miles (97 km) of each other between mid-June and mid-August. Four months later, recoveries were reported from Saskatchewan (11 November), California (17 November), and North Carolina (19 November). It is 2,070 miles (3,331 km) between the Saskatchewan and Carolina recoveries and 2,500 miles (4,023 km) between the two U.S.A. points.

Hunting seasons were open for at least the first half of December in Canada and in all 31 western states. There were no Canadian recoveries, and most of the reports (62 percent) were in a 700-mile band to the southeast, between Missouri and Texas.

The latest hunting seasons closed on 15 January. During the last week of this period, hunting was restricted to the eight states of the Mississippi and Central flyways where it was closed in October and in three to five Pacific Flyway states (California, Arizona, Nevada, Oregon, and Washington), depending on the year. Both the farthest recovery and the bulk of the recoveries indicate that the southern portion of the kill occurred farther north in January than in December. This may have been due to unfavorable hunting conditions in January along the Gulf of Mexico or to movement away from the coast.

BIASES IN THE DATA

The foregoing can be interpreted only as a statement of the distribution of reported recoveries of young Mallards shot during the hunting season immediately following the period of banding. Before interpretations can be extended to the distribution of the first-year harvest of these birds, let alone the autumn movements of the Kindersley-raised population of Mallards, much supplementary information is necessary. Some of the factors involved are discussed briefly below.
In the area in which the birds are banded, population size and the survival of broods from year to year must be considered. Some of the factors adversely affecting the survival of flightless young are different habitat conditions (drought), weather (hail), predation, disease, and, possibly, method of capture. As for the method of capture, the recovery rate for birds caught by dogs was slightly higher (not statistically significant) than the rate for man-caught birds (Gollop, 1958).

Once the banded birds have been recovered, an important assumption usually made is that marked birds represent the same numbers of unmarked birds when recovered in different areas as they did when banded. Crissey (1955) has pointed out the problems involved here. The two premises on which this assumption has rested in the past are: (a) the opportunity to take a duck is equal between years and between areas, and (b) the same percentage of recovered bands is reported from each area each year.

In connection with the first premise, it is conceivable that hunting conditions might be such that 20 percent of the population passing through the Central Flyway was harvested while only 10 percent of that in the Mississippi Flyway was shot. If this were the case and if Kindersley Mallards actually distributed themselves equally between these two areas, band recoveries would show a 2:1 ratio in favor of the Central Flyway. This in turn might be interpreted erroneously as a distribution of 67 percent of these birds in one flyway and 33 percent in the other.

Factors affecting hunting conditions and kill between areas and years are many. Weather is probably the most important. Varying attributes of a waterfowl population itself are another. For instance, the continental kill of a species migrating in one area is probably influenced by the size of that population in relation to populations of the same species raised elsewhere and to the populations of other species once these groups mix with each other in migration. Differential hatching dates and age and sex ratios between years may have an influence. The conditions of late-summer and autumn habitat in both breeding and migration areas affect waterfowl movements and harvest efficiency. Changes in hunting regulations, the number and distribution of hunters, and hunting effort are also factors that have to be measured and evaluated.

In connection with the percentage of recovered bands that are reported, Bellrose (1955) and Geis and Atwood (1961) have conducted investigations with reward and control bands, and with mail questionnaires. Based on corrections resulting from their findings, changes in the distribution of Kindersley recoveries are presented in Table 3.

This adjustment makes little difference between Canada and the United States. It does make a difference in the ratios between flyways.

Even before a banded bird is in the hunter’s hand, there is a bias resulting from differential crippling losses between areas. Crissey (1957) indicated a crippling loss in 1956 of 14 percent in the Pacific Flyway, 14 percent in the
Table 3.—Percentage Distribution Adjusted for Reporting Rate of Recovered Mallards (1955–58)

<table>
<thead>
<tr>
<th>Where Recovered</th>
<th>Unadjusted Distribution</th>
<th>Excluding Mexico</th>
<th>Adjustment Factor</th>
<th>Adjusted Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canada</td>
<td>35.1</td>
<td>35.2</td>
<td>0.82\textsuperscript{a}</td>
<td>33.0</td>
</tr>
<tr>
<td>United States</td>
<td>64.8</td>
<td>64.8</td>
<td>—</td>
<td>67.0</td>
</tr>
<tr>
<td>Mexico</td>
<td>0.1</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Four U.S. Flyways</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific</td>
<td>6.1</td>
<td>6.1</td>
<td>0.69\textsuperscript{b}</td>
<td>4.8</td>
</tr>
<tr>
<td>Central</td>
<td>25.6</td>
<td>25.6</td>
<td>0.83\textsuperscript{b}</td>
<td>24.4</td>
</tr>
<tr>
<td>Mississippi</td>
<td>32.7</td>
<td>32.7</td>
<td>1.00\textsuperscript{b}</td>
<td>37.4</td>
</tr>
<tr>
<td>Atlantic</td>
<td>0.4</td>
<td>0.4</td>
<td>0.77\textsuperscript{b}</td>
<td>0.4</td>
</tr>
</tbody>
</table>

\textsuperscript{a} From Bellrose (1955).
\textsuperscript{b} From Gels and Atwood (1961).

Central, 19 percent in the Mississippi, and 23 percent in the Atlantic. In other words, for every hundred ducks shot in each flyway, the numbers that hunters actually retrieved were 86, 86, 81, and 77, respectively. This factor alone would account for 13 percent more recoveries in the Pacific than in the Atlantic Flyway. Similar data are not available for Canada.

SUMMARY

Geographical and seasonal distribution of 1,104 reported recoveries of young Mallards shot during the hunting season immediately following the period of banding at Kindersley, Saskatchewan, from 1955 through 1958 are presented. Thirty-five percent of the recoveries were from Canada and 65 percent from the United States. Thirty-six percent of the Canadian recoveries were within 10 miles (16 km) of the banding sites, and 70 percent were within 50 miles (80 km). Within the United States 50 percent of the recoveries were from the Mississippi Flyway, 40 percent from the Central, 9 percent from the Pacific, and less than 1 percent from the Atlantic Flyway. On a monthly basis, the reports were distributed as follows: 9 percent in September, 23 percent in October, 41 percent in November, 19 percent in December, and 7 percent in January. Difficulties of interpretation are discussed briefly. Correction factors for differential reporting rates make little difference to the distribution of these recoveries.

LITERATURE CITED


The Use of Great Horned Owls in Catching Marsh Hawks

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Raptor studies have been handicapped by the difficulty of catching breeding adults. Curiously, the use of owls has been largely overlooked by modern bird catchers, although Christian Brehm described the use of Eagle Owls (Bubo bubo) for netting raptors in 1855 and it was plainly not a new technique even then. As recently as 1943, Captain R. Luff Meredith in Wood and Fyfe's *Art of Falconry of Frederick II* gave several ways of setting a dho-gaza and illustrated a rig with four dho-gazas and an owl. I have modified these techniques for catching breeding Marsh Hawks (*Circus cyanus*).

The equipment is simple (Fig. 1). A live Horned Owl (*Bubo virginianus*) is jessed in the traditional manner used by falconers. It is fastened by a leash to a perch under the dho-gaza so that it cannot touch it. The dho-gaza that our group (see acknowledgments) uses is a 6-ft × 8-ft piece of black nylon gill net. The stretched mesh is about 4½ inches. The net is hung with strong fine cord, only around the edges, in such a manner that when all four corners are pulled out there is no sag. There is a loop of cord at each corner. The dho-gaza is then stretched vertically between two slender poles 8 ft to 16 ft high, being fastened at each corner by a hook made of a single strand of soft picture wire run through the corner loop. The hawk stoops at the owl and goes into the net. All four hooks unbend as the hawk takes the net and becomes entangled. Because some of the hawks have flown too far with the dho-gaza, we now always fasten a nylon stocking, containing about a half-pound weight in the toe, to one of the lower corners of the net. Especially in heavy cover, the stocking is easier to find than a netted hawk.

Overcast days with a wind of about 5 miles per hour appear to be optimum for Marsh Hawk netting. The dho-gaza should be set crosswind. If there is sunlight and essentially no wind, Marsh Hawks tend to orientate their stoops in relation to the sun when attacking the owl, usually stooping either directly toward, or directly away from the sun. It is our impression that, when the young Marsh Hawks have eggs or small young, trapping success is highest early in the morning, but after the young are on the wing, the parents are not apt to visit the nest until about 2 hours after sunrise.

Having set up the rig, one retreats to a vantage point prepared to run as fast as possible to grab the hawk, for one is never sure that it is thoroughly

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1This is part of a study made possible by the Josselyn Van Tyne Fund of the American Ornithologists' Union. I also wish to thank those who helped with the field work, and particularly Frederick Hamerstrom, Daniel Berger, Raymond Anderson, Gary Hampton, Glen Fox, Gary Anweiler, and Ross Lein.

caught. Certain individual hawks keep knocking down the net, are entangled only a short time, and then escape, and one may have to reset the dho-gaza repeatedly. Thus, some individuals became so net shy that we never were able to catch them. More often our failures to catch the hawks appeared to be because certain individuals are not especially keen on stooping at an owl. Quite often the mate of such an individual is spectacular at stooping.

Fig. 1. Dho-gaza set to catch Marsh Hawks.

Females are usually easier to catch. We ordinarily do not trap until after the eggs have hatched in order to avoid keeping the incubating female off the nest too long. Males are more easily caught early in the nesting season, but after the young are half grown some of the males seldom, and possibly never, come near the nest again. However, we have several times trapped both adults when the young were already on the wing by setting up where the young spent most of their time, sometimes even when we did not know where the nest had been.

We like to set up at least 2 yd from the nest so that we do not leave a trail to the nest for mammalian predators to follow. We have made several catches 30 yd or more from the nest, where the terrain near the nest was unsuitable.

Usually we use a live owl, which we tether to the perch in such a way that it cannot reach the ground; it will come back onto the top of the perch
if it happens to bate. An owl that is free to leave a low perch often stays
down on the ground, where it is not conspicuous enough. Stuffed Horned
Owls have proven satisfactory, and we have made 14 catches with them. A
few individual Marsh Hawks seem to stoop more vigorously at an owl
placed very close to the nest. In such cases, particularly if the young hawks
have hatched, it is best to use a stuffed owl, or to tether the owl on a high
enough perch so that the young hawks cannot reach it. Young Marsh Hawks

![Diagram of dho-gaza set over water to catch Ospreys.]

Fig. 2. Dho-gaza set over water to catch Ospreys.

have twice crawled under our live Horned Owl, once to escape hot sunlight,
and once to get out of the rain; fortunately our owl was not sharp-set, but
it might have jeopardized their chances for survival.

Sometimes Marsh Hawks are caught on the first stoop in a matter of
moments after they have spotted the owl. Other individuals may warm up
for 2 or even 3 hours before they finally come low enough to hit the dho-
gaza. Occasionally visiting Marsh Hawks, not associated with the nest, may
come from some distance to stoop at the owl. Weakly stooping individuals
tend to increase the vigor of their stoops if another Marsh Hawk appears.

We have made 84 catches of breeding raptors: 63 of these were Marsh
Hawks, 50 percent more females than males, plus one juvenile female about
a week before she started migrating. This method has not proven practical
for catching migrating hawks: At the Cedar Grove Ornithological Station,
Cedar Grove, Wisconsin, only a single Red-tailed Hawk (*Buteo jamaicensis*) has been netted over a Horned Owl.

We have tried for several other species and have caught 4 adult Short-eared Owls (*Asio flammeus*), setting as for Marsh Hawks, and 1 Broad-winged Hawk (*Buteo platypterus*), setting on the ground near the nest tree. Daniel Berger, Helmut and Nancy Mueller, and the Hamerstroms devised an over-water rig for trapping Ospreys (*Pandion haliaetus*), of which we have netted 14. The dho-gaza poles are mounted on a floating cross, which is anchored near the nest (Fig. 2). This is undoubtedly the most efficient device we have tried. On land sets, with each change in the wind direction, one must disrupt trapping opportunities by running out to reset the poles so that the dho-gaza is again crosswind. As our Osprey rigs have been anchored in water without a current, they adjust to the proper wind direction automatically.

Other methods that we have used for catching Marsh Hawks have been a simple bownet with which we caught the females on two nests, and the bal-chatri (Berger and Hamerstrom, 1962) with which we made 99 Marsh Hawk catches, only 4 of which were during the nesting season. Bal-chatris baited with live Starlings (*Sturnus vulgaris*) proved ineffective during the summer when the hawks have an abundant food supply and the cover is so high that the traps are not conspicuous.

Live or stuffed owls in conjunction with dho-gazas are an efficient method of catching a variety of species of breeding raptors. Injuries have been non-existent, or so slight as to be not worth mentioning. One hawk undoubtedly was killed because we neglected to fasten a clog to the dho-gaza and we never could find her.

Several species of owls would undoubtedly prove satisfactory: Marsh Hawks have stooped at a Snowy Owl (*Nyctea scandiaca*) and at a Barred Owl (*Strix varia*). Tame owls, accustomed to handling, adapt well as decoys and are far easier and quicker to use than wild ones.

**SUMMARY**

A dho-gaza set over a tame or stuffed Horned Owl is a practical method for catching adult breeding Marsh Hawks and several other species of raptors (84 catches). The net is set crosswind, with a half-pound weight as a clog; overcast days with a 5-mile-an-hour wind are best. The owl and net on a cross floating on water will catch breeding Ospreys.

**LITERATURE CITED**


Comparative Molt Cycles in the Tyrannid Genus *Empidonax*

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Although there have been a few studies of timing and extent of molt in congeneric, resident species of birds, for example in *Lophortyx* (Raitt, 1961; Raitt and Ohmart, 1962) and in *Aphelocoma* (Pitelka, 1945), to my knowledge no attempt has been made to compare patterns and cycles of feather replacement in closely related, migratory species with a view to revealing possible adaptive modifications. The tyrannid genus *Empidonax* is appropriate for such a study because it comprises a well-knit group of species whose molts, as now understood, reveal striking interspecific differences that provoke an attempt at analysis of molt adaptation.

Dwight (1900), Dickey and van Rossem (1938), Moore (1940), Bent (1942), and Mengel (1952) have provided information on molt in *Empidonax*, particularly for those species breeding in eastern North America. Recently, molt cycles have been outlined in detail for *E. hammondii*, *E. oberholseri*, and *E. wrightii* to provide a partial basis for the segregation of juveniles, first-year birds, and adults for systematic purposes (Johnson, 1963); a discussion of the presumed adaptive meaning of the extent and scheduling of molt in these three species, together with new data gathered by the author for *E. flaviventris* and *E. minimus*, represents the focus of the present report.

**Acknowledgments.**—The author is indebted to the curators of the following museums and universities for the loan of specimens: American Museum of Natural History, United States National Museum, Museum of Comparative Zoology, Carnegie Museum, California Academy of Sciences, University of Arizona, University of California at Los Angeles, Cornell University, Louisiana State University, University of Utah, and the Moore Laboratory of Zoology at Occidental College. Specimens were also examined from the private collection of Gale Monson. Mrs. Ethel McDonald typed the manuscript, Gene M. Christman prepared the figure, and Hans J. Peeters assisted with proofreading. While working on various phases of molt problems in *Empidonax*, I have benefited from discussions with Alden H. Miller and Frank A. Pitelka.

**SYNOPSIS OF MOLTS**

For purposes of discussion, the essential features of the molts of certain species will be described. The sequence and scientific nomenclature of species follow the American Ornithologists’ Union *Check-list of North American Birds* (1957). The molt cycles of five of the species to be considered are illustrated in Fig. 1.

Age categories have been defined as follows: *juvenile*, any individual that has not completed the postjuvenal molt; *immature*, a bird between the end of the postjuvenal molt and the first prenuptial molt; *first-year bird*, an individual between the first prenuptial molt and the end of the first postnuptial molt; and *adult*, any bird that has completed the first postnuptial molt in its life cycle.

**Empidonax flaviventris** (Yellow-bellied Flycatcher)

*Postjuvenal Molt.*—Occurs on or near the breeding grounds, prior to the fall migration, from early (?) July to at least early September. Ten specimens in fresh first-winter plumage (immatures) have been examined from Vermont, Massachusetts, New York, and the District of Columbia, bearing collection dates between 24 August and 6 October. The fact that occasional individuals may complete the postjuvenal molt by late August indicates that this molt possibly begins as early as late June. This molt apparently involves only the body plumage; no evidence is available that the flight feathers are renewed at this time.
Prenuptial Molt.—Occurs on the wintering grounds between mid-February and mid-May. Seven of eight specimens available in the period between mid-February and the end of March that are in the process of prenuptial molt are obvious first-year birds by reason of their retention of juvenal rectrices; the other specimen cannot be aged with certainty because it has recently replaced the tail feathers. This may indicate that the young birds are timed somewhat ahead of the adults in the spring molt, although further material needs to be examined to prove this point. The prenuptial molt is probably complete in most individuals, with the exception that certain adults may retain a few flight feathers. Two specimens from southern Mexico illustrate that occasionally the prenuptial molt of adults may involve only the replacement of those flight feathers that had not been renewed during an incomplete postnuptial molt of the previous fall. For example, an individual collected on 9 May 1961 by L. L. Wolf in Oaxaca, Mexico (La. State Univ. Mus. Zool. No. 24567) has the adult rectrices, left primaries 1 to 6, right primaries 1 to 7, and secondaries 1 to 6 + 8 of the previous fall, but had fresh, newly acquired left primaries 7 to 10, right primaries 8 to 10, and both pairs of secondaries 7 and 9. The difference between these two generations of flight feathers was only detectable upon close scrutiny, and because the bird had recently replaced the body plumage during the prenuptial molt, it appeared to be in sleek new plumage. A second specimen illustrating this point was collected on 12 May 1959 by D. G. Berrett in Tabasco, Mexico (La. State Univ. Mus. Zool. No. 22956). It had recently replaced primaries 7 to 10 on both sides, secondaries 7 to 9, and all rectrices as well as most or all of the body plumage. That the prenuptial molt of first-year birds may occasionally be incomplete is indicated by a specimen taken on 10 June 1934 by A. H. Miller in British Columbia (Mus. Vert. Zool. No. 65634). This individual is in fresh plumage except for a few old coronal region and alular feathers, and rectrices 1–1, which are old and pointed (juvenal generation). All other specimens examined by the author from localities of spring migration or of breeding in eastern North America have been in overall fresh plumage, providing concrete evidence of a complete previous spring molt.

Postnuptial Molt.—Occurs on the wintering grounds after the fall migration. Specimens in active molt have been seen in early October only. Although this molt may be complete in certain individuals, the evidence available to the author suggests that typically it is incomplete. In a series of 15 adults taken on the wintering grounds in southern Mexico and Central America between 5 December and 16 March, after the postnuptial molt and before the prenuptial molt, only one specimen had the appearance of having undergone a complete fall molt. The remaining specimens had retained varying numbers of old coronal feathers, dorsal-tract feathers, distal primaries, and proximal secondaries through the postnuptial molt. One specimen had retained all of the old rectrices, whereas another had retained only the central pair; the others had replaced all the tail feathers. Primary feathers retained
were: numbers 5 to 10 (1 specimen); 6 to 10 (2); 7 to 10 (4); 8 to 10 (2); and 9 and 10 (3). Secondary feathers retained were: numbers 2 to 7 + 9 (2 specimens); 3 to 7 + 9 (3); 4 to 7 + 9 (1); 5 to 7 + 9 (1); 6, 7, and 9 (1); and 7 and 9 only (4). None of the specimens mentioned above was in active molt; the peculiar occurrence of two generations of flight feathers was entirely a result of the postnuptial molt having been arrested “prematurely.”

According to Dickey and van Rossem (1938:375-376), the postjuvenal molt in this species takes place rather late in the fall, on the wintering grounds, and involves only the body feathers. They further state that the first-year birds undergo a complete prenuptial molt beginning in early April. The postnuptial molt of adults is said to occupy the entire period from late fall to early spring and starts with the complete molt of body feathers. After the body plumage is renewed, a protracted primary molt ensues that may last until mid-March. Dickey and van Rossem also reported that the adults, like the juveniles, undergo replacement of the body plumage from late March through April. However, only the first-year birds are said to have a complete prenuptial molt.

My interpretations of the molt cycles of the Yellow-bellied Flycatcher are considerably different from those cited above, and it is now clear that the molts of this species do not differ so strikingly in pattern and timing from those of congeneric forms, as was indicated by the descriptions of Dickey and van Rossem. In other words, there is no evidence of a protracted primary molt in adults that occupies the winter period and that follows an autumnal molt of the body plumage. The chief distinctiveness of the molts of *E. flaviventeris* lies in their extent and in the fact that there are two periods of the year during which complete molts can occur. Furthermore, the prenuptial molt is usually complete for first-year birds and adults, but the postnuptial molt is often not, the reverse of the situation seen in other well-studied species of *Empidonax*. The occasional occurrence of a “split” flight-feather molt is to my knowledge without parallel elsewhere in the genus.

The fact that the juveniles undergo the postjuvenal molt prior to the fall migration, whereas the adults migrate south before the postnuptial molt, has not been generally recognized for this species. In this respect, the Yellow-bellied Flycatcher is similar to the Least Flycatcher. This phenomenon is further discussed below.

*Empidonax minimus* (Least Flycatcher)

*Postjuvenal Molt.*—Occurs from early (?) July to late (?) October on the breeding grounds; late phases are probably completed during migration. Variable in extent; typically this molt involves part or all of the body plumage and, occasionally, secondaries 8–8 and a few upper greater and upper middle secondary coverts. Rarely, secondaries 7–7 and rectrices 1–1 are renewed. A specimen (Mus. Vert. Zool. No. 111182), collected on 15 October 1938 by W. W. Brown in Guerrero, Mexico, that was not active in post-
juvenal molt and yet is largely in juvenal plumage, suggests that in occasional individuals this molt is very limited or even lacking.

**Prenuptial Molt.**—Occurs on the wintering grounds from mid-February to mid-May, with peak activity on a population basis from mid-March to late April. This molt seems to involve first-year birds almost exclusively; from among a series of 52 specimens examined (32 first-year birds and 20 adults) that had been taken during the period of prenuptial molt and in the subsequent spring migration and summer residency period, all of the first-year birds, but only three of the adults, showed positive evidence of any recent feather replacement. Two of the adults were replacing limited dorsal-tract feathers (male, taken by D. G. Berrett on 15 April 1959 in Tabasco, Mexico—La. State Univ. Mus. Zool. No. 22952; and male, taken by H. C. Land on 17 February 1959 in Guatemala—Mus. Vert. Zool. No. 142523), whereas the third had renewed both eighth secondaries (male, taken by John Davis on 21 May 1941 in New York; Mus. Vert. Zool. No. 84209). The prenuptial molt of first-year birds is usually extensive, involving most or all of the body plumage, two or three pairs of inner secondaries (numbers 7, 8, or 9) and their corresponding upper greater and middle coverts, and a variable number of pairs of rectrices (commonly pairs 1–1 and 6–6, or pairs 1–1, 2–2, 5–5, and 6–6 are molted together). Four specimens of the first-year group had molted all their rectrices. Two specimens had renewed secondaries 6–6 in addition to pairs 7, 8, and 9. A point to be stressed, however, is that there is as yet no evidence that the prenuptial molt is ever complete in this species.

**Postnuptial Molt.** Occurs from at least late August to mid-November on the wintering grounds. Apparently complete in first-year birds and adults.

Dickey and van Rossem (1938:379) have stated that the “molts and plumages of the least flycatcher parallel those of *flaviventris* and *traillii*. In other words the ‘first nuptial’ and ‘adult nuptial’ plumages are acquired by molt and not, as supposed by Dwight, by wear.” These remarks imply the existence of a molt program in this species quite different from that indicated by the present study. They suggest that the young of the Least Flycatcher have a complete prenuptial molt whereas the adults have a prenuptial body-feather molt, although unfortunately they do not provide supporting data for their statements. Certainly it is clear that prenuptial molts are significant in at least first-year birds of this species.

To my knowledge it has not previously been reported that a difference exists in timing of fall molts with relation to migration between adults and young of the year, with juveniles undergoing the postjuvenal molt prior to migration, the reverse of the pattern shown by the adults.

**Emidonax hammondii** (Hammond Flycatcher)

**Postjuvenal Molt.**—Occurs from early July to mid-October on the breeding grounds; very late phases may be completed during migration. Involves most or all of the body plumage, never any flight feathers or coverts.
Prenuptial Molt.—Occurs from late February to mid-April on the wintering grounds. Variable in extent in both first-year birds and adults; usually only the body plumage is involved, although rarely secondaries 8 and 9 and rectrices 1–1 and/or 6–6 may be renewed.

Postnuptial molt.—Occurs from mid-June to mid-September on the breeding grounds. Complete in both first-year birds and adults.

Empidonax oberholseri (Dusky Flycatcher)

Postjuvenile Molt.—Occurs from late August to early January on the wintering grounds. All body plumage, from one to three pairs of inner secondaries (no. 7–9), and a variable number of upper secondary coverts are typically replaced.

Prenuptial Molt.—Occurs from early March to mid-May on the wintering grounds. Variable in extent, usually only body plumage is renewed. However, first-year birds may replace from one to three pairs of proximal secondaries and a few inner greater and middle secondary coverts.

Postnuptial Molt.—Occurs from mid-August to early December on the wintering grounds. Complete in both first-year birds and adults.

Empidonax wrightii (Gray Flycatcher)

Postjuvenile Molt.—Occurs from late July to late December on the wintering grounds. Most of the body plumage is typically replaced. Renewal of rectrices is variable; usually either pair 1–1 or pair 6–6 is replaced; more extensive molt is less common. Rarely, all the rectrices are molted. Typically secondaries 8 and 9, less often number 7, are replaced. Some secondary wing coverts are usually renewed.

Prenuptial Molt.—Occurs from early March to mid-May on the wintering grounds. Extremely variable in extent; from a few body feathers to all the body plumage may be renewed. Rectrices 1–1 and/or 6–6 and secondaries 8 and 9 (rarely 7 and 6 also) may be replaced when the molt of body plumage is extensive. This molt mainly involves first-year birds (those individuals that had a relatively incomplete postjuvenile molt?).

Postnuptial Molt.—Occurs from late (?) July to mid-December on the wintering grounds. Complete in both first-year birds and in adults.

The Molts of Other Migratory Species of Empidonax

There are scattered data in the literature concerning the molt cycles of the Acadian Flycatcher (Empidonax virescens), Traill Flycatcher (E. traillii), and the Western Flycatcher (E. difficilis) which will be summarized here. The molts of none of these species have as yet been studied in detail by the author.

Mengel (1952:274–277) has provided certain points of interest regarding the molts of E. virescens. His data suggest the existence of a partial postjuvenile molt (juvenal remiges and rectrices retained) and a complete postnuptial molt in August and September, prior to the autumn migration.
Although he had no evidence concerning prenuptial molts in this species, Mengel believed that either a partial or a complete spring molt does occur in *E. virescens*, as in related forms.

For *E. traillii* (including *E. t. traillii* and *E. t. brewsteri*), Dickey and van Rossem (1938:376–378) report that the postnuptial molt occurs on the wintering grounds from early September to late January. The adults are said to have a prenuptial molt of body plumage that is “finished just before the northward migration in April. The young retain the remiges and rectrices through the winter and in April go through a complete molt.” Thus, they describe the molt cycles of *E. traillii* to be similar to those they attribute to *E. flaviventris* and *E. minimus*. Because my data disagree on numerous points with the statements of Dickey and van Rossem concerning the molts of *E. flaviventris* and *E. minimus* (see above), I also doubt their remarks on the molts of *E. traillii*.

Concerning *E. difficilis*, Bent (1942:250) comments that “What few specimens are available seem to indicate that young birds molt the body plumage late in the fall and have a complete prenuptial molt in late winter or spring. Adults seem to follow a similar sequence, with perhaps a renewal of the flight feathers during the winter.” These very general and tentative remarks indicate that the molts of this species are essentially unknown; the basis for the statement of Bent, that the molts described for the Western Flycatcher “apparently correspond to those of the yellow-bellied flycatcher,” is therefore not clear.

**ADaptation in extent of molt**

In every species of the genus that has been sufficiently studied, the adults undergo two molts per year, a prenuptial and a postnuptial, at least one of which is always complete. Thus, two alternating molts of this extent are apparently adequate for all members of this group. It is of interest to examine the extent of molt from both intra- and interspecific standpoints to see if differences exist that may be adaptive.

For example, there is considerable difference in extent of postjuvenal molt in *E. hammondii*, on the one hand, and in *E. oberholseri* and *E. wrightii* on the other, a divergence that is concerned chiefly with whether or not certain flight feathers and coverts are renewed along with the molt of the body plumage. In *E. hammondii* this molt is the least extensive of the three species and takes place rather early; in *E. oberholseri* and in *E. wrightii* the molts nearly always involve some secondaries and secondary coverts and occasionally rectrices (in the latter species), and the molts are timed relatively late. The latter two species migrate south in their juvenal plumage; this, plus the fact that a relatively long period of time passes subsequent to the postnatal molt, suggests that the feathers would be correspondingly more worn than in *E. hammondii*, hence selection might favor more extensive replacement. Very likely the greater the length of time between the postnatal and the postjuve-
nal molt, the greater the number of feather follicles that are activated by the postjuvenal molt. When flight feathers are renewed in the postjuvenal molt, it is significant that they are those most vulnerable to wear, hence the most in “need” of replacement (the exposed inner secondaries and exposed rectrices). This generalization applies also to the prenuptial molt. The adaptive value of all three species replacing most or all of the fluffy juvenal plumage during the postjuvenal molt is probably a mechanism by which a set of feathers is replaced that might reach a dangerous degree of disintegration if not renewed until a subsequent (prenuptial) molt.

Is there any relationship between the extent of the prenuptial molt and the timing and extent of the postjuvenal molt of the previous summer and fall? In *E. hammondii* an early, relatively incomplete postjuvenal molt on the breeding grounds is correlated with a limited prenuptial molt on the wintering areas. The comparatively early timing of the prenuptial molt, with a peak being reached perhaps 3 weeks earlier in *E. hammondii* than in either *E. oberholseri* or *E. wrightii*, may be related to the early position of the postjuvenal and the postnuptial molts. The back-to-back occurrence of two very incomplete molts in young *E. hammondii* is apparently without parallel elsewhere in the genus. In contrast, *E. oberholseri* and *E. wrightii* have late, relatively extensive postjuvenal molts, and also fairly extensive prenuptial molts. Perhaps these more complete prenuptial molts are related to the fact that the subsequent postnuptial molts in individuals of these species occur late. Thus, the renewal of vulnerable flight feathers in the prenuptial molts may be an adaptive mechanism that helps permit repeated migrations on what is essentially the same set of juvenal rectrices and remiges. Distal primaries and secondaries and certain wing coverts, however, are not renewed by many individuals of *oberholseri* and *wrightii* until they have completed their first three migrations.

There are certain correlations between the completeness of successive molts in *E. flaviventris* that are worthy of comment. The existence of complete prenuptial molts perhaps “compensates” for the early and relatively limited postjuvenal molt and for the postnuptial molt. The latter molt, although timed rather late when compared with the postjuvenal molt in this species, is typically incomplete, hence a complete molt in the spring would appear to be adaptive. The indication that the young may enter the spring molt earlier than the adults in this species also would correlate with their having spent a greater period of time in the plumage that is lost by the prenuptial molt. In *E. minimus* there is an interesting correlation between a comparatively early and limited postjuvenal molt with an extensive prenuptial molt that seems to involve chiefly first-year birds. The adults of this species that have undergone complete and fairly late fall molts have only a very slight prenuptial molt, or may not molt at all during that season.
TIMING OF MOLT

The Relation between Molt and Breeding

Knowledge of the timing of the molt periods in relation to other activities of high energy demand, namely breeding and migration, is of considerable importance because of the general view that physiologically incompatible events do not overlap (see Farner, 1958:18). Regarding scheduling of molt in permanently resident Steller Jays (*Cyanocitta stelleri*) of the Queen Charlotte Islands, Pitelka (1958) concluded that the annual molt is timed as closely as is breeding to coincide with summer food abundance. Molt and breeding activities do not overlap in this species. In the Plain Titmouse (*Parus inornatus*), although molt was occasionally underway at the same time that fledglings were being fed, the overlap in molting and nesting did not “appear critical in terms of additional energy demands on the parents” (Dixon, 1962:136). The same author provided evidence that the relatively early scheduling of molt was correlated in timing with the availability of a richer food supply that occurred prior to the autumn dry season.

Johnston (1961) presented findings that point to an inception of annual molt in the Glaucous Gull (*Larus hyperboreus*) in the Cape Thompson region of Alaska “before or soon after the eggs are laid, that is, by the end of May.” In summarizing, he states that the early molt is an adaptation enabling the completion, or the near completion, of both breeding and molt during the abbreviated summer season. However, earlier in the same paper he concludes that it is “unlikely that this early molt has any present adaptive value” because the Glaucous Gull “evidently does not suffer from a dearth of food even in late autumn and since it does not migrate especially early from arctic Alaska.”

Granted that a species is physiologically constituted so as to permit partial overlap, or even coincidence, of molt and breeding activities, it appears to me that such specific adaptations can indeed be favored if the selective disadvantages of a complete molt at some other time of year are greater than the disadvantages of molt during or immediately following breeding. For example, in the Glaucous Gull serious problems may result from the scheduling of molt after migration when food competition among numerous species of gulls in flocks on their wintering grounds is probably severe. The fact that molt in most migratory passerine birds occurs on the breeding grounds, closely following breeding (Dwight, 1900:127), suggests that it is a widespread adaptation, at least in perching birds, for both of these energy-demanding activities to be generally correlated with the period of most favorable environmental conditions (such as food abundance and optimal temperatures).

The fact that several species of the genus *Empidonax* (*E. flaviventris*, *E. virescens*, and *E. traillii*) either definitely or probably schedule the complete molt in the spring and the partial molt in the fall, the reverse of the pattern shown by *E. minimus*, *E. hammondii*, *E. oberholseri*, and *E. wrightii*, suggests
that whether the complete molt is timed before or after the breeding period is not significant except as it may reflect adaptation within the cycle of a particular species. For example, if it were selectively advantageous for a species of *Empidonax* to be in fresh, bright plumage at the time of pair formation, one could hypothesize that the complete molt (at least of the body feathers) would be scheduled for the spring or prenuptial period. Indeed, this could play a role in determining the extent of the spring molt in *E. flaviventer*. At least in *E. oberholseri* there is no evidence that completeness of prenuptial body molt is correlated with any particular degree of "pairing success." Individuals with fresh, yellowish underparts and individuals that had worn grayish underparts and that evidently had a very limited body molt prior to the spring migration seem to occur as breeders in approximately equal numbers. Members of the genus *Empidonax*, in general, seem to place heavy stress on vocalizations for purposes of sex and species recognition (Johnson, 1963), hence slight importance is attached to the possibility that the variation in plumage color resulting from feather wear affects pairing and breeding success. If such influences do occur, they are at least subtle and easily overlooked.

*The Relation between Molt and Migration*

Tordoff and Mengel (1956) state that the rarity of migrant birds with remiges in molt is strong evidence that molt at least influences the time of migration, although it is "immaterial whether this molt occurs before or after migration." The findings from *Empidonax* agree with this to the extent that migration and heavy molt have not been found to overlap. The chief evidence for this statement is the fact that specimens showing significant molt are available from localities of summer or of winter residence only. Migrants may be involved only in very early or very late stages of molt.

The most obvious relationship between molt and migration in *Empidonax* is that molts occurring after migration tend to be protracted. In other words, an early molt on the breeding grounds is correlated with a leisurely, prolonged southward migration, and an early and rapid fall migration is associated with a subsequent protracted molt. For example, the postnuptial molt of *E. hammondii* occurs on the breeding grounds, and on a population basis takes approximately 3 months, a period comparable to that taken by three sedentary, temperate-zone species in California: the Plain Titmouse as reported by Dixon (1962), the Scrub Jay (*Aphelocoma coerulescens*) as reported by Pitelka (1945), and the House Finch (*Carpodacus mexicanus*) as reported by Michener and Michener (1940). The autumn migration of *E. hammondii* in western North America is considerably more protracted than in related species of the genus; in California, for example, this species may linger in mountainous areas into early October and pass through the southern lowlands in late October (Johnson, MS.). This prolonged fall migration is correlated with a rather late arrival on wintering areas in central America. October 14 is the earliest date for arrival in Guatemala, as based on specimens reported
by Griscom (1932), and 21 November is the comparable date for El Salvador (Dickey and van Rossem, 1938), although the latter authors state that “It is probable that the date of arrival is somewhat in advance of that given above, for the birds were present in numbers on November 21.”

On the other hand, *E. oberholseri* moves southward hurriedly in the late summer, then undergoes the postnuptial molt over a period of nearly 4 months, on a population basis, after settling in wintering areas in Mexico. *Empidonax wrightii* has a similar rapid migration from western North America prior to a postnuptial molt period of approximately $4\frac{1}{2}$ months in Mexico (see Fig. 1). These species do not migrate as far south as does *E. hammondii*, hence their early arrival times on wintering areas (middle to late August at least in northern portions of the wintering range) may not be too surprising. However, other species that do migrate as far as *E. hammondii*, but differ from that species in that the adults molt after the fall migration, also arrive in Central America rather early: 15 August for *E. flaviventris*, 26 August for *E. t. traillii*, and 13 August for *E. minimus* in Guatemala (Griscom, 1932); and 8 October for *E. flaviventris*, 25 August for *E. t. traillii*, 14 August for *E. t. brewsteri*, and 3 September for *E. minimus* in El Salvador (Dickey and van Rossem, 1938). I tentatively conclude that the distance of the fall migration does not influence the timing of the autumnal molt.

The striking variation observed in the placement of the postnuptial molt in relation to the fall migration suggests that the timing of these important events in the annual cycle is largely a matter of adaptation at the species level. As stated earlier, there is now solid evidence that both the postjuvenal and the postnuptial molts of *E. hammondii* occur prior to the fall migration (Dickey and van Rossem, 1938; Johnson, 1963); *E. virescens* may time these events in similar fashion (Mengel, 1952), although the fall molts of this species are too poorly documented to permit generalization at this time. All worn fall specimens of “*E. hammondii*” from Mexico that have lent support to the idea that some individuals molted after arriving on their wintering grounds have proved to be misidentified specimens of other species in the genus, notably *E. minimus* and *E. oberholseri* (see Moore, 1940:356).

With the exception of all age groups of *E. hammondii*, and probably *E. virescens*, and juveniles of *E. flaviventris* and *E. minimus*, the evidence suggests that all other North American species of *Empidonax* undergo the fall molts on their wintering grounds. Sufficient knowledge of the molts of *E. hammondii* enables us at least to inquire why this species follows an apparently “atypical” molt-timing system. Furthermore, it will be profitable to compare this species with *E. minimus*, which is probably the most closely related form to *E. hammondii* in the genus (Johnson, 1963). The fact that all individuals of *E. hammondii* accomplish the postnuptial molt on or near the breeding areas suggests that there is perhaps selection operating to avoid molting on the wintering grounds. This species is exceptional among forms of *Empidonax* that winter in Central America by virtue of the fact that it
inhabits highland forested regions, rather than concentrating in the lowlands and foothills as do *E. flaviventris*, *E. traillii*, and *E. minimus*. For example, in El Salvador, Dickey and van Rossem (1938) reported that *E. flaviventris* was “fairly numerous and evenly distributed” between sea level and 3,600 ft; *E. t. traillii* was a “very common fall migrant and winter visitant to the lowlands” between 200 and 1,000 ft; *E. t. brewsteri* was “common, locally abundant, in fall, winter, and spring throughout the lowlands”; *E. minimus* was “most numerous” below 2,500 ft, and “rare and local” as high as 3,500 ft; and *E. hammondii* was a “common winter visitant” between 3,500 and 8,700 ft (rare at the latter elevation). A similar altitudinal distribution of these species of *Empidonax* is known for other regions of Central America and southern Mexico. Two points are suggested by the fact of *E. hammondii* wintering in the highlands: (1) It is physiologically constituted so as to be able to exploit a region essentially unoccupied by other, possibly competing, species of the genus; (2) the species is ill-adapted for wintering at low elevations in the tropics, both from the standpoints of physiology and tolerance of competition.

Considering the habitats occupied by *E. hammondii* for breeding purposes in western North America, cool boreal forests of spruce–fir and northern aspen woodland, it is apparent that this species probably is physiologically adapted to coolness to a degree that permits the occupancy of highland forests of the tropics during the winter. Two other species of *Empidonax* that live in cool-temperate forests in eastern North America, *E. minimus* and *E. flaviventris*, winter only in foothill or lowland regions of the tropics; the explanation for their rarity at higher elevations is not clear. Perhaps this rarity is related to both competition and physiological tolerance. At least the fact that these “cool-adapted” species are able to winter successfully at low elevations in the tropics suggests that *E. hammondii* is probably physiologically able to do likewise; perhaps competition with other small flycatchers keeps it from doing so.

Probably correlated also with the ability to inhabit cool environments for breeding and wintering is the protracted autumn migration of *E. hammondii*. Because of the assumed existence of inherent physiologic adaptation, and because the birds are then in new plumage, it is suggested that this species is better prepared to withstand the cool or cold autumn temperatures of mountains in western North America than are other forms in the genus.

Furthermore, the fact that *E. hammondii* is the only migratory species of *Empidonax* that winters commonly in the highlands of southern Mexico and Central America, whereas several other species of *Empidonax* simultaneously winter in the lowlands, points to the conclusion that these highland regions are not as favorable as are the lowlands for occupancy during the winter by North American members of the genus. Continuing this line of reasoning, it may also be disadvantageous because of food shortages and/or cool temperatures for a species wintering in the highland forests to undergo
the postnuptial molt there. This could also explain why the prenuptial molt of this species (that *does* occur on the wintering grounds) is relatively limited in extent, as compared with other species of the group. I believe that it is highly significant that this species accomplishes both the fall and spring migrations with the same set of flight feathers; the tentative explanation to be proposed here is that, for reasons as yet unknown, it is selectively disadvantageous for this species to molt on the highland wintering areas.

Although proper data are not yet available to permit an extended discussion, the situation of a postnuptial molt prior to migration to wintering areas at predominantly high elevations in Central America and northern South America by *E. virescens* agrees with the argument advanced for *E. hammondii*.

Selection probably does not favor protracted fall molts among temperate or high-latitude migratory species that accomplish their molts on the summering grounds. Thus, it is likely that the length of the period occupied by such an early molt is a compromise that reflects the “need” (1) to be rapid in order to complete the process in the abbreviated time between the waning of breeding and the time of migration (whether or not the latter is correlated with the onset of unfavorable environmental conditions at middle or high latitudes), and (2) to be slow enough to avoid excessive rates of energy drain, impairment of flight, and reduction of body temperature control resulting from extensive feather replacement. Furthermore, if there is selective pressure in favor of a protracted fall molt, it appears that the only way in which this molt can be accommodated into the cycle of a temperate- or high-latitude species is for it to occur after the fall migration.

Among passerines, two groups in particular are notable for containing numerous species that undergo fall molts on the wintering grounds subsequent to migration, the flycatchers and the swallows (Dwight, 1900; Rintoul and Baxter, 1914). These also possess species characterized by protracted fall molts (Dickey and van Rossem, 1938; Bent, 1942). The question that immediately arises is whether the molts are protracted because a previously completed migration permits them to be leisurely, or whether there is indeed selection operating among the flycatchers and swallows to promote protracted molts. I subscribe to the latter view for the reason that both groups consist of species that are primarily aerial-insect predators whose foraging maneuverability could theoretically be reduced by rapid molts.

**SUMMARY**

The sequence and timing of molts are outlined in detail for five congeneric species of North American tyrantids: *Empidonax flaviventris, E. minimus, E. hammondii, E. oberholseri*, and *E. wrightii*. The limited information available in the literature for three other species of the genus, *E. virescens, E. traillii*, and *E. difficilis*, is also briefly summarized. These eight species illustrate striking differences in their scheduling of molts. *Empidonax flavi-
ventris, E. minimus, and E. hammondii undergo postjuvenal molts on the
breeding grounds prior to migration, whereas the postnuptial molts of all
species except E. hammondii, and possibly E. virescens, occur after the fall
migration on the wintering areas. Postnuptial molts are complete in at least
E. minimus, E. hammondii, E. oberholseri, and E. wrightii; that of E. flaviventr
is is usually incomplete. Premoltual molts may be relatively slight (as
in E. hammondii) or complete (as in E. flaviventris).

There is a general correlation between early postjuvenal and postnuptial
molts and subsequent protracted migrations, as well as between early, com-
paratively rapid migrations and subsequent protracted molts.

Intraspecific adaptations in extent and timing of particular molts for each
species are discussed. One complete and one partial molt per year seem to
be a general requirement for adults of each species; the degree of inter-
specific variation in timing is so great as to suggest that the exact position
in the annual cycle of these molts is chiefly a reflection of adaptation at the
species level.

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Thermodynamics of Incubation in the House Wren, *Troglodytes aedon*

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One of the first studies of the thermodynamics of incubation in wild birds was that of Bergtold (1917). He believed that for each species "the true length of incubation is fixed or determined by the temperature of the incubating parent." Inclement weather or excessive absence of the incubating bird may extend the incubation period beyond its true length. He recognized the importance of the nest structure to serve for heat insulation of the eggs and of the brood patch on the adult bird for applying heat to the eggs. He was wrong, however, as will be shown below, in stating that "the optimum incubation temperature for any species is the temperature of the incubating parent."

There have been a number of measurements of egg or incubation temperatures both in wild and domestic species since the time of Bergtold (see citations below). The objective of many of these studies was to determine the best temperature to use in artificial incubation. A recent study in some detail is concerned with the heat exchange in the domestic duck egg during incubation (Kashkin, 1961).

The present study is designed to measure the heat exchange in the eggs of the House Wren (*Troglodytes aedon*) from the time they are laid until they hatch. This involves measurement of the rate at which the eggs lose heat, the relation between egg and nest temperatures, the amount of heat applied to the eggs, and the work performed by the incubating bird. The original data were obtained at the Baldwin Bird Research Laboratory, near Cleveland, Ohio, principally between 1934 and 1936. The present analysis was undertaken with the support of a grant from the National Science Foundation.

*Relation between Egg and Air Temperatures.*—The actual temperature that is effective in the incubation of bird eggs is not the air temperature surrounding the eggs but the temperature of the embryo. During the first several days of incubation, the embryo is a small mass on the upper surface of the yolk and moves with the rotation of the egg so that it maintains a position between the center and top of the egg. As the embryo becomes more fully formed during the latter days of incubation, it comes to occupy most of the egg interior except for the air space at the larger end.

Several years ago we attempted to measure the temperature of the House Wren embryo during various stages of incubation and under various conditions (Baldwin and Kendeigh, 1932). Thin delicate thermocouples were inserted into the egg through small holes drilled through the shell and the opening then sealed with collodium. The sensitive warm junction of the thermocouple was centered as closely as possible halfway through the widest
part of the egg, although the instrumentation was not sufficiently sensitive to detect differences in temperature at various depths in the egg as long as the warm junction did not touch the shell or penetrate the air space. We were measuring the internal egg temperature, but doubtless the temperature of the embryo approximated closely the temperature of the egg and for our present objectives they may be considered identical. Readings were taken with an indicator potentiometer and special galvanometer with a tested sensitivity and reliability of 0.1° C.

In order to determine the relation between egg and air temperature under constant conditions, eggs were removed from the nest and placed in the laboratory until they established equilibrium with room temperature, usually after one hour's time. The egg temperature then measured slightly below (0° to -0.3° C) air temperature during the first half of the 14-day incubation period. From the tenth to twelfth days of the incubation period the egg temperature reached an equilibrium slightly above (0° to +0.4° C) room temperature (Baldwin and Kendeigh, 1932). These temperatures indicated that during the early part of incubation the rate of heat loss through evaporation of moisture from the egg exceeded the heat production of the embryo, but during the latter part of the incubation period the rate of heat production was greater than the rate of heat loss (Kendeigh, 1940). Similar relations between egg and air temperatures and between heat loss and heat production have been demonstrated for eggs of the domestic fowl (Romijn and Lokhorst, 1956) and domestic duck (Kashkin, 1961), the change coming on the tenth or eleventh day for the much longer incubation periods of these precocial species. Kashkin has measured the relative importance of radiation, convection, and evaporation in the heat loss from the egg.

An average of 15 measurements on eight House Wren eggs throughout the incubation period was -0.05° C compared with the air temperature. It is obvious that the difference between egg and air temperatures under constant conditions is so small that it lies beyond the sensitivity of the recording potentiometers used at the nests and may be disregarded.

Relation between Egg, Nest, and Air Temperatures.—Egg temperatures were obtained in the nest by means of a thermocouple inserted into an egg with the thermocouple leads extending through the bottom of the nest to a nearby observation blind. Another thermocouple was inserted in the bottom of the nest cavity just above the feather nest-lining to obtain nest temperatures below the eggs. Temperatures were read with an indicator potentiometer for periods of an hour or longer, both while the adult female incubated during attentive periods and while she was away during inattentiveness.

Twelve separate series of recordings of egg and nest-bottom temperatures were obtained during 4 years on five separate nests over a period of 11 hours and 46 minutes. A total of 355 egg temperatures and 283 nest temperatures were taken at an average rate of one egg temperature per 2.0 minutes and
one nest temperature per 2.5 minutes. The lengths of the attentive and inattentive periods were determined during several recordings and averaged approximately normal, 11 and 9 minutes, respectively.

When nest and egg temperatures are plotted against air temperatures (Fig. 1), it is apparent that at air temperatures up to 32° C nest temperature rises progressively \( b = 0.34°/1.0° \) while egg temperatures remain nearly constant \( (35.1° \) C). The goodness of fit of the regression line for nest temperature is significant \( (P < 0.001) \), but that for egg temperatures \( (b = 0.045°/1.0° \) C) is questionable \( (P = 0.3) \). At air temperatures of 31.5° and 32.0° C, egg temperatures were below nest temperatures. The embryos in these two eggs had been incubated for 12 and 2 days, respectively. At 32.7° C air temperature, both nest and egg temperatures were exceptionally high. The embryo of this egg had been incubated for 9 days. The relation between egg temperatures \( Y \) and nest temperatures \( X \) is linear \( Y = 31.08 - 0.88X \), the difference between the two increasing with the drop in the latter \( (b = -0.88°/1° \) C).

The ability of the incubating bird to maintain an egg temperature constant at approximately 35° C in spite of a rise of 11.4° C in air temperature and of 4.2° C in nest temperature is of considerable interest. This is done principally by decreasing the length of time spent on the eggs by the incubating female as the air temperature rises. In these particular cases, the total time spent incubating during the daytime by the females decreased from a mean of 84 percent at 20° C to 29 percent at 32° C air temperature \( (b = -4.6%/1.0° \) C). Other studies (Kendeigh, 1952) have shown that this behavior is general in the species and is effected by a decrease in the length of the attentive periods. At 15° C, attentive periods average 14 minutes; at 30° C, 7.5 minutes. The length of the inattentive period remains approximately the same at all except extremely high temperatures.

Huggins (1941) found the average egg temperature during incubation for 37 species of birds from 11 orders to be 34.0° ± 2.38° C. Internal egg temperatures during incubation, measured by other investigators (Kossack,
1947; Eklund, 1961; Howell and Bartholomew, 1962) for a variety of non-passerine species, fall generally between 34° and 36° C. Temperatures obtained by thermocouples placed between but not inside the eggs for a number of species vary between 33° and 37° C (Rolnik, 1939; Koch and Steinke, 1944; Barth, 1949; Irving and Krog, 1956; Baerends, 1959; Kessler, 1960). The incubation temperature of the House Wren appears to be representative, therefore, of birds in general. A possible exception is the domestic fowl where measurements of egg temperatures are commonly 38° to 39° C or above (Eycleshymer, 1907; Atwood, 1917).

This incubation temperature of 35° C is to be contrasted with the body temperature of the adult bird, which varies from 40.2° to 40.6° C at rest to about 44.2° C after intense excitement and activity (Baldwin and Kendeigh, 1932).

Rate of Cooling and Warming of the Egg under Controlled Laboratory Conditions.—In order to maintain the egg at a constant temperature, the incubating bird must compensate for the rate of heat loss from the eggs by giving the eggs an equivalent amount at the same rate. The problem, then, is to determine the rate of heat loss from the eggs at various nest temperatures.

Five eggs were used to determine both the rate of heat loss when placed at low air temperatures and the rate of heat gain at high air temperatures. These eggs had received 0, 4, 5, 9, and 12 days' incubation, but the amount of incubation of the eggs gave no significant variation in the results. All eggs had normal embryos when examined at the end of each experiment. The eggs were removed from the nest to the laboratory, a thin thermocouple inserted halfway, the egg then put on cotton in a small cardboard box approximately 6.5 × 4.0 × 1.5 cm in dimensions, another thermocouple fastened in the box about 2 cm away from the egg and above the cotton to get the air temperature to which the egg was exposed, and the setup then maintained at room temperature until an equilibrium was reached. The egg and box were then placed in an incubator at a high temperature until it reached another equilibrium, after which it was returned again to the room. Readings were taken at 3- to 4-minute intervals of both egg and air temperatures.

The box and cotton doubtless affected the rate of heat loss and heat gain of the egg itself. On inserting the setup into the incubator and then out of it, the egg was not immediately exposed to the extreme air temperature since the temperature of the box and cotton also underwent an adjustment. This should not be much different, however, than the changes in the egg and nest temperature as they affect each other in the nest, as the nest as well as the egg warms up while the bird applies heat during attentive periods and they both cool down while heat is lost during her inattentive period. In the analysis of the data, the air temperature used is the final or extreme air temperature when the egg, box, and air have reached equilibrium.
In order to determine the rate of cooling of the eggs at various low air temperatures (18°–23°C), starting with the eggs at various high temperatures, the differences between egg and air temperatures were first plotted against minutes from the beginning of the cooling period. This gave a series of shallow curves, concave in reference to the time base. A plot of the logarithms of the differences between egg and air temperatures against time gave a straight line, as similarly found by Morrison and Tietz (1957) for the cooling of animal bodies. Since 10 minutes is approximately midway between the mean lengths of the inattentive period (8.5 minutes) and attentive periods (12.1 minutes) (Kendeigh, 1952), the drop in temperature was determined over 18 such periods and plotted against the difference between egg and air temperature midway during each period (Fig. 2). This gave a straight line in agreement with Newton’s law of cooling \[ b(t - t') \]. That the regression line does not reach zero at zero difference between egg and air temperatures is an inaccuracy, but may be disregarded as the slope of the line is the important factor. The coefficient of cooling \( 0.86°/1°\,\text{C}/10\,\text{min} \) for the small egg of the House Wren (1.364 g) with its relatively large surface area is to be compared with the coefficient of cooling (about \( 0.13°/1°\,\text{C}/10\,\text{min} \) for the much larger (78 g) duck egg (Kashkin, 1961:fig. 4).

Conversely, when the rise in egg temperature, after the egg was placed at high air temperatures, was determined for 24 ten-minute periods and plotted against the difference between egg and air temperatures, the relation appears to be curvilinear (Fig. 3). A significant straight line, however, can be fitted to the upper range of temperatures which are most important in relation to normal fluctuations in the nest. The difference in the coefficients for cooling
(0.86°/1° C) and heating (0.54°/1° C) means that it takes 1.6 times as long to heat the egg back to a certain temperature level as it takes for the egg temperature to drop below that level. This is the result of evaporation accelerating cooling but retarding heating. Both coefficients need to be multiplied by 6 to be put on a 1-hour instead of a 10-minute basis.

Rate of Cooling and Warming the Eggs in the Nest.—In order to determine whether these cooling and warming rates for the eggs maintain also in the nest, an analysis was made for 23 inattentive and 22 attentive periods when eggs underwent normal cooling and warming in the nest. The drop in egg temperature during the intervals of time when it could be measured was at an average rate of 4.2° C/10 min. The average rate of rise in egg temperature was 3.3° C/10 min. Here again, the rate of heating the egg is slower than its rate of cooling, the time required for heating the egg being 1.3 times longer than the time required for an equivalent amount of cooling.

In order to equate these rates of cooling and warming of the eggs in the nest with those measured in the laboratory, it was necessary to determine the temperatures in the nest to which the eggs were exposed during the inattentive and attentive periods. The temperature at the top of the eggs when the bird is incubating is actually the skin temperature of the bird in contact with the upper surface of the eggs. When the bird is away, the top of the eggs is most exposed to radiational and convectional loss of heat and hence cools the most rapidly. On the other hand, the temperature in the bottom of the nest under the eggs is much more stable (Baldwin and Kendeigh, 1932:153). The
nearest approach we can come to the temperature to which the eggs are exposed in the nest is to average the temperature just above and below the eggs by means of thermocouples. The temperature of the eggs is, however, also affected by radiation and conduction of heat laterally to adjacent eggs and nest wall. Although temperatures above the eggs as well as in the nest bottom were taken, no measurements of heat lost laterally were obtained during the course of the present study.

Since the temperature of the nest air (average of the temperature above the eggs and in the nest bottom), as well as the temperature of the egg, falls gradually during the inattentive period and rises during the attentive period, the temperatures at the ends of these two periods usually but not invariably represent the extreme fluctuations that occur. An average of temperatures at the end of 22 inattentive periods gives 32.2° for the nest air and 34.3° C for the egg. An average of temperatures at the end of 20 attentive periods gives 37.4° for the nest air and 36.0° C for the egg. These temperatures for the egg are somewhat less extreme than the real minimum and maximum temperatures during the inattentive and attentive periods given by Baldwin and Kendeigh (1932). The inattentive and attentive periods are seldom long enough to permit the egg temperature to reach an equilibrium with the temperature of the nest air. The effective drop in surrounding temperature to which the eggs were exposed during the inattentive period should be considered the difference between the last egg temperature during the preceding attentive period and the last nest-air temperature during the inattentive period, or 3.8° C. Likewise, the effective rise in temperature is the difference between the last egg temperature during the preceding inattentive period and the last nest-air temperature during the attentive period. In the House Wren data cited above, this value is 3.1° C.

Reference to Fig. 2 shows that the drop in nest-air temperature of 3.8° C should produce a rate of cooling of the egg of 3.9° C/10 min, which, in view of the difficulties involved, is reasonably close to the 4.2° C actually measured. This means also that the average of the temperatures directly above and below the eggs is a reasonably accurate measurement of the nest-air temperature to which the eggs are exposed during the inattentive periods when the bird is not incubating.

On the other hand, the rise of 3.1° C in nest-air temperature while the bird is incubating corresponds to a warming rate for the egg under laboratory conditions of only 1.8° C/10 min (Fig. 3), slightly over half of the rate of 3.3° C/10 min that was measured in the nest. The source of heat to the egg during incubation is primarily the conduction of heat from the skin of the bird to the upper surface of the egg. In the laboratory measurements, the eggs were warmed as the result of heat convection currents affecting all sides of the egg except the bottom. Apparently, transfer of heat to the eggs by conduction is 1.6 times as efficient or rapid as transfer of heat by convection alone.
No measurements were taken of the egg temperatures at night. The body temperature of the bird at night, and hence the temperature applied to the eggs, is less than during the day, but as the bird then sits more steadily the equilibrium of egg temperature is probably about the same as its mean temperature during the day.

**Specific Heat of the Eggs.** — The specific heat of House Wren eggs has not been measured. For the entire egg of the domestic fowl, it is 0.772 g-cal/g/° C (Romanoff and Romanoff, 1949); for the duck egg, it decreases from 0.80 to 0.78 (Kashkin, 1961). The percentage of water in the hen’s egg (about 74) appears to be less than in songbird eggs (about 83, Kendeigh et al., 1956). We may assume for our purposes here that the specific heat of entire House Wren eggs is around 0.80.

**Weight of Eggs.** — The average weight of 294 fresh eggs of the House Wren is 1.461 g with a standard deviation of approximately 0.1 g. Daily weights of 22 eggs in 4 clutches indicated that 13.3 percent of the fresh weight is lost by the time of hatching. This loss in weight is due largely to water evaporated through the shell. The mean weight of the egg for the entire incubation period is therefore 1.364 g. Variations in the weight of individual eggs will, of course, affect the rate of cooling and the amount of heat required to keep them at a constant temperature.

**Measurement of Heat Applied to the Eggs by the Incubating Bird.** — Since we know the rate at which the eggs cool at various air temperatures, we can compute the amount of heat energy that must be applied to the eggs at each air temperature in order to maintain them at approximately 35° C, since the input of heat must balance the outgo. The caloric value of a degree-hour of cooling for an average-sized egg is calculated to be 5.6 g-cal (1.364 × 0.86 × 6 × 0.80).

To determine the amount of heat transferred from the incubating bird to the eggs throughout the incubation period, it would be desirable to measure the total degree-hours of cooling involved. One should be able to compute accumulative degree-hours of cooling from the differences between eggs and the temperatures to which the eggs are exposed in the nest, if the latter could be accurately and continuously recorded.

The cooling rate of eggs in the nest has been shown above to be related to the average temperature above and below the eggs (nest air). However, the continuous recording of the nest-air temperature is not suitable, since the nest-air temperature is not representative of conditions during the attentive period, when the bird is sitting on the eggs. The nest-bottom temperature responds to the cooling and warming of the eggs and, during the attentive periods, is not otherwise affected by the presence of the incubating bird. It appears, therefore, that this temperature would best be used for continuous recording and determination of the potential cooling rate of the eggs. During
19 inattentive periods when both temperatures were measured, the nest-bottom temperature averaged 0.5° C higher than the nest-air temperature. Data obtained from recorded nest-bottom temperatures should therefore be corrected by subtracting this amount.

Still another correction is necessary. When the incubating bird is attentive, heat loss from the top surfaces of the eggs is prevented by the presence of the bird on the eggs. The cooling rate is therefore less than it is during an inattentive period. Since the eggs are more or less pointed, more so however at one end than the other, radiation is most effective from the sides. Without exact measurements available, it may be assumed that the attentive bird may reduce heat lost by 25 percent. The amount of heat required to maintain the eggs at incubation temperature should therefore be reduced by 25 percent for the proportion of the day when the bird is sitting on the eggs. The incubating House Wren is on the eggs an average of about 75 percent of the 24-hour day.

The House Wren during incubation is adapted to transfer heat from its body to the eggs as rapidly and efficiently as possible. While incubating, the feathers on the lower surface of the body are separated so as to give maximum contact between the skin and the eggs. Furthermore, the skin is developed into a brood patch to give increased flow of blood and transportation of heat from inside the body to the skin and then to the eggs (Bailey, 1952). The outer surfaces of the clutch of eggs then becomes the exposed surface for heat loss in place of the skin of the body of the nonincubating bird. The nest lining, usually of chicken feathers with the House Wren, assumes the role of reducing this rate of heat loss from the eggs in the same manner as do the body feathers on the nonincubating bird.

The heat applied to the eggs is, however, lost to the nest and box and finally to the outside environment. Loss of heat by conduction from the eggs to the surrounding nest material continues during both the attentive and inattentive periods. When the bird is away during inattentive periods, the eggs lose much heat by radiation to the top of the box and by convection to the box as a whole. It is for this reason that the nest-bottom temperature is always higher than the temperature of the air outside the box. The difference between the nest-bottom and outside air temperatures increases (0.66° C/1° C) in proportion to the drop in the latter. In calculating the amount of heat applied to the eggs, it is not necessary, however, to consider the air temperature if nest-bottom temperatures are measured, as variations in air temperature are reflected in the variations of nest-bottom temperature. The amount of heat applied by the incubating bird is determined by the cooling rate of the eggs, which is related directly to the nest-bottom temperature.

The following equation brings together these various considerations in a form capable of use in a practical way (values of the constants for the House Wren are given in parentheses):
Kcal = \frac{n \cdot w \cdot h \cdot b \cdot (t_e - t_{na}) \cdot i \cdot (1 - c \cdot a)}{1,000}

where

- \( n \) is the number of eggs in the clutch,
- \( w \) is the mean weight of the eggs,
- \( h \) is the specific heat expressed in small calories per gram-egg (0.80 g-cal),
- \( b \) is the rate of cooling of the eggs expressed as degree change per hour per degree difference between egg and nest-air temperatures (5.2°/hr/°C),
- \( t_e \) is the egg temperature \((35.1° C + 0.045 [X - 26.3° C])\) where \( X \) is the outside air temperature,
- \( t_{na} \) is the nest-air temperature (nest-bottom temperature minus 0.5° C),
- \( i \) is the interval in hours (24, if computations are made on a daily basis),
- \( c \) = percentage of total surface of eggs covered by attentive bird (assumed to be 25%),
- \( a \) = percentage of total 24 hours that the bird is attentive (approximately 75), and
- 1,000 is the factor for converting gram-calories to kilogram-calories.

**Amount of Heat Applied to the Eggs during Incubation.**—Table 1 gives information for those nests where the heat applied during the entire period of full incubating was measured. The thermocouple to register temperature was inserted in the nest under the eggs as soon as possible after egg laying began and left in position until all the young had hatched. Temperatures were measured by a recording potentiometer accurate to about ±0.3° C. The period of full incubating was considered as beginning at midnight after the last egg was laid and ending at midnight before the first young hatched. The number of days involved in the averages are for nest 25, 13; 49, 12; 75, 11; 43, 11; 43A, 10; and 10, 11.

<table>
<thead>
<tr>
<th>Nest No.</th>
<th>Date of Record</th>
<th>Mean Air Temperature</th>
<th>Exposure</th>
<th>No. of Eggs</th>
<th>Mean Weight of Eggs (g)</th>
<th>Calculated Egg Temperature</th>
<th>Measured Nest-air Temperature</th>
<th>Hours Incubating per Day</th>
<th>1 - c \cdot a</th>
<th>Kcal/Day</th>
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</thead>
<tbody>
<tr>
<td>25</td>
<td>26 May–7 June 1935</td>
<td>17.0°C Mostly shade</td>
<td>6</td>
<td>1.36°</td>
<td>34.7°C 30.7°C 24</td>
<td>0.81</td>
<td>2.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>49</td>
<td>4–15 June 1936</td>
<td>17.1 Shade</td>
<td>6</td>
<td>1.44</td>
<td>34.7</td>
<td>31.5</td>
<td>24</td>
<td>0.82</td>
<td>2.2</td>
<td></td>
</tr>
<tr>
<td>75</td>
<td>14–24 June 1935</td>
<td>18.0 Sun</td>
<td>6</td>
<td>1.47</td>
<td>34.7</td>
<td>32.1</td>
<td>24</td>
<td>0.81</td>
<td>1.8</td>
<td></td>
</tr>
<tr>
<td>43</td>
<td>30 June–10 July 1936</td>
<td>22.2 Shade</td>
<td>6</td>
<td>1.33°</td>
<td>34.9 (32.0)</td>
<td>21.4</td>
<td>0.80</td>
<td>1.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>30 June–10 July 1934</td>
<td>22.9 Partly sun</td>
<td>4</td>
<td>1.36°</td>
<td>35.0</td>
<td>30.6 (32.0)</td>
<td>21.5</td>
<td>0.81</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>43A</td>
<td>2–11 Aug. 1935</td>
<td>22.3 Sun</td>
<td>6</td>
<td>1.50</td>
<td>34.9 (35.2) (33.7)</td>
<td>21.6</td>
<td>0.80</td>
<td>1.1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*a Correction factor for reduced rate of heat loss from eggs while bird is sitting on them.

*b Mean weight of eggs for species used.

c Egg No. 4 lacked yolk and germ cell and weighed only 800 g.

d Data in parentheses are for entire period where different from actual hours bird incubating.
Outside air temperatures were calculated from Weather Bureau records obtained at Cleveland, Ohio, about 19 km from where the study was made. Actual air temperatures were recorded at Gates Mills, where the laboratory was located, during the summers of 1929 to 1931 inclusive, but not for the years in which the nest temperatures were measured. Comparison of mean daily temperatures at Gates Mills and Cleveland for 224 days between 15 May and 1 August indicated that air temperatures averaged 1.0°C lower at Gates Mills. This difference held at all air temperatures, with extreme differences ranging only from -3.3°C to +2.2°C.

When the eggs were weighed in the particular nests where measurements were taken, these weights have been used in the calculations, otherwise the mean weight of eggs for the species as given above. The average weight of eggs during full incubation was calculated as 6.7 percent less than fresh weights, because water is continually evaporating from the egg.

The exposure of the nest box is indicated, since its position in full sunlight or in shade affected the nest temperature and consequently the amount of heat that the incubating bird applied to the eggs. When the internal box temperature became very high, the bird did not incubate, and this had to be corrected for as shown. The value of $1 - ca$ is given only for the time the bird was incubating. The attentiveness of the bird to incubation could be calculated, since the time of beginning and ending the daytime activities could be determined from the record, and it was assumed that the length of the inattentive periods during the day remained constant at 8.5 min but that the attentive periods varied inversely with temperature, as shown in Kendeigh (1952: fig. 5).

Although its effect on the data is not known, it should be noted that in nest 25, egg No. 1 proved to be infertile and the embryo in egg No. 3 died when incubated four or five days. In nest 43A, egg No. 6 did not hatch and was removed by the bird at the time the other eggs hatched. Egg No. 4 in nest 43 was a runt, lacking yolk and germ cell. All the other eggs in the various nests hatched in apparently normal manner.

There is evident a progressive decrease with time in the average daily amount of heat applied to the eggs at the six nests. However, the time of summer is probably not the significant factor, as there is also an inverse correlation with the prevailing air temperature.

*Correlation with Air Temperature.*—Table 1 indicates that with a rise in air temperature there is generally a rise in the temperature of the nest air and a corresponding decrease in the amount of heat applied to the eggs by the bird, but that this relation is modified by whether or not the nest box is exposed to the sun during the day. The inverse relation between air temperature and the amount of heat applied to the eggs is shown in more detail in Fig. 4 where the data for individual days are plotted.

Nest boxes exposed to the sun maintain an equilibrium between absorption
and loss of heat at a higher level of temperature than in boxes continuously in shade. The effect of this difference on the amount of heat applied to the eggs is evident from the two regression lines. The difference in slope of the lines is significant at better than the 5 percent level; the difference in elevation of the lines is significant at better than the 1 percent level.

When air temperatures are low, there is advantage in the nest box being exposed to full sunlight, as less heat then needs to be applied to the eggs by the incubating bird. Such an exposure is disadvantageous at high air temperatures since nest temperatures may reach the limit of tolerance of the embryos.

![Fig. 4](image_url)

**Fig. 4.** Relation between amount of heat applied to eggs and air temperature and between shaded and sunlit boxes.

_Daily Rhythm._—The average amount of heat applied per hour to the eggs by the incubating bird varies almost threefold with the time of day when hourly averages are computed for 3-hour intervals, being least at midday and greatest in early morning (Fig. 5). The lowest outside air and nest-air temperatures usually occur at daybreak, in the 3:00 to 6:00 A.M. period. However, the bird sits steadily on the eggs until about 5:09 A.M., so that the eggs and nest do not get a chance to cool off as they do during the inattentiveness of the bird in the 6:00 to 9:00 A.M. period. The bird undoubtedly applies heat to the eggs at the fastest rate during the first hour or longer after beginning her activity in the morning. There is no marked difference in the amount of heat applied before and after she retires at about 7:29 P.M., as air temperatures are generally high during this time of day.

As air temperatures rise during the day, the bird spends less and less time incubating, and when nest-air temperatures exceed 35°C she generally stays away entirely until nest-air temperatures again drop below this level. This
period of absence extended to 12 hours at one nest on the twelfth day of incubation. At nests 10 and 43A, fully exposed to the sun, nest-air temperatures went above 35° C when air temperatures rose above 21.2° and 25.6° C, but at nest 43, which was mostly shaded, nest temperatures did not get above 35° C until air temperatures rose above 28.4° C.

Absence of the bird on the eggs at high nest temperatures permits more rapid loss of heat from the eggs and may help to reduce embryo mortality from excessively high egg temperatures. At nest 43A, the failure of egg No. 6 to hatch may have been due to high egg temperatures, as the nest-air temperature reached 42.7° C on the day the egg was laid and 42.1° C on the first day of hatching. On both these days, the mean daily temperature was 26.8° C. Previously, we have found that an hour's exposure of eggs to temperatures of 41.1° C may cause a 50 percent mortality of embryos (Baldwin and Kendeigh, 1932). At no other nest did nest-air temperatures get above 38° C.

**Egg-laying Period.**—The egg and nest-air temperatures were determined in a different manner for the egg-laying period. The reason for this is that full incubating behavior does not usually develop until the day the last egg is laid, regardless of whether it is a 5- or 6-egg clutch. As a general rule, each day an additional egg is laid, a larger number of attentive periods is spent on the eggs, the longer these periods become, and the less time is spent away from the nest. Likewise at night, although the bird may be in the box, she may not at first sit on the eggs, or, if she sits on the eggs, she may not apply full incubating heat to them. However, the amount of heat applied to the

![Figure 5](image-url)

**Fig. 5.** Daily rhythm in heat applied to eggs by incubating birds.
eggs increases each night until full incubating behavior is established, usually the night after the fifth egg is laid. There is evidence that the brood patch develops gradually during the laying of the clutch and is not fully formed so as to transfer heat efficiently from the body to the eggs until the last egg is laid. There appears to be some regression of the brood patch after a first nesting, since the application of full incubating temperatures is gradual even for second clutches during a season (Bailey, 1952; Kendeigh, 1952).

The egg temperature during the laying period was considered to be the same as the recorded nest-air temperature, since attentive periods were few and scattered and there was plenty of time for the eggs to reach the equilib-

![Graph](image)

Fig. 6. Measurements of heat applied to eggs, egg temperature, and air temperature during laying and incubation periods.

rium with air temperatures such as was demonstrated under experimental laboratory conditions. It was also possible to estimate what nest-air temperatures would have been throughout the day had no incubation occurred. The number of calories of heat applied to the eggs was calculated from the difference between these two temperatures. On the day the last egg was laid, the egg temperature and heat application was calculated in the same manner as during the incubating period proper. The factor, $1 - ca$, was calculated from the record separately for each bird for each day during the laying period.

It is apparent (Fig. 6) that the amount of heat applied to the eggs increases day by day and is higher on the day the last egg is laid than the average for the full incubating period. It is also apparent that the egg temperature remains relatively low until the day the last egg is laid. The greater amount of heat applied on the day the last egg is laid, compared with the amount applied during the following days of incubation, may in part be required to raise the temperature of the eggs and establish the temperature gradient through the nest that is held throughout incubation. The way the nest-air temperature becomes raised on the day the last egg is laid is well
shown in Fig. 7 where the bird had her first clutch for the season and air temperatures were low, 10.1° and 14.6° C, respectively, for the 2 days. The nest-air temperature was raised from 10.3° to 30.7° C over a period of 3.5 hours from 6:15 to 9:45 A.M. From 9:45 A.M. until noon the nest box was exposed to the sun and nest-air temperatures rose for a brief period to 35° C. Cadman (1923) states that the domestic fowl requires 6 hours for this initial heating of the eggs to incubation temperature.

At nest 10, the clutch consisted of only four eggs. One egg was laid on 25, 26, and 27 June, then a day was skipped, and the fourth egg was laid on 29 June. Egg temperatures on the third and fourth days at this nest were unusually high, as the nest box was exposed to the sun, and during midday, even with the bird absent, nest-air temperatures rose to over 37° C. The amount of heat applied to the eggs by this bird was, as a result, exceptionally low throughout the laying period.

**Source and Regulation of Heat Applied to Eggs.**—The sources of heat for maintaining egg temperatures are the heat production of the embryo itself (which, however, is too small to be significant), atmospheric heat, solar insolation, and the incubating bird (Fig. 8).

Whether or not atmospheric heat contributes to the development of the embryo depends on whether the air temperature is above the temperature threshold for development. Evidence is presented elsewhere (Kendeigh, 1963) for placing the temperature threshold at 17.2° C. On many days, of course, air temperatures do not exceed this level, so that the eggs are unaffected in their development. On those days when the air temperature is higher, the number of calories of heat received by the eggs from the at-
mosphere is calculated by subtracting 17.2° C from the mean daily air temperature, multiplying by the weight of the clutch, by 24 (hours per day), by 5.16 (rate of cooling per hour), and by 0.80 (specific heat).

When the nest box is located in an exposed situation, it receives direct insolation from the sun, but, even if not fully exposed, there is absorption of diffused radiational heat at a faster rate than it is lost so that nest-air and egg temperatures rise. The amount of this radiational heat was measured during the second and third day of egg laying, before the bird had begun to incubate, by using the difference between nest-air and outside air temperatures in the above multiplications. It was assumed that the amount of radiational heat received by the eggs remained about the same thereafter.

Atmospheric and radiational heat during incubation are sufficient on the average to maintain the egg temperature at about 5.3° C above the threshold temperature, or at approximately 22.5° C. The heat required for bringing the eggs to the average incubation temperature (34.9° C) comes from the incubating bird, principally on the day the last egg is laid, as discussed above. Once the incubation temperature and full incubating behavior become established, this heat is never entirely lost. The heat that is retained in the nest by reason of its insulation is called residual heat. It is calculated by multiplying the difference between nest-air and outside air temperatures by the series of factors listed in the second paragraph above and subtracting the radiational heat.

Because of the good insulation, residual heat may be more important in hole-nesting birds than in those that build nests in the open and is doubtless more important with those species that have good substantial nests than with those that do not. Palmgren (1939) inserted a container of water in various nests and noted the rate at which the water cooled at a constant environ-
mental temperature. Some variation occurred between different nests of the same species and considerable variation occurred between nests of different species. Cooling was more rapid with air movement than in quiet air. Linsdale (1936) found a correlation between the color of nest linings and the nest location, which he believed was influenced by the need for heat regulation. Nests exposed to the sun in hot situations had pale or pallid nest linings, while concealed nests or nests in cool locations had dark-colored linings. Irving and Krog (1956), however, did not find that nests in the Arctic were any better insulated than those in temperate regions, although the eggs were maintained at similar incubation temperatures. This problem of the insulating efficiency of nests of different structure and type is worthy of more detailed investigation.

The amount of heat provided the eggs by the atmosphere and by insolation varies, of course, from day to day, dependent upon the air temperature, cloudiness, and other factors. Likewise the amount of residual heat tends to dissipate. Variations in heat derived from these sources are uncontrollable but are compensated for by the amount of heat applied by the incubating bird. The bird must also apply sufficient heat to maintain the egg temperature (34.8° C) above that of the average nest-air temperature (33.4° C). Hence, her contribution varies inversely with air temperature and insolation. Because her regulating behavior is so well adjusted, there is very little variation in average egg temperature and no correlation can be found in these records between the length of incubation and air temperature.

The Work of Incubation.—A bird is continually losing body heat, and it has been suggested that the mere roosting of the bird in the nest box may allow sufficient accumulation of heat for incubation. If true, no work would be performed. In my study of a House Sparrow (Passer domesticus), roosting during the winter in a nest box similar in proportions and structure but slightly larger in size than the ones used by House Wrens (Kendeigh, 1961), I found that at 17° C the box temperature was raised on the average about 1.5° C, at 22° C it would have been raised 0.5° C, and at 24.7° C too little to be readily measured. This decreasing effect with rising air temperature results from the decrease in gradient between body temperature and air temperature and from the lower rate of heat production of the bird at the higher temperatures. The House Wren usually roosts in the nest box after the first egg is laid and may at times actually sit on the eggs, but, until her brood patch becomes fully developed and effectively used, the temperature of the eggs is only slightly changed (Fig. 6 and 7). We may, therefore, consider practically the entire heat application of the bird to the eggs as extra energy that would not otherwise have been expended. Although perhaps not satisfying the strict definition of "work" as given in physics, nevertheless incubation is an achievement that results from the expenditure of energy, and hence may be considered work as far as the bird is concerned.
The chief source of energy in the body is from the oxidation of carbohydrates and fats derived directly from the ingested food or from stored deposits on the body. An appreciable amount of energy taken in as food is lost in the excreta, and considerable amounts are required for maintaining existence. Energy requirements for existence increase linearly with drops in air temperature. Only that energy left over after the requirements for existence are satisfied is available for such activities as incubation. This "productive energy" has not been measured in the House Wren, but may be calculated from data that are available for the House Sparrow, proportionate to their difference in weight, $W^{0.66}$ (King and Farner, 1961). Productive energy in the House Wren would increase linearly from zero at about $0^\circ$ C to approximately 8.3 kcal/bird/day at $20^\circ$ C air temperature. A maximum of perhaps 8.4 would be reached between $20^\circ$ and $25^\circ$ C and a rapid decline would occur at still higher temperatures.

The efficiency of mobilizing and transferring productive energy into heating of the eggs has not been measured but is probably high compared with the efficiency of energy use in other physiological processes, but it would not be 100 percent. Heat is lost to warming the air around the eggs and to the nest structure. With a higher rate of metabolism, heat loss over the rest of the bird's body and through respiration would also be greater than for a bird not incubating. If we are conservative and assume an efficiency of heat transfer of 75 percent, the average percentage of the total potential productive energy needed for incubation would vary from about 17 at an air temperature of $22.3^\circ$ C to 51 percent at $17.0^\circ$ C (Table 1). On one day at nest 49 with air temperature at $14^\circ$ C, the incubating bird applied 4.3 kcal to the eggs. This represents an expenditure equal to the entire productive energy the bird could acquire at this temperature. Using quite a different procedure, West (1960) estimated that the energy cost of incubation in the Tree Sparrow ($Spizella arborea$), at the prevailing summer temperature of $9.2^\circ$ C on its breeding grounds, would require 28 percent of its productive energy.

The work of incubation should also be considered to include the extra energy required for traveling back and forth between the nest and the surrounding territory where the bird finds its food. At the present time we are unable to estimate the size of this demand. It is apparent, however, that at moderate temperatures the House Wren experiences no difficulty in meeting the energy demands for incubation, but at low air temperatures the amount of energy required for incubation would draw seriously or excessively upon what the bird could mobilize.

*Work Requirements during the Egg-laying Period.*—Energy is, of course, incorporated into the bird's egg. We estimated this in the House Wren to be 1.572 kcal, and that most of the energy in a 6-egg clutch was deposited over a 9-day period at a daily rate of about 1.048 kcal (Kendeigh et al.,
1956). Net efficiency in converting energy above that required for maintenance into energy deposited in the egg is estimated for the domestic fowl at 77 percent (Brody, 1945). This would make the energy requirement for egg formation 1.361 kcal/bird/day. If this amount is added to the heat applied to the eggs during the laying period, the total energy expenditure from the second to the fifth days would increase from 24 to 53 percent of the productive energy. On the day the last or sixth egg is laid, when egg temperatures are raised to the incubation level, the average heat input alone, since no new egg is being formed, averages 78 percent of the calculated productive energy.

If these calculations are correct, one can understand why the onset of incubating behavior progresses gradually during the egg-laying period. The bird would be overtaxed physiologically to supply energy both for constructing the egg and for maintaining full incubation temperature. On the day the last egg is laid, however, the drain on the bird's energy resources for egg formation is eliminated, thereby freeing extra energy in the form of heat to be applied to the eggs. It would be of considerable interest to study the thermodynamics of incubation and bioenergetics of the incubating bird in those species when apparent full incubation begins with the laying of the first egg.

**SUMMARY AND CONCLUSIONS**

The temperature of House Wren eggs in equilibrium with room temperature averages 0° to 0.3° C below the air temperature during the early part of the incubation period, and 0° to 0.4° C above the air temperature during the latter part of the incubation period. Egg temperatures \( T \) are maintained at nearly a constant mean temperature of approximately 35° C throughout the incubation period \( T = 33.92 + 0.045X \), where \( X \) is air temperature.

Nest temperatures \( T \) under the eggs vary directly with air temperatures but at a proportionately slower rate \( T = 24.56 + 0.34X \). The difference \( (T) \) between egg and nest-bottom temperatures increases linearly with drop in air temperature \( T = 31.08 - 0.88X \). The rate of cooling of the eggs is 0.86° C per 1° C difference between egg and air temperature per 10 minutes.

Heating the eggs by conduction from the brood patch of the incubating bird is more efficient than heating by convection, as performed under laboratory conditions. The amount of heat applied to the eggs by the incubating bird is a function of the number of eggs in the clutch, their mean weight, their specific heat, and their rate of cooling. This amount \( T \) varies inversely with air temperature, being greater for nest-box locations in the shade \( T = 5.34 - 0.17X \) than when exposed to solar radiation \( T = 3.42 - 0.10X \).

There is a daily rhythm in the amount of heat applied to the eggs, varying about threefold between the least amount at midnight and the greatest amount in early morning. There is also a gradual increase in the amount of heat applied to the eggs during the laying period, with the greatest amount coming on the day the last egg is laid as the egg temperatures are raised to
the level maintained during the incubation period. The sources of heat for incubation are atmospheric, radiational, residual, and the incubating bird. Residual heat is considered to be the heat retained in the nest by reason of its insulation. Incubation is considered to be work because it requires an extra expenditure of energy from the incubating bird. The work of incubation is calculated to be 17 percent of the productive energy that the bird has available at air temperatures of 22° C, 51 percent at 17° C, while at 14° C the entire productive energy of the bird is required for maintaining egg temperatures. Energy requirements for egg formation and egg care during the laying period are approximately equal to the energy requirements for incubation.

LITERATURE CITED

Avian Body Weight, Adaptation, and Evolution in Western North America

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Through the years the adaptive significance of body size in birds has received much study and has been the subject of a number of generalizations. The best known of these is Bergmann's Rule, according to which larger size is correlated with low temperatures in the coldest months (Rensch, 1939) or on the wintering grounds (Salomonsen, 1955). Properly speaking, the basis for Bergmann's Rule is a purely empirical correlation with low temperature, but frequently it has been explained as an adaptation for increased heat conservation. Scholander (1955) criticized this view, arguing that the heat conservation produced by size increase within the usual observed range was insignificant compared with the adaptive value of increased insulation of feathers. Mayr (1956) disagreed with Scholander, arguing that the validity of the rule depended on observed correlation and not on the presumed explanation for its existence.

Most of the support for Bergmann's Rule comes from studies on European birds. In North American birds, Pitelka (1951) found that Aphelocoma coerulescens, for example, followed Bergmann's Rule. He did see an additional correlation between small size and dense vegetation as well as the correlation with warmer climate. However, neither Miller (1941) working with Junco, nor Hamilton (1958) working with Vireo, could see any expression of Bergmann's Rule in these genera.

Reinig (1938) proposed an entirely different theory to account for geographic variation in body size. According to him, populations of a given species became progressively smaller as they spread outward from the point of species origin, or of ice age refuge, because of gene depauperization and resulting loss of hybrid vigor. Timoféeff-Ressovsky (1940), however, demonstrated that just the opposite had occurred during the documented spread of the Yellow-breasted Bunting (Emberiza aureola) into Europe from its original home in Siberia. In this species the birds got progressively larger with distance from the ancestral home.

In the 53 species of birds of western North America that I have studied, I find phenomena similar to that described by Timoféeff-Ressovsky. There is a species center at which the birds are smallest. Outward in all directions from this center the birds get larger, the increase in size being roughly proportional to the distance from the center. For reasons of metabolic and population efficiency, I postulate that the greatest degree of specific adaptation to habitat conditions exists at the center, and that larger size represents a mechanism for nonhabitat specific increase in efficiency as a temporary

adaptation to new conditions pending evolution of specific adaptation to the individual conditions in the newly occupied habitat.

In this study, body size was measured by weights from specimens in the Museum of Vertebrate Zoology, University of California, Berkeley. Only weights of adult summer-taken birds were used, thus avoiding complications of growth and migration. If the weights for the two sexes were statistically different \((P \leq 0.05)\), only males were considered. For each species a map was prepared on which were plotted the mean weights of the sample populations. A population sample consisted of all the usable records from several adjacent counties and was usually a small number (under 30).

The maps showed that variation existed in nearly every species; in some it was quite regular, in others less so. Various analyses and classifications were tried in order to characterize these patterns of variation and to permit comparisons between species and to reveal underlying ecological relationships. The most satisfactory method proved to be to relate all the populations to that having the lowest mean weight. This population of smallest birds was designated the center. Viewed thus, the maps showed a tendency in all species for the weight to increase outward clinally in all directions from the center. In some species this pattern was very marked, although in every case there was at least one population out of sequence.

The geographic centers of the species did not coincide. To group the species, they were segregated according to the location of their centers in the major biogeographic regions of western North America. Five groups resulted: three montane—Sierran–Cascade, Coastal, and Montane Great Basin–Desert; and two lowland ones—Californian and Lowland Great Basin–Desert. Fig. 1 shows the pattern for the Yellow Warbler \((Dendroica petechia)\), which falls in the Coastal Montane group. The pattern is one of increasing weight from the center in north coastal California northward to British Columbia, southward to southern California, and importantly, eastward to the Great Basin. A contrasting pattern can be seen in Fig. 2 for Audubon's Warbler \((Dendroica auduboni)\) of the Great Basin Montane group. With its center in the mountains of northern Nevada, it also gets heavier going north, south, and, by contrast with the Yellow Warbler, westward. The third montane group, the Sierran–Cascade, is illustrated by the Purple Finch \((Carpodacus purpureus)\) (Fig. 3). The patterns found in members of the lowland groups are illustrated by the House Finch \((Carpodacus mexicanus)\) of the Great Basin–Desert group (Fig. 4) and the Yellowthroat \((Geothlypis trichas)\) of the Californian group (Fig. 5). The total membership in the montane groups is shown in Fig. 6 and the lowland groups in Fig. 7.

The regularity present in this geographical variation suggests that some sort of correlation with ecological factors exists. Since not all species, nor even members of the same genus, respond in the same way, it appears un-
Fig. 1. Geographic variation in weight in the Yellow Warbler (Dendroica petechia). Sample areas are shaded. The large open circle encloses the center population. Large numbers are the sample mean weight in grams. The small numbers are $P$ values for significance of difference between the population weight and that of the center population.
Fig. 2. Geographic variation in weight in Audubon's Warbler (Dendroica auduboni).
Fig. 3. Geographic variation in weight in the Purple Finch (*Carpodacus purpureus*).
Fig. 4. Geographic variation in weight in the House Finch (*Carpodacus mexicanus*).
Fig. 5. Geographic variation in weight in the Yellowthroat (*Geothlypis trichas*).
likely that the response is to a single factor such as temperature. It is more likely a response to the total complex of environmental conditions. This reasoning prompted a summarization of known relationships between body weight and various energy-requiring activities.

When an activity rate, such as food intake, is plotted against body weight on a logarithmic graph, the relationship between them is usually a straight line for which the regression equation of \( y \) on \( x \) is \( \log y = a \log x + \log b \). Here \( a \) is the slope of the line, and \( b \) is the intercept of the line on the \( y \) axis when \( \log x = 0 \). If the energy demand per gram is the same for large and small birds, the slope equals one. Most frequently, the slope is less than this, indicating that the large bird is performing the same function at less energy cost per gram than the smaller one. By the definition I use, the larger bird is more efficient. The degree to which it is more efficient is indicated by the amount by which the slope departs from a value of one.

With these ideas in mind, we may consider Table 1 wherein the slopes of regression lines of various energy-demanding functions or indices to them are plotted as functions of body size. They are listed in order of increasing value, which means that those nearest the top are those in which larger birds have the greatest advantage in efficiency.
Fig. 7. Lowland biogeographic areas of the western United States and the species centered in each area.

Large birds, for instance, are more efficient in food utilization in that they support a larger amount of tissue without a proportional increase in food requirement. One can also see, for example, that large birds have no advantage over small ones in terms of energy to replace feathers at the molt. The weight of feathers per gram is the same in birds of all sizes. The material in

<table>
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<th>Function or Character</th>
<th>Slope</th>
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<td>Kendeigh, 1945</td>
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<td>Food consumption</td>
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<td>Nice, 1938</td>
</tr>
<tr>
<td>Basal metabolism</td>
<td></td>
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<td>Many species</td>
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the table supports the general conclusion that larger birds have, all activities considered, a higher efficiency in generalized activities than small ones.

The question arises whether the interspecific relationships implied in the table also hold for size differences among birds of the same species. According to Kendeigh (1945) they do, while Meunier (1959) considers that the intraspecies slopes are even lower than the interspecies ones. If Meunier is correct, then, within a species, larger birds have an even higher efficiency relative to smaller individuals than would be indicated in the table. It will be seen that large birds have relatively smaller internal organs, which suggests that their locomotor apparatus, muscles and skeleton, are proportionally larger than in small birds.

One may ask whether greater efficiency is of selective value. Are more efficient birds likely to survive and breed longer and leave a greater number of offspring? It would seem to depend on the character of the habitat. If, for instance, food is scarce, or widely scattered, so as to require much travel to gather it, then greater efficiency in flight and feeding is likely to be an advantage, since large birds are better able to withstand food shortage (Kendeigh, 1945). The number of young produced is also influenced by the food supply (Lack, 1954).

However, the situation may be quite different. For example, food may not be scarce. Since smaller birds eat an absolutely smaller quantity of food than large ones (Gibb, 1957), they may require smaller territories and hence have higher densities. Kluijver (1951) found in the Great Tit (*Parus major*) that in a favorable habitat the birds had a density of about 5 pairs per 10 ha and that each pair produced about 11 eggs and fledged about 6 young. In an unfavorable habitat, deficient in food, the density was lower, about 0.8 pair per 10 ha, but each pair produced about 14.5 eggs per pair and fledged about 8.6 young. Certainly the birds in the unfavorable habitat appear to be more efficient.

But calculations on a per-pair basis obscure the comparative performances of populations in the two habitats. If one calculates the total production of young per 10 ha, it turns out that the greater density in the favorable habitat more than compensated for the lower productivity of the individual pairs. The total production was 31 young fledged per 10 ha in the favorable habitat, as compared to 6.6 young fledged per 10 ha in the unfavorable area, nearly five times greater in the favorable environment.

To relate all this to geographic variation in weight, one needs to know the relationship between habitat character and relative body size. In studies of the California avifauna, Grinnell and Miller (1944) and Miller (1951) gave for many species the areas of most favorable habitat as indicated by high density. With few exceptions their areas of highest density correspond with the species centers—the areas of minimum weight—of this study. As a further indication, the Bobwhite Quail (*Colinus virginianus*) exists in higher fall densities in Florida than in Wisconsin, 0.2 bird per acre having been reported.
on Florida study areas by Stoddard (1931) and 0.06 on a Wisconsin area by Errington (1945). The Florida birds weigh 165 g on the average, and the Wisconsin birds 202 g (Ripley, 1960). Again, the birds weigh the least in the area of most favorable habitat, as judged by densities.

A word must be said here about this expression "favorable habitat." A habitat cannot be judged either favorable or unfavorable except as it relates to a single species. Obviously a habitat may be favorable for one species and not for another. A habitat is favorable or unfavorable according to the goodness of fit that exists between the morphological, physiological, and behavioral characteristics of the birds and the characteristics of the habitat. In favorable habitat—species relationships the fit is good. As the fit becomes poorer, the habitat becomes progressively less favorable. The effect is to force the inhabiting birds to operate under less and less suitable conditions and the species—habitat relations become less and less efficient. Since the birds cannot change the habitat, the only course open is a reduction in the inefficiency of the relationship by selectively modifying the characteristics of the birds to make their operations more efficient. The obvious manner in which this might be brought about would be by selective modification of morphological and other characteristics of the birds of the population toward closer adaptation to specific habitat structure. But the stringent limitations imposed on avian structure and function by the requirements for flight would appear to inhibit abrupt and rapid evolutionary changes. One might expect that change could take place only by gradual steps, with considerable delay for internal adjustment and alignment so as not to disturb the complex mechanisms necessary for flight, cooling, and so on.

On the other hand, as a quicker temporary measure for improvement, the inefficiency in the relationship could be countered in part by a nonspecific increase in the overall efficiency of the bird. This could be achieved without any change in internal relationships by an increase in size. At a slower rate, specific adaptations to the individual habitat conditions might be evolved and perhaps permit a concomitant reduction in size and a related increase in breeding density.

If this hypothetical process operates, we would expect to find the closest adaptation to specific habitat conditions—and the smallest size—in the area occupied for the longest time. Least specific adaptation, and largest size, would be expected in areas most recently occupied. The gradient in weight from small to large populations would provide an index to the rate of spread of the species over its contemporary range.

Allowing these postulates, I would suggest the following generalized picture. The species center, identified by the lowest body weight, is the center of evolutionary origin or of postglacial spread of the species. Because of climatic and vegetational shifts in time, this center may not now coincide with the original geographic location, although habitat conditions may be the same or very nearly so. The best ecologic fit between the population and
habitat exists at the center simply because adaptive evolution has been going on there longest. In the peripheral populations the ecologic fit is poorer because there has been less time for adaptive evolution. To counteract this inherent inefficiency in the relationships, the individual birds are larger and hence generally somewhat more efficient. The degree of increase in size over that of the center population provides an index to the relative unfavorableness of the habitat for the species and an indication of the length of occupation of that habitat. The heaviest birds are found in the most recently occupied regions where the lowest degree of specific adaptation to habitat conditions exists.

**SUMMARY**

Populations of birds of western North America vary geographically in body weight. In many species, the variation is regular and forms a pattern in which the lightest populations are central and the peripheral populations become progressively heavier with increasing distance from the center. Species are grouped according to location of their centers in major biogeographic regions.

Considerations of metabolic advantages and disadvantages of larger size lead to the hypothesis that the central location is the optimal habitat. Examination of the center location relative to inferred ages of avifaunas and the paleofloristic history of western North America suggests that species differentiated in areas ecologically similar to their centers.

**LITERATURE CITED**


The Arrangement and Action of the Feather Muscles in Chickens

Peter Stettenheim, Alfred M. Lucas, Effie M. Denington, and Casimir Jamroz


Birds frequently adjust the posture of their feathers. Starting from a normal, relaxed condition, the feathers can be depressed against the body, producing the sleeked condition, partially erected to give the fluffed condition, or fully erected to the ruffled condition. These postures have been analyzed by Morris (1956) and found to have numerous functions. They are primarily employed in regulating the insulation and hence the heat balance of the body. Other functions include cleaning activities, defecation, brooding, and—in diving birds—the control of buoyancy. The posturing of feathers may also act as a social signal, occurring, for example, during threat or courtship displays.

Two categories of muscles are involved in feather control. First are the cutaneous components of body muscles such as the cucullaris, pectoralis, serratus superficialis, and latissimus dorsi. These are composed of striated muscle tissue and are readily visible to the naked eye. They originate on the skeleton or on the main part of a body muscle and insert on the inner surface of the skin. The second category is that of the tiny nonstriated muscles in the dermis. This category includes the feather muscles (pennamotor muscles, arrectores plumarum) and the deeper network of muscular and elastic fibers.

The cutaneous muscles were apparently discovered by Jacquemin (1836) and the feather muscles by Nitzsch and Burmeister (1840), but both accounts were brief. Helm (1886) noticed that the size of the feather muscles varied over the body in relation to the size of the feathers and the frequency of their movement. The structure, innervation, and action of the feather muscles were described in detail by Langley (1904). These subjects were further investigated by Dreyfuss (1937), who was particularly interested in the course of the nerves to the follicle and the feather. The reticular structure of the nerve endings in the nonstriated muscles was demonstrated by Schartau (1938). The relationship of feather muscles to displays is a fascinating topic, but we know of only one study of it, that by Pycraft (1905) on the Lesser Bird-of-Paradise (Paradisea minor).

Our research on the feather muscles began several years ago as part of our program in avian anatomy. We have been studying the arrangement of the muscles and their associated structures in Single Comb White Leghorn

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Proc. XIII Intern. Ornithol. Congr.: 918-924. 1963
chickens (*Gallus gallus*). The preparation of illustrations, an important phase of the project, has been done by Casimir Jamroz and John Metheany.

The basic pattern of the feather muscles can be seen in an area where contour feathers are fairly evenly spaced and the musculature is not too heavy. The femoral tract is one such area on a chicken. Bands of muscles link adjacent feathers, forming intersecting rows across the tract (Fig. 1a). In most places these form square or rhomboid figures; but where the feathers are unevenly spaced, the shape of these figures is altered. Typically, each feather is connected by a pair of muscles to each of four surrounding feathers (Fig. 2). One muscle runs from the basal end of one feather to a higher level on a feather anterior or dorsal to it. Contraction of this muscle swings the basal end of the first feather anteriorly or dorsally, and swings the upper end of the second feather posteriorly or ventrally. The result in both cases is depression of the feather, so this is termed a depressor muscle. Its antagonist, the elevator muscle, goes from an upper level of a feather to the basal end of a more anterior or dorsal feather. The size of the muscles varies, as will be seen, but in each pair the depressor is usually thicker than the elevator. Each muscle may be either entire or composed of several bundles of fibers, and the bundles of opposing muscles usually interdigitate as they cross.

For convenience, we have said that the muscles go to the feathers, but actually they attach to the wall of the follicle. At the end of each muscle

![Fig. 1. Nonstriated muscles in skin of a White Leghorn chicken; internal view. (a) Left femoral tract, posteroventral portion. (b) Dorsal cervical tract, midline, and right side at thoracic end of neck. (c) Left crural tract, anterior portion to the left, medial portion to the right.](image-url)
belly, there is an abrupt transition from the contractile fibers to fine elastic fibers. These form a very short, tight bundle and then spread out to join the outer layer of elastic fibers that encircle the follicle.

We can now consider some variations in the basic pattern of muscles. The arrangement is quite regular on the dorsal and pelvic tracts, although there may be minor differences between right and left sides. The muscles parallel to the long axis of the body are longer and thinner than those oblique to this axis. The latter set consists of a depressor muscle and a muscle that attaches at the same level to both follicles. In the pelvic tract this band is at the base of the feathers, but in the dorsal tract it is broader and is inserted for some distance along the lower ends of the follicles. Contraction of this muscle draws the feathers together without raising or lowering them.

On the interscapular tract the oblique rows have both elevator and depressor muscles, but the longitudinal rows consist only of thin depressors. Additional muscles of the same kind run diagonally from each follicle to the one anterolateral to it. The feathers here are thus depressed by three sets of muscles: lateral, anterior, and anterolateral.

The feather musculature of a chicken is heaviest and most complex on the dorsal cervical tract. This is related to the fact that the most conspicuous displays of these birds entail pronounced raising of the hackles. Elevation

![Diagram](image-url)

**Fig. 2.** Basic arrangement of feather muscles as found on left femoral tract of a White Leghorn chicken; external view.
of the neck feathers also occurs during courtship performances of the Red-necked Grebe (Podiceps grisegena), the Ruff (Philomachus pugnax), and certain grouse and birds-of-paradise.

The muscle pattern is fairly regular over the thoracic end of the neck, but it becomes irregular near the back of the head (Fig. 1b). Both antero-laterally and posterolaterally directed rows have elevator and depressor muscles, except along the border of the tract. The anterolateral muscles are the larger, consisting of as many as five bundles, whereas the posterolateral ones contain no more than three. In addition, the upper parts of the depressor muscles in the anterolateral rows have become distinct entities, the retractor muscles. These broad bands join adjacent follicles at the same level and their contraction pulls the feathers together. Finally, there are often a few elevator and depressor bundles crossing a diamond diagonally, from one feather to the one anterior to it.

A feature of the feather muscles that is especially evident in the dorsal cervical tract is that they may meet a follicle either perpendicularly or tangentially. In the latter case, contraction of the muscle twists the feather while raising or lowering it. Some muscles even have divided attachments on opposite sides of a follicle; this apparently permits finer adjustment of the angle of the feather.

The contrasting condition of a lightly developed musculature occurs in the crural tract (Fig. 1c). There is no characteristic arrangement here because the pattern varies considerably over the tract. The follicles on the external (lateral) surface of the leg are linked together, whereas many of those on the internal (medial) surface are not. The arrangement on the anterior and posterior surfaces is transitional between these conditions. Both the feather muscles and the musculoelastic bands in the apteria terminate at the border of scaly skin on the ankle.

One arrangement found in the external region of this tract is that in which only the anterodorsally directed rows of muscles are well developed. The elevator and the depressor muscles both consist of three bundles which interdigitate as they cross. The posterodorsally directed rows regularly have only thin retractor bands, but very weak elevators and depressors are sometimes present. Diagonal muscles may run either dorsoventrally or anteroposteriorly, but only one set is present in a given diamond.

The muscles tend to have a random arrangement in areas where the feathers are widely spaced, such as the internal surface of the leg. They go out from the follicles in many directions, and since they may not shift to higher or lower levels they can no longer be identified as elevators or depressors. Aponeuroses of elastic fibers are especially evident in such muscles. These tendinous segments anastomose freely, connecting the feather muscles with each other and with the deeper network of muscular and elastic fibers.

The posterior end of the pectoral tract illustrates the situation in which feathers are closely spaced along the transverse axis but not along the longi-
Fig. 3. Nonstriated muscles in skin on ventral side of the body of a White Leghorn chicken; internal view. From left to right are the posterior end of the pectoral tract, pectoral apterium, anterior end of the sternal tract, and sternal apterium. Isolated semi-plumes and down feathers occur in the pectoral apterium. Deep musculoelastic fibers are present in the pectoral apterium but not in the sternal apterium.

The adjustment of feathers involves the combined action of the striated dermal muscles and the nonstriated feather muscles. The former are inner-
vated by afferent and efferent branches of spinal nerves. Their contraction causes a wrinkling or twitching of the skin, thereby moving groups of feathers. The feather muscles are believed to be innervated only by efferent branches from the thoracolumbar division of the autonomic system. These fibers accompany the branches of spinal nerves that go to the follicle wall, dermal papilla, and feather pulp. According to Schartau (1938:9–13), the nerves have two types of terminal in the muscle—a syncytial reticulum and a small loop. Our preparations, however, have shown only simple, pointed endings. As described above, the feather muscles can elevate, depress, and twist the feathers or pull them together. The muscles can act separately, but the autonomic system normally stimulates them to have a tonic depressor action (Langley, 1904:237–238).

The sensory input concerning the posture of a feather probably comes from the general afferent nerves in the follicle wall and from the Vater-Pacini (Herbst) corpuscles. These end organs have been found in the skin all over the body of the rooster (Winkelmann and Myers, 1961:27–28). In the tracts they are associated with the follicles, usually one or two per follicle. They have been reported (loc. cit.) to be situated just above the attachments of the feather muscles, but we have found them at lower levels as well. They usually lie at right angles to the long axis of the feather, roughly parallel to the wall of the follicle.

The Vater-Pacini corpuscles are generally considered to be pressure receptors (Winkelmann, 1960:80), but Schwartzkopff (1955:204–207) has shown that they are also extremely sensitive to vibration. Both sensations can be expected in the follicle wall when a feather is moved by its muscles or an external force. The corpuscles may thus aid in monitoring the posture of feathers, not only for flight but also for other functions.

**SUMMARY**

The posture of feathers is adjusted chiefly by the feather muscles (arrectores plumarum), bands of nonstriated fibers in the dermis. In the basic arrangement, the follicle of a contour feather is connected by pairs of muscles to each of four adjacent follicles. There is typically a depressor and an erector muscle in each pair, the former being the larger. A band attaches to the basal end of one follicle and to a higher level on the next follicle. Antagonistic muscles often interdigitate as they cross. The length and thickness of muscle bands vary over the body in relation to the size of the feathers and the frequency with which they are moved. The feather muscles are innervated by the thoracolumbar division of the autonomic system. The Vater-Pacini corpuscles, located near the follicles, may sense the vibration of feathers and thus play a role in the control of feather posture.

**LITERATURE CITED**

GENERAL BIOLOGY AND MISCELLANEOUS STUDIES

The Annual Cycle and Zugunruhe in Birds

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One of the recent trends in modern biology is a concern for the temporal, and particularly, the cyclical organization of life. This trend is manifest not only in studies of short-term physiological functions, but is also implicit in evolutionary studies. Investigation of the temporal dimensions of life in individuals and populations is one of the active areas of current inquiry: However, it is the "circadian" organization that has received most attention, while "circannual" phenomena are neglected or treated in a fragmentary fashion.

In spite of the fact that temporal studies of the annual cycle must be pursued as though seasonal phenomena were separate and separable events, the essential unity of these events cannot be overlooked. The annual cycle in birds must be viewed as an adaptive and functional whole.

Study of the annual cycle can be approached in two ways. An annual cycle could be defined as the totality of overt and covert manifestations of cyclical, and usually rhythmical, morphological, physiological, and behavioral changes in an organism or population of organisms with a periodicity of about a year. These changes are clearly related proximately and/or ultimately to a seasonal environment. In most birds, this cycle can be divided into the following periods: (1) a contranuptial (or hiemal) period; (2) a prenuptial (or vernal) period of at least partial molt, followed by or overlapping (3) a period of vernal migration in some species; (4) nuptial (usually aestival) period of breeding; (5) a postnuptial (or serotinal) period of complete molt; and (6) a postnuptial (or autumnal) period of migration in some species. It will be suggested that period (5) or (6) is followed by (7) a transitional period preceding (1), the contranuptial period. Although this conceptual scheme is a useful point of departure, it leads to and encourages the fragmentary treatment of portions of the annual cycle.

A second way of looking at an annual cycle might be as the totality of regular, characteristic, and seasonally synchronized manifestations of internal and external "activity," where activity is used in its broadest sense. Although these manifestations must be viewed as an adaptive and functional whole, they may be divided into three or more theoretically separate "cycles." These are (1) seasonal cycles in the physical and biological environment of the individual, (2) ethological cycles of externally directed activity by the individual, and (3) morphological, physiological, and psychological cycles within the individual. Only the latter two "cycles" are part of the annual cycle in the strictest sense, but proximately or biologically important aspects of the seasonal cycle are perceived and act as effective stimuli synchronizing

or triggering internal cycles. These internal cycles are interrelated and, in turn, control externally directed behavior. Environmental factors acting as synchronizing stimuli (Zeitgeber of Aschoff, 1958) might be viewed as first-order proximate factors; second-order proximate factors might be regarded as nontiming factors which nevertheless are effective stimuli modifying the cyclical activities as releasers, accelerators, decelerators, or inhibitors. In terms of annual cycles where the functional integration of many different activities is complex, such a distinction is important. In an ultimate sense, the seasonal cycle has acted and is interacting in a selective fashion upon populations producing or modifying the seasonal adaptations illustrated by the extant annual cycles.

Although these conceptual schemes are different ways of fragmenting the annual cycle, the latter approach permits study without losing the cyclical structure of individual phenomena.

One aspect of the annual cycle with physiological, psychological, and behavioral overtones is illustrated by Zugunruhe, the characteristic “migratory” activity of caged migrant birds. Zugunruhe has been accepted as a useful index, even though its causation and precise nature remain unknown (see Farner, 1955; Weise, 1956). Because nocturnal activity can be easily measured, is clearly a cyclical manifestation, and is a widely used tool in experimental studies of the annual cycle in passerine birds, it is timely to explore and compare the temporal aspects of this cyclical activity in field populations and in individuals housed under natural conditions. Some clearer statement of the nature of Zugunruhe is also desirable. For illustration and discussion, let us turn to the annual cycle and Zugunruhe in the White-throated Sparrow (Zonotrichia albicollis).

**ZUGUNRUHE IN THE WHITE-THROATED SPARROW**

*Methods*

My study of the annual cycle of the White-throated Sparrow began in 1956 at Harvard University and the Hatheway School of Conservation Education, and is continuing at Bucknell University, although only data obtained prior to 1960 are reported here. The White-throated Sparrow was chosen for intensive study because, (1) as a seed-eating species, individuals would keep well in captivity; (2) it is primarily a nocturnal migrant; (3) the study area in Massachusetts is located in a region of overlap between the normal summer and winter ranges of the species and, it was inferred, year-round conditions would not exceed normal adaptational limits of the species; and (4) some physiological and field data on the species were available, and much work was and is being done on the closely related White-crowned Sparrow (Zonotrichia leucophrys) in other laboratories by investigators working in this area of biology.

Field study of the annual cycle in the White-throated Sparrow has been concentrated on a measurement of seasonal variations in body weight and
visible-fat class as these fluctuations reflect bioenergetic processes. (Results of this aspect of the study will be reported elsewhere.)

Laboratory study has involved four essentially different measurements or index determinations made upon captive individuals at regular intervals: (1) molt, (2) gonadal development, (3) body weight and visible-fat class, and (4) nocturnal activity. Weekly qualitative determinations of molt (see Weise, 1956) and the development of the cloacal protuberance, reflecting gonadal development (see Wolfson, 1954), were recorded. Quantitative determinations of body weight to the nearest 0.1 g, coupled with related estimates of visible-fat class (see Helms and Drury, 1960), were also made. All captives were housed in activity cages. Two movable perches in these cages, resting on microswitches, served as activity transducers, with continuous recordings being made on an Esterline-Angus Operations Recorder. Duration of nocturnal activity was measured from these graphic records and converted to a percentage of the duration of darkness to eliminate or partially correct for changes in daylength during the year. All of these data were then tabulated graphically by individual bird for yearly periods (see Fig. 1–3).

Individual cages were optically isolated from one another in one of two small unheated rooms in front of open south-facing windows. Daylengths were normal and room temperatures were free to fluctuate with outside changes, although minima were not as low in the room as outdoors. Thus, the physical environment was roughly normal for the study area. However, the biological environment was highly modified, since all social and sexual interactions (except those dependent upon vocalization and hearing) were normally excluded. Food was also held constant throughout the study. These conditions are subsequently referred to in this paper as “natural conditions.”

Five males and five females were involved in this study over a period of 136 bird months. Further details of the methods used and results obtained in this study are given by Helms (1960).

I would like to thank William H. Drury, Jr., and the Massachusetts Audubon Society for providing the facilities of the Hatheway School where this work was performed. Weather instruments were graciously supplied by the U.S. Army, Quartermaster Research and Development Command. Kenneth S. Rawson and Donald R. Griffin made suggestions regarding the original activity-recording equipment and cages. Many individuals have aided in various ways throughout this study. I am also indebted to the National Science Foundation (G4811) and the Milton Fund of Harvard University for financial support during this work. I am particularly grateful to Ernst Mayr for his interest, support, counsel, help, and patience in, with, and during this study.

Results and Discussion

Activity Patterns in the White-throated Sparrow.—Graphic presentations of nocturnal activity and other variables recorded during this study are given
for three White-throated Sparrows housed under natural conditions (Fig. 1, 2, and 3).

As Wagner (1930) pointed out, the presence or absence of nocturnal activity divides the year into four periods: vernal and autumnal periods with activity, and serotinal and hiemal periods without. The periods of activity persist somewhat longer than natural ones in the field, the vernal period ending only with the onset of postnuptial molt and the autumnal period with the onset of climatic winter. As Fig. 4 shows, this latter activity can persist throughout much of the winter in a bird not exposed to low winter temperatures, ending only prior to vernal gonadal development and the onset of prenuptial molt. Similar prolongations of activity in spring and fall are reported by Merkel (1938), Palmgren (1944), Wagner (1955), and others working with migratory restlessness. In addition, nocturnal activity can be released by elevated temperatures under short photoperiods (Farner and Mewaldt, 1953), and is generally variable under a variety of temperature

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**Fig. 1. Annual cycle data for White-throated Sparrow 01♀.** This bird was housed under natural conditions from capture, 25 September 1957, to death, 21 June 1959. She was exposed to 02♂ (Fig. 2) from early May to early June 1959, but at other times was held in optical isolation from other birds. Months are indicated by Roman numerals. Each line of the chart covers a maximum of 1 year of records from 1 February to 1 February.

NA, nocturnal activity: duration of activity as percentage of dark time (breaks in the record indicate nights of questionable data which are not plotted).

BWF, body weight and fat: heavy line, body weight in grams; light line, fat in fat-class units (*f.c.*, see Helms and Drury, 1960).

*M*, molt: open rectangle, contour molt; dark rectangle, flight molt.

*CIP*, cloacal protuberance: open rectangle, marked cloacal development.
Fig. 2. Annual cycle data for White-throated Sparrow 02♂. This bird was housed under natural conditions from capture, 25 September 1957, to release 12 August 1960. He was exposed to 01♀ (Fig. 1) from early May to early June 1959, but at other times was held in optical isolation from other birds (the 1960 records are not included in this figure). Months indicated by Roman numerals. Each line of the chart covers a maximum of 1 year of records from 1 February to 1 February.

NA, nocturnal activity: duration of activity as percentage of dark time (breaks in the record indicate nights of questionable data which are not plotted).

BWF, body weight and fat: heavy line, body weight in grams; light line, fat in fat-class units (f.c., see Helms and Drury, 1960).

M, molt: open rectangle, contour molt; dark rectangle, flight molt.

CIP, cloacal protuberance: open rectangle, marked cloacal development; dark rectangle, functional cloacal development.

Exp, experimental: a, disregard experimental administration of gonadotropin in this context.

situations, depending partly upon season and species, although there is no universally accepted pattern to this variability (Eyster, 1954; Merkel, 1954 and 1956; Palmgren, 1937 and 1944; Siivonen and Palmgren, 1936; Wagner, 1937 and 1955; Weise, 1956). Restricted food can also elevate nocturnal activity (Eyster, 1954; Wagner, 1937, 1957), although in my experience with
Fig. 3. Annual cycle data for White-throated Sparrow 14♀. This bird was housed under natural conditions from capture, 10 October 1957, to release on 12 August 1960. He was held in optical isolation from other birds throughout this period (the 1960 records are not included in this figure). Months are indicated by Roman numerals. Each line of the chart covers a maximum of 1 year of records from 1 February to 1 February.

NA, nocturnal activity: duration of activity as percentage of dark time (breaks in the record indicate nights of questionable data which are not plotted).

BWF, body weight and fat: heavy line, body weight in grams; light line, fat in fat-class units (f.c., see Helms and Drury, 1960).

M, molt: open rectangle, contour molt; dark rectangle, flight molt.

CIP, cloacal protuberance: open rectangle, marked cloacal development; dark rectangle, functional cloacal development.

Exp, experimental: a, severely restricted weight, fat, and activity due to lack of drinking water; b, disregard experimental administration of gonadotropin in this context.

buntings, the limitation must be severe, and generally elevates total diurnal as well as nocturnal activity. Light intensity during the night is also significant, total darkness suppressing activity completely (Wagner, 1937, 1957; Helms, unpublished data). Although molt normally suppresses nocturnal activity (Eyster, 1954), one female Lark Sparrow (Chondestes grammacus)
Fig. 4. Annual cycle data for White-throated Sparrow 40♀. This bird was housed under natural daylengths, but held at room temperature from capture, 29 September 1957, to 24 June 1959 (Exp g), when she was exposed to natural conditions of all variables as described in the text. This bird was released 12 August 1960. She was held in optical isolation from other birds throughout this period (the 1960 records are not included in this figure). Months are indicated by Roman numerals. Each line of the chart covers a maximum of 1 year of records from 1 February to 1 February.

Note particularly the differences in the intensity and seasonal pattern of nocturnal activity in the fall of 1958 and 1959. During the former year, this bird was excluded from normal environmental variations in temperature (see text).

NA, nocturnal activity: duration of activity as percentage of dark time (breaks in the record indicate nights of questionable data which are not plotted).

BWF, body weight and fat: heavy line, body weight in grams; light line, fat in fat-class units (f.c., see Helms and Drury, 1960).

M, molt: open rectangle, contour molt; dark rectangle, flight molt.

Exp, experimental: disregard all experimental treatments (labeled a–h) in this context.

PL, perch light: dim light in experimental room, off between vertical bars and on at other times.

showed appreciable and relatively undiminished activity throughout the postnuptial molt periods for 2 years. Both the prolongation of nocturnal activity under natural conditions and its apparent lability at any phase of the annual cycle in experimental situations need careful attention, and suggest caution in applications where it is labeled “migratory” restlessness or Zugunruhe. It is preferable to use the neutral term “nocturnal activity” or
Nachtunruhe in view of these considerations. It is particularly misleading to speak of migration in caged birds as some authors have done. As generally defined (Farner, 1955), migration is a behavior permitted only in free-living individuals.

Thus, although migratory restlessness is a cyclical phenomenon displayed by caged nocturnal migrants during the migratory seasons and as such is a part of the annual cycle in caged individuals, its congruence with actual migration is open to doubt. Perhaps even its use in studies of migratory phenomena might be questioned, since the psychological and physiological causation of this activity would seem to be an open matter at present.

Before discarding this experimental tool, however, it is instructive to look more carefully at the seasonal and diel patterns of nocturnal activity.

In spring, diurnal activity normally increases in the afternoon hours, but drops sharply with the onset of nocturnal activity in the hours prior to midnight (Palmgren, 1944). Within several nights of first activity or onset, the nocturnal activity is fully developed, with a normal duration of 90 percent of the dark period. It begins shortly after the onset of darkness and may last into the morning hours with no or very few breaks. In other words, the vernal nocturnal activity is typically intense and continuous. Later in the spring or early summer, the nocturnal activity becomes broken by periods of no activity and is less in amount and more variable, although onset of the first nocturnal activity remains early in the dark period.

Following postnuptial molt, nocturnal activity begins once more, usually with first movements occurring late in the night, frequently after midnight. This nightly activity is broken by rest periods throughout the autumnal period. Although activity begins earlier in the night later in the fall, it is seldom found prior to 1½, and usually 2 or 3, hours after the beginning of darkness. Maximal activity builds slowly, taking at least 1 and often 2 weeks to reach duration values of 60 percent of the dark time. There are no marked changes in diurnal activity in the White-throated Sparrow during this period, and an evening maximum, lacking in spring, is present in fall. Later in the period of autumnal unrest, amounts of activity decrease, and nights of activity are often separated by 1–3 nights of no activity. The evening period of sleep or rest prior to the beginning of nightly activity normally becomes longer, and, in the last nights of unrest prior to extinction, activity is concentrated in the morning hours.

In summary, vernal unrest is characteristically more intense, more continuous, and begins earlier in the dark period than autumnal unrest. In addition, both periods are marked by increased variability of activity, as well as reduced activity later in the seasonal periods of unrest. My consideration of these patterns over a 5-year period has suggested that, in White-throated Sparrows housed under natural conditions, not only can vernal and autumnal activity be separated, but both periods can be subdivided. In practice, either the inflection point following maximal vernal and autumnal activity or that
point preceding a marked increase in variability of the nocturnal activity (usually preceding the first night of markedly reduced activity) has been used to effect this subdivision. In both migratory periods, the first period of more intense activity is termed “motivational” and the nocturnal activity, motivational migratory restlessness (Zugunruhe, sensu stricto). The later, more variable period of activity is termed “adaptational” and the nocturnal activity called merely nocturnal activity or adaptational migratory restlessness (Zugunruhe, sensu lato). The justification for this separation and the operational terms employed will follow.

Temporal Comparison of the Annual Cycle in Captive and Wild White-throated Sparrows.—Temporal onsets of periods of the annual cycle are given in Table 1 by date and may be compared with crude median dates for events in wild populations in New England areas. First field movements in the spring are noted about 5 April with peak movements during the last week of April, and latest movements end with the onset of breeding activities about 23 May. Allowing 7 days for the establishment of territory, courtship, and pair formation, 5 days for nest building, 4 days for egg laying, 12 days for incubation, and 20 days until the young are independent, breeding would last until 10 July. Although no dates are available in the literature and a few July nests are recorded with eggs, this date agrees well with the onset of molt in captive individuals. Fall movement begins about 5 September with peak movements during early October. Migration in field populations is essentially over by 15 November.

If we accept these dates for wild populations and compare them with the phases of the annual cycle displayed by captive birds (Table 1), it can be seen that the onset and cessation dates for vernal motivational Zugunruhe agree with the field dates. This suggests that this period of caged activity does indeed correspond to the migratory period of wild birds and might be regarded as an expression of some aspect of migration (however, correlation does not necessarily imply causal or functional relationship).

Adaptational nocturnal activity persists throughout the normal breeding period, terminating at the time of the onset of molt. The White-throated Sparrow frequently sings at night on the breeding grounds, indicating a degree of wakefulness during this period of the annual cycle. Merkel (1956) suggests, however, that experiences of the free-living birds on their breeding grounds tend to end restlessness. Comparison of 1959 records of 01♀ and 02♂ White-throated Sparrows (Fig. 1 and 2) supports this contention. These birds were in adjacent cages and were allowed full view of one another from early May to early June. The female showed extinction of nocturnal activity by the last week in May and marked development of the cloacal protuberance (death presumably due to an attendant physiological malfunction). The nocturnal activity of the male decreased markedly until the partition was restored, when activity returned to high levels. These evidences suggest that the adaptational nocturnal activity of caged birds may be inhibited by inter-
Table 1.—Temporal Aspects of the Annual Cycle in Captive White-throated Sparrows

<table>
<thead>
<tr>
<th>Period of the Annual Cycle</th>
<th>Onset of Period (Mean ± s.e.)</th>
<th>s.d. of Onset (Days)</th>
<th>Sexual Difference in Onset</th>
<th>MEAN LENGTH OF PERIOD</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Contranuptial period</td>
<td>4.5 Dec. ±6.2</td>
<td>20.5</td>
<td>δ δ 11.7 days before ♀ ♂</td>
<td>126.5</td>
<td>34.7</td>
</tr>
<tr>
<td>Spring migration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Motivational Zugunruhe</td>
<td>9.9 April ±2.6</td>
<td>9.6</td>
<td>δ δ 5.4 days before ♀ ♂</td>
<td>39.7</td>
<td>10.9</td>
</tr>
<tr>
<td>Adaptational Zugunruhe</td>
<td>19.6 May ±1.8</td>
<td>6.5</td>
<td>♀ ♂ 5.9 days before δ ♂</td>
<td>53.3</td>
<td>14.6</td>
</tr>
<tr>
<td>Postnuptial period</td>
<td>11.9 July ±3.0</td>
<td>10.9</td>
<td>♀ ♂ 6.7 days before δ ♂</td>
<td>61.7</td>
<td>16.9</td>
</tr>
<tr>
<td>Fall migration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Motivational Zugunruhe</td>
<td>11.6 Sept. ±3.4</td>
<td>9.6</td>
<td>♀ ♂ 16.5 days before δ ♂</td>
<td>40.0</td>
<td>11.0</td>
</tr>
<tr>
<td>Adaptational Zugunruhe</td>
<td>21.6 Oct. ±3.0</td>
<td>8.8</td>
<td>♀ ♂ 2.8 days before δ ♂</td>
<td>43.9</td>
<td>12.0</td>
</tr>
</tbody>
</table>

individual stimulations and is normally so inhibited in wild birds. In the event that climatic conditions are unfavorable, this extended period of preparedness for migration may permit a delay in reaching breeding areas, a reversal of direction and reverse migration, or continued flight in either direction if nesting is unsuccessful. This assumes that this period of nocturnal unrest may reflect migratory capability in some way. Hence, this period of activity has been called adaptational.

Similar considerations apply in the fall. The onset of early movements in caged and wild birds correspond closely, and much of the field movement is over by mid-October. However, local flock movements and limited migration may be noted into November. The cessation of autumnal nocturnal activity is highly variable (standard deviation 20.5 days), and is, in caged birds, correlated with the onset of climatic winter between mid-November and late December. Since the caged birds were not exposed to full temperature minima, this date appears to be late in these captives. However, at similar periods, Tree Sparrows (Spizella arborea) in the local study area shifted from lowland areas, river bottoms, and fields to upland wintering areas, and remained in the latter areas throughout the remainder of the contranuptial period. These relationships suggest that motivational Zugunruhe in the fall again corresponds to a period of normal seasonal migratory movement, while adaptational Zugunruhe corresponds to a period in which stragglers and other individuals, delayed by late broods, illness, or injury, etc., are still able to move, although the majority of the species is largely sedentary within the normal range. The extinction of caged nocturnal activity corresponds with
the loss of migratory capability as reflected by depot fat in wild populations and a shift to typical winter habitat. This is a transitional period between fall migration and the contranuptial period.

These temporal relationships are summarized in Fig. 5, utilizing the conceptual scheme of the annual cycle outlined in the introduction (other data used in constructing this figure will be discussed elsewhere).

![Annual Cycle Diagram]

**Fig. 5.** The annual cycle of the White-throated Sparrow. This figure utilizes the conceptual scheme of the annual cycle presented in the text to illustrate some of the major seasonal cyclical features of importance in the life of the White-throated Sparrow. Months of the year are indicated by number around the periphery of this circular diagram. The outer circle represents the seasonal cycle, and includes all environmental events of biological importance to the species, although only a few of these events can be suggested. The middle circle includes behavioral events associated with varying phases of the annual cycle, while the inner circle includes a variety of internal cycles emphasizing the phases of the annual cycle delimited by nocturnal activity in caged birds. The internal and external activities included in these two circles are normally synchronized with events in the seasonal cycle.

**What Is Zugunruhe?**—In the light of this discussion, it could be argued that all nocturnal activity in White-throated Sparrows housed under natural conditions is migratory in a broad sense, in that it does appear to reflect some aspect of migratory capability and that the classical utilization of this tool is justified.

However, a certain, usually very low-level activity is sometimes found during winter periods, and more frequently during periods of complete molt.
Multiple-regression and correlation analysis of activity and weather variables, which are under way, suggest that these nights of activity are closely related to (1) wave cyclones in winter with heavy snowfall and low temperatures, and (2) intense frontal storms after squall-line passages in summer, and that this activity may not in any sense be regarded as migratory. (However, some changes in winter territories of foraging groups occur with the wave storms in winter.) Thus, a note of caution must be interjected into the direct application of nocturnal-activity data to functional interpretation and study of migration per se. In caged birds the progressive exclusion of normal environmental variables induces a progressive increase in variability of activity patterns. This increased variability suggests that experimental application, or rather the interpretation of experimental results using activity data, may be difficult or even hazardous unless the patterns are clearly defined. Because the patterns are most clearly defined under natural conditions, it would seem that, at least under experimental situations, we are led into an impasse, dependent in part on what we are measuring when we measure nocturnal activity and how we evaluate such data.

Farner, Mewaldt, and King (1954:151) state that "Zugunruhe is probably best regarded as an expression, under very abnormal conditions, of a profound change in activity pattern which, in itself, is one facet of the complex of altered physiologic and psychologic processes of the migratory bird." Although it might be well to strike "physiologic and" from this statement, this is a reasonable and current view of Zugunruhe that is not disputed. This definition might be both broadened and narrowed, however, by saying that nocturnal activity is a cyclical expression of psychological processes during the annual cycle bearing an unknown relationship to other annual phenomena. As such, it is endogenously controlled (Cycle 3) under environmental proximate setting (Cycle 1: first-order factors), but exogenously released or inhibited within limits by environmental stimuli (Cycle 1: second-order factors) that may differ seasonally, or the relative thresholds of which may vary with the endogenous mechanisms in back of the behavioral manifestation, nocturnal activity (Cycle 2). Hunger, adverse weather, experimental conditions, and other internal or external factors may modify, initiate, or suppress this activity. However, from the normal seasonal and diel patterns of this activity, it may be inferred that the normal drive relationship is migratory. In this context, Wagner's (1955) hypothesis is rejected as an oversimplification that does not fit this picture. Merkel's (1956) approach, developed at the Helsinki Congress in 1958, deserves further elaboration.

However, this discussion does not appreciably contribute to an understanding of what exactly migratory unrest is, because "drive" and "psychological" are suitable but vague and rather meaningless terms. The only conclusion to be drawn is that "Zugunruhe" does indeed represent an expression of a process or processes in a migratory bird which are usually related in some unknown way to migration of wild birds of the same species.
The practical problem of interpreting data on nocturnal activity under experimental conditions remains. In the first place, both physical and biological environments should be known. Under natural conditions, important parameters such as daylength, light intensity, temperature, humidity, etc., should be recorded. Under experimental conditions, control points must be known and held. Under both conditions, at least visual, interindividual interactions should be excluded unless they are being studied. In the second place, long-term recordings to establish patterns of activity for the species under natural conditions should accompany experimental analyses. Preferably, individuals should also be studied for longer periods in captivity prior to experimental treatment so that phases of and variations in activity are well established. In the third place, since high fat reserves and a general lability of these reserves normally accompany periods of migratory capability, measurements of a bioenergetic nature greatly aid in the interpretation of activity data. Molt records, gonadal conditions, etc., also are of use in phase interpretation.

However, it is not improbable that the mechanisms controlling these other cyclical phenomena, although normally coupled, can be experimentally uncoupled. In this event, pattern and intensity of activity alone may have to serve in the interpretation of activity data. This eventuality does not simplify the experimental problems. Nevertheless, under carefully defined and well-known conditions, as outlined, nocturnal activity, or migratory unrest in the broadest sense, is an operational tool worth using simply because of its temporal correspondence with migratory movements in wild populations, although it must be interpreted continuously.

Under natural conditions, periods of restlessness in caged birds can be tentatively separated into two phases in both the spring and the fall, termed motivational and adaptational. Where the activity is motivational in nature, congruence with field behavior is suggested; but precise relationships remain unknown. Detailed phenological analyses of activity during this period may help to clarify this problem. As a basis for further research, I tentatively suggest that motivational migratory unrest is more sensitive to second-order control by the physical environment than adaptational nocturnal activity, except in the late fall when low temperature seems to be responsible for extinction (perhaps as a first-order proximate factor?). Directional components of nocturnal activity may also be less labile during motivational periods, although the converse of this situation is very likely.

Under experimental conditions where separation of activity into motivational and adaptational phases may be impossible, acceptance of a certain intensity and duration of activity as migratory activity may be permissible. Analysis of directional components of experimentally induced nocturnal activity would be desirable, particularly if a planetarium were available for controlled study.

In spite of the apparent usefulness of nocturnal activity, a number of
methodological as well as theoretical problems remain unsolved. Fresh approaches and new study methods are needed.

CONCLUSIONS

Because of the unsatisfactory nature of our knowledge about causal and functional aspects of migratory unrest and the relative difficulties in precise interpretation of activity data, Zugunruhe alone is a less than satisfactory tool for the experimental study of cyclical phenomena in the annual cycle of birds. Such data, however, represent only monovariable information, and it is doubtful that study of any other single variable, gonadal cycles for example, is any more valuable (except as the functional and causal interrelations may be known more completely). As a cyclical phenomenon in caged birds, obviously a part of the annual cycle as defined, it does warrant more study and perhaps wider application. Because it can be recorded continuously and automatically, moreover, it does offer certain advantages in the study of proximate timing of cycles, and as an adjunct to other assays of cyclical phenomena, it defines certain phases, if recorded continuously, rather precisely.

The annual cycle is a totality of seasonally synchronized activities; and in this light, the objects of study become these activities, the periods of which are used in classification, rather than the reverse. Methodologically, this point of view recommends a horizontal rather than a vertical separation of such cyclical phenomena as migratory activity, fat deposition, gonadal development, etc., for study. This preserves and emphasizes the unitary nature of these phenomena. Integration of studies of these cyclical phenomena into studies of a polyvariable nature must be made for the further clarification of the adaptive and functional integrations of these independently assayed cycles at higher organizational levels.

SUMMARY

The annual cycle of birds must be viewed as an adaptive and functional whole. In spite of the fact that investigations of the cycle must be pursued as though various phenomena were separate and separable events, the essential unity of cyclical phenomena cannot be overlooked.

Migratory restlessness (Zugunruhe) is widely used in studies of migratory passeresines known to fly at night. In some experiments any nocturnal activity has been considered "migratory." In the White-throated Sparrow (Zonotrichia albicollis), graphic presentation of the annual cycle, which includes records of body weight and visible fat, gonadal stages, molt, and nocturnal activity, suggests that so-called "restlessness" may have other meanings than migration per se.

When nocturnal activity is viewed in this context, restlessness may be separated into two phases, one termed motivational (Zugunruhe, sensu stricto), and one termed adaptational (Zugunruhe, sensu lato). Separation of these two phases is difficult in the short-term experimental situation, al-
though certain criteria (onset time, duration and pattern of activity, variability in duration, responsiveness to exogenous stimuli, etc.) may suggest differences.

For the present, results of monovariable approaches to the annual cycle should be regarded as being applicable only in the given experimental situation. An overall view of the cycle can be obtained only through a polyvariable approach considering adaptive and functional integrations at a higher level of organization.

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Autumnal Migratory-fat Deposition in the White-crowned Sparrow

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One of the most prominent indications of the physiological preparation for migration in many species of birds is the intensive deposition of fat that immediately precedes migratory departure and that recurs during each stopover in the migratory itinerary (for pertinent reviews of the occurrence and magnitude of migratory fattening in different species of birds see Wachs, 1926; Zedlitz, 1926; Groebbels, 1930; Wolfson, 1945, 1952; Farner, 1955; Odum 1960b; Odum et al., 1961). Because of the widespread correlation of fat deposition and migration, and because of the lengthy migratory flights accomplished by many species of birds, energy storage in the form of fat is a necessary metabolic adaptation to the muscular work of migration (Odum et al., 1961) and to the survival of other exigencies of the journey. In the investigation of the environmental factors and internal responses that time this important adaptation and regulate its magnitude, attention has been directed chiefly to the vernal phase of migration and to species that breed at high northern latitudes. It is the intention of this paper to examine the characteristics of autumnal fat deposition in the White-crowned Sparrow (Zonotrichia leucophrys), and to compare these with the corresponding events of the spring.

Characteristics of Vernal Fat Deposition

In several fringillid finches, many physiological and behavioral events of the vernal season, including molt, testicular recrudescence, sexual song, fat deposition, and locomotor activity (Zugunruhe) manifesting the migratory urge, can be unseasonally induced in caged birds by experimental extension of the daily photoperiod (for reviews see Farner, 1955, 1960; Wolfson, 1945, 1960). Accordingly, for the species involved, the increasing vernal photoperiod is implicated as a major factor inducing these events under natural conditions.

One of the most intensively studied groups of birds are the crowned sparrows of the genus Zonotrichia. With regard specifically to vernal fat deposition, the underlying metabolic adaptation includes, at least for Z. leucophrys gambelii (King and Farner, 1956; King, 1961a) and Z. albicollis (Odum and Major, 1956; Weise, 1956; Odum, 1960a), a distinct hyperphagia during the establishment of the increased premigratory fat reserves. In Z. l. gambelii, and probably in the related taxa, this adaptive increase in appetite is photoperiodically induced (King, 1961b; see also Odum, 1960a) and persists, as will be shown below, at least through the early phases of migration, thus assuring that lipid reserves will be replenished rapidly during stopover pe-
periods. These reserves are clearly regulated at a higher level during the migratory seasons than during other phases of the annual cycle. Adaptive hyperphagia is, of course, a major psychophysiologic consequence of the tendency toward increased energy storage.

Other important characteristics of vernal premigratory-fat deposition include its typically rapid development (cf. Fig. 1) and its impressive temporal precision, at least in *Z. l. gambelii*, from year to year as well as among in-

Fig. 1. Seasonal variation in mean midafternoon body weight of male *Zonotrichia leucophrys gambelii*. Data compiled from several years. Numerals at each point indicate the number of birds in the sample. Open circles: feral birds in southeastern Washington; blackened circles: captive birds at Pullman, Washington.

dividuals within a given year (King and Farner, 1959). Like the case of photoperiodically induced gonadal development, the natural or experimental photic induction of vernal fattening is accompanied by the development of a *photorefractory period*. During this period, which persists at least into December in northern latitudes (Miller, 1948, 1954; Wolfson, 1952; Farner and Mewaldt, 1955; Shank, 1959; King et al., 1960), experimental prolongation of the daily photoperiod will not produce a second or additional gonadal or metabolic response. It is well established for the case of the gonadal response that the hypothalamohypophysial axis is the site of blockade to photoperiodic stimulation (for review, see Laws, 1961). We assume that this is true also for metabolic photorefractoriness, although the mechanisms are at least partially independent, as indicated by the longer duration of the
metabolic photorefractory period in some species (Shank, 1959; King et al., 1960).

AUTUMNAL MIGRATORY-FAT DEPOSITION

The occurrence of fat deposition in many passerine species during autumn migration has been abundantly documented through the investigation of captive birds (e.g. Groebbels, 1932; Merkel, 1938, 1958; Wallgren, 1954; Rautenberg, 1957) and by the sampling of feral populations (Millar, 1960; Odum, 1960b; King et al., 1963). These investigations show that long-distance overseas migrants, such as Dolichonyx oryzivorus, Piranga olivacea, and P. rubra, are extremely obese (lipid content equal to 33–52 percent of body weight) during autumn migration, although intracontinental migrants that traverse shorter distances (e.g. Zonotrichia albicollis, Z. leucophrys gambelii) are less fat during autumn. In the relatively few investigations of autumnal migratory-fat deposition that have been accomplished thus far, attention has been confined to the study of captive birds or to observation and sampling of wild populations in transit, considerably after departure from the breeding grounds. Practically no information is available concerning fat deposition, if any, in feral populations during the autumnal premigratory period. Our knowledge of the metabolic adaptations for autumnal migration is thus restricted on the one hand by the uncertainties of projecting laboratory observations to feral populations, and on the other hand by uncertainties in the interpretation of data from samples of transient populations. These samples undoubtedly vary temporally in many factors that influence the fat reserves, and therefore bias our assessment of the magnitude of these reserves in autumn migrants. These factors include, for instance, the age and sex composition of the flocks, the length of the most recent migratory flight and the duration of refeeding since its completion, the abundance of suitable food, the weather conditions, and so forth. Samples of vernal premigratory populations (e.g. Odum and Perkinson, 1951; Blanchard and Erickson, 1949; King and Farner, 1959) that are obtained from stationary and relatively stable populations are, of course, not statistically biased in this way.

With these precautions in mind, we may examine the data available on the autumnal migratory fattening of Zonotrichia leucopyhrs gambelii. Questions of particular interest concern the temporal and quantitative characteristics of fattening, compared with the vernal counterpart, and the factors involved in the induction and regulation of the metabolic changes that result in increased lipogenesis and storage.

Data from captive and feral populations of male Z. l. gambelii at the northern boundary of the wintering ground of this race are displayed in Fig. 1. The vernal changes in body weight (reflecting mainly changes in stored fat) are very similar in the captives and in the stationary wintering population. We have previously compared in detail the vernal premigratory responses of wild and captive White-crowned Sparrows and have shown that captivity has a surprisingly minor effect on the timing and intensity of pre-
nuptial molt, premigratory-fat deposition, and the initial stages of testicular growth. Zugunruhe develops concurrently with the departure of the feral population from the nearby wintering grounds (King and Farner, 1959, 1963; King 1961a, 1961b). This leads reasonably to the assumption that data from captive birds may be used also to reveal, at least qualitatively, the metabolic tendencies of the feral population in the autumn.

There is an abrupt increase of the body weight of captive *Z. l. gambelii* in the vernal phase (Fig. 1). Autumnal fat deposition occurs more slowly and attains a lower maximum. The data for individual birds reveal that in the autumn there is much greater individual variability in the onset of premigratory fattening, the rate at which it proceeds, and the maximum reserves attained. These prominent differences between vernal and autumnal fattening have been found also in captive *Zonotrichia atricapilla* and *Z. querula* maintained at our laboratories in Pullman (King and Farner, 1963).

A comparison of the data on the autumnal body weight of captives and of samples of the wild population (Fig. 1) indicates some conspicuous differences. Unlike the situation in the vernal premigratory period, there is little conformity between the autumnal variation in the body weight of the two groups. I submit that this is at least partially the result of sampling a heterogeneous transient population which includes in the autumn individuals that have just arrived in the trapping area after sustained migratory flights, individuals that are stopping over to refeed and replenish the fat reserves, and individuals with reserves restored at the termination of a stopover period. Other aspects of the data lend support to this contention.

The lipid indices (percentage of live body weight as ether-extractable fat) of samples of feral *Z. l. gambelii* during selected phases of the annual cycle are shown in Table 1. These data reveal that during autumn migration there is a definite tendency toward increased storage of fat. This is not reflected clearly in the data on total body weight because the lean fat-free weight of both adults and first-year birds in autumn tends to be approximately 1 g less than in the spring. The difference in the lean weight of males in September (25.5 g) and March (26.5 g) is highly significant statistically (*P* = 0.01). It is therefore quantitatively misleading to compare total body weights of feral migrants in spring and fall as a method for assessing the relative fat deposition.

A further consideration of Table 1 shows that maximum mean lipid reserves during autumn migration tend to approach those of the spring period. Maximum lipid indices for individual birds have been found to be 22 percent and 27 percent in autumn and in spring, respectively. The increase in mean lipid index during the autumn migration possibly reflects the arrival in the trapping area of elements of a more northern population of *Z. l. gambelii* which has a more marked propensity for the deposition of migratory fat. In this connection, Merkel (1958) has shown that captive *Erithacus rubecula* from northern Europe have a greater migratory increase in body weight than
do individuals from middle European populations. The possibility should not be overlooked, however, that the seasonal increase in autumn represents a physiological tendency toward increasing energy storage as migration progresses. This is suggested by the increasing mean body weights of captive \textit{Z. l. gambelii} in autumn (Fig. 2; see also King, 1961b). Odum (1958) found no similar seasonal change in lipid indices in autumn in \textit{Zonotrichia albicollis}, but it is significant that the collection site in Georgia was at the southern

### Table 1.—Mean Lipid Indices* of Feral \textit{Zonotrichia leucophrys gambelii}

<table>
<thead>
<tr>
<th>Dates</th>
<th>MALES</th>
<th></th>
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<th>FEMALES</th>
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<tr>
<td></td>
<td>N</td>
<td>Mean</td>
<td></td>
<td>N</td>
<td>Mean</td>
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<tr>
<td><strong>AUTUMN MIGRATION</strong></td>
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<tr>
<td>1–10 September</td>
<td>4</td>
<td>5.5 ± 0.43(^b)</td>
<td></td>
<td>10</td>
<td>7.0 ± 0.68</td>
<td></td>
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<tr>
<td>11–20 September</td>
<td>16</td>
<td>8.7 ± 0.94</td>
<td></td>
<td>21</td>
<td>10.2 ± 0.98</td>
<td></td>
</tr>
<tr>
<td>21–30 September</td>
<td>20</td>
<td>8.4 ± 0.76</td>
<td></td>
<td>22</td>
<td>8.7 ± 0.81</td>
<td></td>
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<tr>
<td>1–10 October</td>
<td>4</td>
<td>12.5 ± 3.25</td>
<td></td>
<td>5</td>
<td>13.7 ± 1.10</td>
<td></td>
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<tr>
<td><strong>WINTER FLOCKS</strong></td>
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<tr>
<td>11–20 December</td>
<td>24</td>
<td>8.2 ± 0.41</td>
<td></td>
<td>6</td>
<td>10.3 ± 1.53</td>
<td></td>
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<tr>
<td>11–20 January</td>
<td>2</td>
<td>9.8</td>
<td></td>
<td>1</td>
<td>(6.1)</td>
<td></td>
</tr>
<tr>
<td>11–20 February</td>
<td>14</td>
<td>8.0 ± 0.40</td>
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<tr>
<td><strong>VERNAL PREMIGRATORY PERIOD AND MIGRATION</strong></td>
<td></td>
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<tr>
<td>11–20 March</td>
<td>18</td>
<td>6.0 ± 0.25</td>
<td></td>
<td>1</td>
<td>(6.5)</td>
<td></td>
</tr>
<tr>
<td>21–31 March</td>
<td>3</td>
<td>6.3 ± 0.34</td>
<td></td>
<td>1</td>
<td>(5.9)</td>
<td></td>
</tr>
<tr>
<td>1–10 April</td>
<td>23</td>
<td>6.0 ± 0.20</td>
<td></td>
<td>5</td>
<td>5.6 ± 0.24</td>
<td></td>
</tr>
<tr>
<td>11–20 April</td>
<td>6</td>
<td>6.7 ± 0.76</td>
<td></td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>21–30 April</td>
<td>32</td>
<td>13.8 ± 0.95</td>
<td></td>
<td>5</td>
<td>13.6 ± 1.43</td>
<td></td>
</tr>
<tr>
<td>1–10 May</td>
<td>6</td>
<td>20.2 ± 1.80</td>
<td></td>
<td>3</td>
<td>17.8 ± 2.95</td>
<td></td>
</tr>
</tbody>
</table>

* \(\text{g ether-extractable lipid/g live body weight} \times 100\).

\(^b\) Standard error of the mean.

terminus of the migration. It is to be expected that birds would arrive there with relatively reduced lipid reserves.

In résumé, it seems clear for \textit{Z. l. gambelii} that the metabolic adaptations for autumnal migration include a distinct increase in the regulated level of lipid reserves, resembling the vernal increase but of lesser magnitude and probably involving greater variation among individual responses. These observations are concordant with the data of Millar (1960) for \textit{Zonotrichia albicollis} in Wisconsin. On the basis of the data from captive \textit{Z. l. gambelii}, which perhaps exaggerate quantitatively the migratory metabolic responses, but which appear otherwise to conform with observations of the feral population, we may also infer that the onset of premigratory fattening is less precisely timed in autumn and that the rate of fat deposition is slower. Investigation of the species on its breeding grounds prior to migration is obviously required before a rigorous definition of these characteristics can be presented.
Fig. 2. Effects of fasting and of ad libitum refeeding on the body weight of captive Zonotrichia leucophrys gambelii at Pullman, Washington. Blackened circles: mean weights of untreated control groups (N = 14 in autumn, N = 6 in winter and spring groups); open circles: weight variation of individual experimental birds; broken line: no food available; continuous line: food freely available.
THE REGULATION OF AUTUMNAL MIGRATORY-FAT DEPOSITION

A fundamental change in the factors regulating energy metabolism, lipid storage, and intermediary metabolism accompanies both of the annual migratory phases (Farner et al., 1961; King et al., 1963). For the spring, I submit that the evidence is sufficient to support the conclusion that these metabolic adaptations are photoperiodically induced. In the autumn, with decreasing daylength and with a persisting photorefractory period, we cannot explain the fat-deposition response on the basis of the photoperiodically induced hyperphagia of the spring. It is nevertheless evident from data obtained from captive birds that the tendency to maintain increased lipid reserves is as strongly developed during autumn as during spring migration.

In order to extend some preliminary observations reported earlier, a series of simple experiments was designed to identify the regulated levels of body weight during different phases of the annual cycle. Captive *Z. l. gambelii* were periodically fasted to minimal body weight and then permitted to refeed *ad libitum*. It was reasoned that, in the absence of some special stimulus to appetite, the body weight would be restored only to ordinary nonmigratory levels (26–27 g). This was the case during the winter, as shown in the middle graph in Fig. 2, although by chance the control group was composed of especially heavy birds, and several of the experimental birds, stimulated by particularly cold weather in February, were maintaining the high lipid reserves characteristic of cold periods (cf. Table 1). This pattern was evident also during the premigratory period in April (lower graph in Fig. 2), but was markedly altered after 20–24 April as the birds became hyperphagic and were regulating body reserves at an increasingly higher level. The pattern was very similar during autumn migration (upper graph in Fig. 2), indicating that the birds at this time also were stimulated to eat in excess of current requirements, and were therefore hyperphagic by definition.

It appears that the simplest working hypothesis concerning the stimulus for autumnal fat deposition in *Z. l. gambelii* is that it is a continued expression of the metabolic events initiated in spring by the increasing photoperiod, which therefore serves as an immediate timer for vernal fattening and as a remote timer for the autumnal phase. The evidence to support this hypothesis is clearly tenuous, but I suggest that the viewpoint is consonant with the diminished temporal precision and intensity that characterizes autumnal fat deposition in captives in comparison with the vernal phase. One would expect to find just such a deterioration of regulatory efficiency in a free-running annual timer as the interval following its initiation increases and error accumulates.

In order to maintain this viewpoint, it is necessary to propose that some inhibitory process during the breeding period prevents the expression of the tendency toward fat deposition. Upon arrival on the breeding grounds, the body weight of *Z. l. gambelii* promptly drops to a nonmigratory level (Blanchard and Erickson, 1949; Oakeson, 1954; Irving, 1960), where it remains,
apparently, throughout the breeding season. This tendency is clearly expressed also in the captive birds (Fig. 1). It is possible that intense breeding activity represents a sufficient caloric drain to suppress the body weight during this time, but the midsummer depression of body weight observed also in captives indicates that this can at best be only a contributory factor. An alternative suggestion is that secondary neuroendocrine influences accompanying the development of the gonads eventually suppress lipogenesis and fat storage, and that this inhibition is removed with the postnuptial regression of the gonads. The fact that it is possible at present to make only such patently ephemeral hypotheses concerning the regulation of autumnal fat deposition emphasizes the necessity for additional basic investigations of the wild population during the postnuptial period and for a program of definitive laboratory experiments.

ACKNOWLEDGMENTS

Several aspects of the investigations reported herein were accomplished in collaboration with Donald S. Farner and S. Barker. Their fundamental contributions are gratefully acknowledged. Fiscal support was provided by a research grant from the National Science Foundation (No. G-3416) and by funds provided for medical and biological research by the State of Washington Initiative Measure No. 171.

SUMMARY

Fat deposition occurs during the vernal and autumnal migratory seasons in feral *Zonotrichia leucophrys gambelii* and in captives exposed to normal weather and photoperiod on the wintering grounds. In spring, fat deposition begins very rapidly and shows impressive temporal precision annually and among individual birds. Experiments suggest strongly that vernal fat deposition is photoperiodically induced and depends calorically upon a specific stimulation of appetite (hyperphagia). Autumnal fat deposition in captives develops relatively slowly and lacks conspicuous temporal precision; the quantity of fat accumulated appears, in samples of the feral population, to be less than that of the spring. Part of the difference may result from sampling artifacts, but it is also possible that a real difference occurs. Spring migration proceeds rapidly toward areas of uncertain food supply and inclement weather; autumnal migration occurs more slowly at a time of ample food supply and usually mild weather. Hence, there may be an adaptive basis to the greater lipid reserves of the spring.

Because of the persisting photorefractory period of late summer and autumn, it does not seem reasonable to propose that autumnal fat deposition is directly influenced by change in photoperiod. Nevertheless, experiments suggest that captives are hyperphagic in autumn and that the tendency toward fat deposition is equally intense in spring and autumn. It is possible that the increasing vernal photoperiod serves as a proximate timer for vernal fattening and as a remote timer for the autumnal phase.
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Long-term Effects of Constant Photoperiods on European Robins and Whitethroats

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Working for the past 20 years on two European birds, the Robin (Erithacus rubecula) and the Whitethroat (Sylvia communis), I have shown that the annual cycle of these birds, kept under natural light conditions, is the same in the first year of captivity as in later years, even in the fourth and fifth (Merkel, 1958). The cycles in captivity are similar to those in nature except for some differences in the period during which the birds are prevented from breeding. This could be best shown by the fact that a number of caged Robins laid eggs and continued to do so in succeeding years almost at the same time (Merkel, 1961a).

The experimental studies on the regulation of annual cycles initiated by Rowan and reviewed by Farner (1959) and Wolfson (1959) showed the significance of photoperiodic control in a great number of species, mostly Fringillidae, that winter in the temperate zones and never leave areas with large annual changes of daylength.

While the Robin never occurs south of the Sahara, the Whitethroat is a long-distance migratory bird, wintering in the equatorial and even trans-equatorial parts of Africa where increasing daylength could never stimulate development of the gonads and migration back to the breeding areas. So it was of interest to compare the behavior of these species, both kept under different photoperiods. In a manner different from most previous investigations, I began these experiments when the natural photoperiod was equivalent to the experimental photoperiod, in order to avoid as far as possible any stress from an abrupt change in photoperiod and to find out the differential long-term influence of the various photoperiods on the metabolism.

Three groups of Robins and Whitethroats were kept in rooms with constant temperature (20°C) on daily photoperiods of 18, 12, and 9 hours for 1–2 years, some even longer. Body weight and motor activity were measured regularly and periods of singing and molting noted. To investigate the development of gonads and the activity of endocrine glands, birds were killed from time to time and at the end of the experiments. This paper will deal mainly with the effect of different photoperiods on the annual weight cycle and the development of gonads and molt.

Photoperiod 18L:6D

In 1958 at the XII International Ornithological Congress at Helsinki I presented two slides showing the annual average weight cycles of 7–10 Robins

and 8–11 Whitethroats kept 1 year under natural photoperiod and in two following years in a constant 18-hour photoperiod. I intended first to publish these results as evidence that, in these birds too, the photoperiodicity is the exclusive basis of the annual cycle and that the metabolic condition stays on a level equal to that of the period June to August, releasing a number of succeeding body molts. But later, when I got the results of the experiments performed in 9- and 12-hour daylight and checked more carefully the individual weight cycles of the 18-hour birds, certain doubts began to arise in my mind.

As indicated by the curves (Merkel, 1961b), both species kept in the 18-hour day were no longer able to attain high weights as they did in the normal photoperiod. The average weight for the year as well as the amplitude of the weight curve decreased. But there were sometimes weight increases of lower amplitudes, which were mostly accompanied by a body molt. These sequences of weight increase appeared in more or less regular frequencies, performed differently in individual birds (Fig. 1). Very frequently these fluctuations appeared at intervals of about 3–4 months, at least in the first year. In the second year some individual birds still continued with this be-
behavior, but showed in most cases fluctuations that deviated more from the normal pattern. The amplitude of these was smaller and the frequency shorter. There were also birds that for a long time showed almost no greater fluctuations but later suddenly increased in weight, sometimes at a very rapid rate and to a high degree. In some Whitethroats (Fig. 2), however, a weight cycle corresponding to that of the first year under natural light conditions was observed, but the fluctuations were small and not as extended.

In both species on 18-hour days I found no indications of gonadal activity, at least as far as I could decide without detailed histological investigation. Furthermore, I never noticed any intensive singing in this group. Birds, when returned after 1 year to normal photoperiods, again developed normal cycles, while birds after 2 years in the long day remained on a weight cycle with slight fluctuations but nearly normal in frequency.
PHOTOPERIOD 9L:15D

In the short-day experiments I kept 14 Robins for periods longer than 1 year and up to 31 months (Fig. 3). Most of these birds started to get fat, and some reached a weight much higher than that attained previously under a normal photoperiod. These birds also showed weight fluctuations, but with a much longer frequency. A molt was never noticed. Some birds increased their weight only during the first year and dropped gradually in the second year. In these birds also there was no indication of increased gonadal activity, and I seldom heard them sing and then only in weak notes.

Fig. 3. Weight of three European Robins in natural photoperiod (1958) and in an 8-hour daily photoperiod in the following 2^{1/2} years.

So I was surprised that Whitethroats, brought in in the short day in September and October, showed quite a normal weight cycle, started to sing in January, and developed gonads in the same way as under normal photoperiods. In the beginning of June, when I killed these birds, the gonads were large and showed spermatozoa (Fig. 4).

PHOTOPERIOD 12L:12D

I made similar observations with Whitethroats subjected to a 12-hour photoperiod. After being transferred in the middle of September to a constant artificial 12-hour day, these birds also showed normal weight changes and molt in the first winter, and also started singing in March; gonadal development occurred at the normal time. Also in the next autumn, all birds began to increase their weight after a normal summer molt and started
Zugunruhe. Some birds were able to reach nearly the same weight peak as in the first fall. But irregularities later began to appear. Weight increased and decreased, and the normal weight cycle was thus disturbed more and more in most birds (Fig. 5). Like birds on 18-hour photoperiods, they very frequently showed body molt. All these birds, killed in the second spring, were found to have undeveloped gonads except one bird (D13), which was conspicuous from the others in having an almost normal weight cycle and enlarged testes.

The Robins were different. Most of those subjected to 12-hour photoperiods beginning in the fall did not show any weight fluctuations. After a small weight increase followed soon by a decrease, the weight oscillated within a range of 1 g only (Fig. 6). But here, too, were some exceptions showing a weight cycle very near the normal one. As in the other long-term photoperiods, Robins never developed gonads in the 12-hour group.

To learn when the refractory period of these two species is terminated, I transferred birds in the beginning of November from the natural photoperiod to the 18-hour day. As I had expected, the Robins acted differently from the
Whitethroats. Only the first species started loud singing. Killed after 35 and 67 days, respectively, the Robins had highly developed gonads, while the gonads of the Whitethroats showed slight, if any, enlargement.

In a similar experiment, 2 of 4 female Robins laid eggs (Merkel, 1961a). The first egg of each clutch of three was laid after 53 days and 84 days, respectively, in the 17-hour photoperiod—in other words, after 974 hours and 1,510 hours of light. On the other hand, Robins kept in the 12-hour photoperiod never developed gonads, as in the birds that had been exposed to 2,360 hours of light throughout and killed after 197 days.

So at least in the Robins, gonads do not develop after a distinct number of hours of exposure to light, but from the stimulation of increasing hours of daylength.

Thanks to an invitation from D. S. Farner, I worked during the winter of 1961–62 in Pullman, Washington, with White-crowned Sparrows (Zonotrichia leucophrys). I found in this species, too, by chance, that out of 7 females 3 laid eggs about 50 days after having been transferred from 8 hours to 18 hours of daytime.

We have seen that the annual cycles of the European Robin and the Whitethroat both are affected by photoperiod but to a different extent.
Further, I believe that we have to distinguish a photoperiodic long-term effect on the metabolism of the birds and the stimulation that results from changing daylength.

The long-term photoperiods are, of course, artificial for these species, but they are suitable to demonstrate the real static and common effect of different hours of daylength.

Fig. 6. Weight cycles of European Robins in the 12-hour daily photoperiod. In experiments begun in spring (above), the cycles of most birds remained nearly normal in the first year. In birds placed on a 12-hour daily photoperiod in the fall (below), the weight oscillations disappeared in 4 out of 5 birds.

The 18-hour day in both species brings about a high metabolism, high motor activity, and inclination to molt. It seems that this effect in putting the organism under stress is maintained at least for about 1 year. Later, the birds become more adapted, or perhaps we can even say disturbed, by the permanent stimulation.

In a short-day photoperiod on a long-term basis the Robins never molt, and the energy consumption and activity in hours per day are small. All experimental birds gain more and more weight in the first year, and the majority of them also succeed in doing this later. All these facts, I would conclude, prove that the metabolic rate is low and the energy consumption small.

In comparison with the results obtained earlier (Merkel, 1958) in measurements of the gas metabolism of these species, it may be concluded that
the metabolic level in the 18-hour day corresponds with that of June to August and the level in the short day with that of December, January.

The metabolic rate in the 12-hour day seems to be more like that of the 18-hour day, but the metabolism of the bird is not stimulated as much (Fig. 7).

So I believe that the well-known effect of photoperiodicity in timing the annual cycle depends on the effectiveness of different long days and nights, respectively, in changing the metabolism of birds from a low to a high level and vice versa.

As the patterns of the annual weight cycles of the two species show, there are—in addition to the immediate photoperiodic effect—internal mechanisms which are significant for continued sequences of metabolic events for at least 1–2 years. The frequency of the weight oscillations, as seen in the Robins, is again affected by daylength, moving faster in the 18-hour and slower in the 9-hour day. In Robins kept in the 12-hour day, they nearly disappear.

It is improbable that the cycles themselves are endogenous in the sense of inheritance. The established differences among the Robins may have their origin in individual genetic differences or may be the expression of different populations, since the ancestry of the birds is unknown. In Robins, it is further difficult to establish the significance of these internal cycles under natural conditions; it may be that they are the basis on which the effectiveness of the photoperiodicity starts. In any case, in Robins the internal cycles
are not sufficiently connected with the gonadal cycle to be able to develop gonads without the stimulating help of increasing daylength.

In Whitethroats, the internal metabolic cycles are much more fixed. They are nearly normal for about a year in birds kept in the 12- and 9-hour days and are able to produce cycles in weight nearly normal in frequency and amplitude. They are so strongly linked with the gonadal cycle that male Whitethroats develop mature gonads in the first spring after having been changed to 12- or 9-hour photoperiods in autumn. Only the strong stimulation of the 18-hour day disturbs the internal cycle, so that the annual pattern of weight changes becomes abnormal in the first year and the development of gonads ceases. It is evident that the established internal cycle is of great significance in the Whitethroats, which migrate to equatorial and trans-equatorial areas.

It seems to me, therefore, that the old concept of Weigold (1926) and Putzig (1937) distinguishing “Aussenwelt- und Innenwelt bedingte Zugvögel” still has its significance in some different way.

SUMMARY

In contrast to the customary experimental methods for the investigation of the effect of different daylengths on birds, European Robins and Whitethroats were transferred into artificially lighted rooms (20° C) in June, December, and September and were held up to 2 years on constant daily photoperiods equivalent in duration to daylength at the time of transfer. In birds subjected to 18- and 9-hour photoperiods, there was a persistence of cycles in body weight at least for 2 years, although with different frequency and amplitude. In contrast to the Robins, the Whitethroats underwent complete gonadal development as well in 12L–12D as in 9L–15D during the first spring, after having been transferred in the late autumn. The weight cycle of the latter remained normal throughout the first year and deviated from the normal only during the second year.

ZUSAMMENFASSUNG


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F. W. Merkel: Long-term Effects of Constant Photoperiods


Molt, Body Weights, Gonadal Development, and Migration in
Motacilla flava

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Various species of Palaearctic migratory birds living at or just around the Equator in Africa, where the length of daylight is almost constant throughout the year, show specific physiological rhythms, which are expressed by several phenomena such as molt, increasing body weights, and gonadal development. These changes in the birds' physiological state precede the vernal migration and are, apparently, not induced by photoperiodicity or other external factors, at least not during the stay in the tropical, equatorial winter quarters.

The physiological cycles in different Palaearctic birds wintering around the Equator are usually timed differently in various species, although sometimes synchronized action may occur, probably due to factors dependent on the geographic situation (latitude) of the breeding grounds. This is, for instance, the case in several species of waders. It is, however, characteristic that within each Palaearctic species wintering in the tropics there is a great individual variation in molt, body weight, and status of gonads. There is also within each species a wide variation in the seasonal initiation of northward migration. Most probably, this physiological differentiation and varying schedule of migration in monotypic species can be explained by the fact that each "physiological category" represents a certain geographic population, although it cannot be distinguished morphologically. That this is so is clearly shown by the Yellow Wagtail (Motacilla flava), which, unlike other Palaearctic species wintering in the tropics, is divided into several subspecies. These races show different physiological rhythms in spite of the fact that they mingle for long periods and, consequently, are exposed to exactly the same external factors.

During two expeditions (1951–52, 1958–59) in the former Belgian Congo and Ruanda-Urundi during the periods from November to May, I studied the mechanisms, especially internal (physiological) and external (ecological) factors, that might release spring migration in Palaearctic birds. Investigations were concentrated on environmental (climatic and photoperiodic) changes such as length of day and variations in the intensity of light, moisture, temperature, radiation, and so forth in relation to physiological changes and manifestations such as molt, body weight, gonadal growth, and migration. The work was based primarily on M. flava, but also on Tringa glareola and T. hypoleucos, as well as on other Palaearctic and Ethiopian species for control. Data on the Yellow Wagtails consist of 405 specimens collected in the Congo during December–May 1951–52 and 1958–59, 44 in Camargue,

France, during April–May 1960 and 1962, and 106 in Sweden north of the Arctic Circle in May–June 1960. The Camargue area is situated about 5,500 km from the Equator and about 4,000 km from the Arctic Circle.

The results of the expedition in 1951–52 have been preliminarily dealt with in previous papers (Curry-Lindahl, 1953, 1958). Five subspecies of *M. flava* (*flavissima*, *lutea*, *flava*, *thunbergi*, and *feldegg*) spend 5–7 months a year around the Equator in the eastern (Belgian) Congo, where they flock together indiscriminately.

The different patterns of physiological rhythms in various races of *M. flava*, living together under natural conditions on their wintering areas in tropical Africa with almost constant length of daylight, demonstrated that the internal timer works independently of external factors produced by the environment in the equatorial winter quarters.

The internal cycle seems to be genetically stabilized and functions in a rhythm that is synchronized to conditions in the breeding areas (Curry-Lindahl, 1953, 1958). This interpretation may explain the differentiated physiology in *M. flava*, in which various populations are recruited from very large areas in the Palaearctic region, arrive in equatorial Africa in autumn, spend several months of the northern winter in the tropics mingling together, and have still-inactive gonads in December and January. This is the general pattern. In February, however, several physiological features indicate that something is going on with some of the Yellow Wagtails wintering together. Molting and fat deposition start, followed by gonadal development. Finally, it appears from the more or less completed molt that the birds showing all these physiological processes and now ready to migrate belong to the southernmost populations of the species, while great numbers of other Yellow Wagtails are still undeterminable and show no physiological changes. In March and early April other birds of this species undergo the same development: the process of molt, increasing body weight, activation of gonads, and migration. This time such birds usually belong to *M. j. flava*, representing central populations of the species. Simultaneously, other Yellow Wagtails present in exactly the same area and environment do not show any morphological changes. In April and May, however, they do. This last contingent of migrating birds generally belongs to *M. j. thunbergi*, the northernmost race wintering in Africa.

**MOLT**

Yellow Wagtails in general acquire their adult winter plumage by a complete molt in August–September. The molt to summer plumage normally takes place from January–February to March–April. The species is sexually dimorphic. There is great individual variation in the different stages of molt in all subspecies occurring in the Congo. This is also the case, but to a minor degree, when the birds are to be found on the Palaearctic breeding grounds during the summer months.
The general pattern for birds that are still in their tropical winter quarters is that their molt to summer plumage is entirely or almost completed before they take off for the vernal migration. There are, however, exceptions to this rule.

Some Yellow Wagtails (*M. f. flava* and *M. f. thunbergi*) are still in molt when breeding or resting at Camargue in France, and this may also be the case for individuals (*M. f. thunbergi*) after their arrival in Swedish Lapland north of the Arctic Circle. This variation is probably due, at least partially, to age groups, and in Swedish Lapland it may in some cases be attributed to interracial hybridization (cf. Sammalisto, 1958, 1961).

In the present stage of this study no attempt has been made to separate the material into different age categories on the basis of plumage and molt characteristics. There are timing differences between the two sexes. In general, the molt of the males is completed earlier than that of the females.

In *Motacilla flava* no indication was found that the initiation and the progress of the molt are induced by environmental factors such as light intensity. The molt precedes the other physiological changes that take place in *M. flava* during the prenuptial period, and it is not correlated in time with either increase of body weight or gonadal development.

Thus, the molt in *M. flava* seems to be independent of gonadal hormones. This is also the case in the tropical nonmigratory *Quelea quelea* (Witschi, 1935; Disney and Marshall, 1956). Marshall and Williams (1959) have come to the same conclusion concerning the Yellow Wagtail. Of course, this view does not exclude the molt being under the cyclical influence of the pituitary gland, which is probably involved in all changes in the physiological state of migratory and nonmigratory birds (cf. Wolfson, 1954; Assenmacher, 1958).

The sequence of the different stages of molt in *M. flava* during two different years in the Congo was found to be remarkably similar. It normally begins in December–January and continues to April.

**Body Weights (Fat Deposition)**

Extensive studies of lipid deposition in birds have shown that the fat-free weight, in marked contrast to the total live weight, is remarkably constant for a given species and sex. A migratory male of the Red-eyed Vireo (*Vireo olivaceus*), for example, may weigh from 16 to 28 g, while the weight of the body minus the fat will vary but a gram or so from 15 to 16 (Odum and Perkinson, 1951; Odum and Connell, 1956; Odum, 1958; Connell, Odum, and Kale, 1960). The variation in weights of Yellow Wagtails in my material had almost the same amplitude as in *V. olivaceus*: For 555 examples of *M. f. flava*, *M. f. thunbergi*, *M. f. flavissima*, *M. f. lutea*, and *M. f. feldegg* from Africa and Europe for the period from December to June the extreme weights are 14 and 28 g.

It is generally presumed that an accumulation of fat in visceral and sub-
cutaneous depots provides the necessary energy resource required by a bird for extended migratory flights. Odum (1960) has shown that migration in the sense of long-continued, sustained flight is possible only within fairly narrow metabolic limits. Odum, Connell, and Stoddard (1961) distinguish between three patterns of fat deposition in relation to migration. One of these categories includes long-range migrants that become extremely obese with a considerable fat accumulation (up to 50 percent of the body weight) just prior to migration.

*Motacilla flava* is a long-distance migrant, flying during the spring migration from the equatorial regions of Africa along the Nile valley and/or across the Sahara to Europe and Asia, where it spreads over an enormous area from the Mediterranean countries in the South to subarctic regions in the North.

Fig. 1 shows the average weights of *M. f. flava* and *M. f. thunbergi* from December to June and geographically from the Congo, southern France, and northern Sweden. This period represents three stages of the Yellow Wagtail's annual activities: wintering in tropical Africa, vernal migration to Eurasia, and arrival at the breeding grounds and initiation of reproduction.

As seen in Fig. 1, there is a pronounced similarity in the general pattern of the weight curves in males and females of two different races of *M. flava* during two different years. As was to be expected, the weight increase of the southern subspecies, *M. f. flava*, precedes that of the northern race, *M. f. thunbergi*, in both males and females. The decrease in weight for males of *M. f. thunbergi* in December–January may not be significant, for it is based on only two males collected on 30 December 1958. Both specimens had exactly the same weight. Also, the December weight of males of *M. f. flava* is based on a small number of birds. On the other hand, it is not certain that the weight curves for males of both subspecies would have been parallel if material from November had been available, because the weight pattern of *M. f. flava* seems always to be ahead of that of *M. f. thunbergi*. There is, for instance, a male (undetermined as to subspecies), collected in the Congo by Herroelen (in litt.) on 1 November 1958, weighing 19.5 g. In my own material there are several racially uncertain males from December with weights between 18 and 19 g. The fact that the weight in the males of *M. f. flava*, after increasing in January–February (1959), drops in February–March (1952, 1959) may probably be due to southern populations of this race initiating their migration in March. The individuals of the same subspecies remaining in the winter quarters in March have not yet reached the stage of migration readiness (*Zugdisposition*), but they do so in April when their weight has increased to the same (or a higher) level as that of their predecessors when starting migration.

Another picture is shown by *M. f. thunbergi*. Members of this race steadily increase in weight from January to the very early days of April, when they leave for migration.
Fig. 1. Mean weights of *Motacilla f. flava* and *M. f. thunbergi* collected from December to June.
It seems as if both males and females of *M. f. flava* increase their weights while in migratory flight from tropical Africa to Camargue in southern France; but as soon as breeding activities begin, the weights drop abruptly. *M. f. thunbergi*, however, follows another pattern. This race (at least the males, probably also the females) keeps its weight at the same level during the long-distance flight between the Equator and Camargue, but both sexes lose weight during the last part of their migration to Swedish Lapland. After their arrival there, they soon regain weight and start to breed. Like the Yellow Wagtails breeding in northern Scandinavia, the long-distance migrants arriving in Alaska in the spring had also lost weight and fatness (Irving, 1960). Males and females of *M. f. tschutschensis*, collected at Anaktuvuk on their arrival between 4 and 10 June, weighed from 15.1 to 17.7 g. The average weight of *M. f. thunbergi* in May, on its arrival north of the Arctic Circle in Swedish Lapland, was 17.5 g for males and 16 for females.

Males of *M. f. thunbergi* passing on migration south of the Caspian Sea show the same picture as those from Camargue; they do not seem to have lost any weight (cf. figures in Schüz, 1959).

Of course, Fig. 1 is only indicative. Its curves do not tell us anything about the geographical migration pattern. There is no evidence that the populations of Yellow Wagtails that we have studied in the Congo, in France, and in Swedish Lapland are connected with each other. This fact must be strongly emphasized when Fig. 1 is studied. On the other hand, the schedule of migration of *M. flava* from its departure from tropical Africa to its arrival at the Palaearctic breeding areas is well known (cf. literature in Curry-Lindahl, 1958), hence we may presume that Fig. 1 is not very far from being correct.

It is interesting to compare the different weight patterns in the two races of migrating Yellow Wagtails with the results obtained by Odum (1958) for four species of American long-range migrants, the Red-eyed Vireo, the Tennessee Warbler (*Vermivora peregrina*), the Bay-breasted Warbler (*Dendroica castanea*), and the Magnolia Warbler (*D. magnolia*), and one short-range migrant, the White-throated Sparrow (*Zonotrichia albicollis*). These birds pass south toward Florida on their fall migration. The four long-range migrants continue their journey across the Gulf of Mexico in a nonstop flight, while *Zonotrichia* does not migrate farther south than Florida, which is the southern edge of its winter range.

Samples of these five species of migrants were collected in Florida only a few miles from the Gulf Coast. The White-throats had used up all or almost all of their stored fat, which is not unexpected, since the Gulf Coast is near the "end of the line" for fall migration. In sharp contrast to *Zonotrichia* were the four long-range migrants. Most of these birds were fat, and many were still at their maximum level of weight. Apparently they were prepared to continue the migration; that is, they carried stored energy which
would enable them to fly for a long time (Odum, 1958). The same pattern of fat deposition has subsequently been found in other American passerines—tanagers, thrushes, and others, which are considered to be trans-Gulf migrants (Odum, Connell, and Stoddard, 1961).

The situation described for the long-range migrants in Florida appears to explain why the migrating individuals of *M. f. thunbergi*, collected in France, do not seem to have lost any weight during their flight from tropical Africa, and why, when arriving at their final destination in Swedish Lapland, they have lost considerable weight. It is, however, still difficult to explain how members of the southern race, *M. f. flava*, gain weight during their migration from tropical Africa to France. Perhaps the explanation is that the birds increased their weight when resting somewhere in southern France before they appeared at Camargue, where they were collected. The material representing the nominate form for April from this locality consists of only five specimens.

The initiation of fat deposition in *M. flava* begins in the Congo about 3 months before the birds reach readiness for migration, which means that fat accumulation begins in December in *M. f. flava* and in January in *M. f. thunbergi*. This deposition of fat occurs simultaneously with the molt, but precedes the initiation of gonadal development. The magnitude of the increasing weight is not as striking in *M. flava* as in many other migratory birds, in which it can reach very high percentages. The premigratory weight increase in the Yellow Wagtail does not exceed 3 g in the males and 2 g in the females, which is an increase of 16.7 percent and 18.8 percent, respectively, of the calculated mean weights.

Males and females of *M. flava* do not exhibit an abrupt and extensive deposition of body fat just prior to the spring migration, as do many other migratory species, for example the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), in which the adjustment in the level of fat reserves occurs during a span of about 10 days immediately preceding northward migratory movement and results in an approximate doubling of the quantity of reserve fat (King and Farner, 1959).

The slow fat accumulation in *Motacilla flava* is combined with an individual variation in fat deposition. On 9 February 1959 I collected a male of *M. f. flava* weighing 28 g, the heaviest Yellow Wagtail I have ever collected. It was heavily loaded with premigratory fat, but the gonads were entirely undeveloped and the molt seemed to have just begun. Two days later another male of the same race showed almost exactly the same stage of molt and gonads as its heavy congener, but this bird weighed only 16 g.

The weight curves of *M. f. flavissima* differ from those of *M. f. flava* and *M. f. thunbergi*. Both males and females of *flavissima* collected in March have the same mean weight, 17.5 g, which differs from the weight dimorphism showed by three other subspecies (*lutea, flava*, and *thunbergi*) which were collected in the Congo. Thus, in March males of *flavissima* weigh less than
males of *flava* and *thunbergi*, while the females of the former race are heavier than those of the latter races. The average weight of *M. f. lutea* in March was exactly the same as in *M. f. flavissima*, 17.5 g, which means that individuals of this subspecies weigh less than those of *M. f. flava* and *M. f. thunbergi* in spite of the fact that they have reached a much more advanced stage of sexual development than the others.

**GONADAL DEVELOPMENT**

In *Motacilla flava* there is only a slight increase in the size of the gonads before the birds leave their tropical winter quarters. The first sign of gonadal growth in *M. f. flava* was found on 18 February 1959, when among two males and three females collected the same day, a male showed slightly enlarged testes. This male weighed 17 g, which is 2 g more than that of its congener with undeveloped testes, collected simultaneously. In 1952 the first male of *M. f. flava* with enlarged gonads was found on 22 February. It also weighed 17 g. In 1959 the second male of the same subspecies with growing gonads was obtained on 20 February. This individual weighed 18 g. In March, males of *M. f. flava* with enlarged testes were collected more frequently. A male of *M. f. lutea* with gonads in an advanced stage of development was obtained on 3 March (weight 18 g). A male of *M. f. flavissima*, collected the same day, also had enlarged testes but to a lesser degree than *lutea*. Of 15 males of *lutea* collected between 3 and 17 March, 9 had enlarged gonads. They weighed from 17 to 20.5 g, while those with undeveloped gonads had weights from 16.5 to 17.5 g. Of 19 *M. f. flavissima* collected between 3 and 17 March, not one was found with enlarged gonads, while of 47 *M. f. flava* obtained in March 1959, 11 had enlarged gonads. Of these birds all except one had reached this stage in the period 20–31 March. In 1959 the first *M. f. thunbergi* with enlarged testes was found on 23 March, the second male on the day after, and the third on 31 March. In 1952 we did not obtain any *thunbergi* with enlarged testes as early as March. In April all Yellow Wagtails of *flava* and *thunbergi*, except six individuals, had swollen gonads in different degrees of size. The same general pattern of gonadal development in the different races of *M. flava* wintering in the Congo in 1959 was also found in 1952.

Table 1 shows percentages of birds with activated gonads (= gonadal growth) among the material collected. There is clear correlation between the growth of gonads and the departure for migration. *M. f. feldegg* was only observed during the second half of February, and one individual collected on 25 February had enlarged testes. Probably this bird, as well as its congeners, was on migration to breeding areas. Data on the spring migration of *M. f. feldegg* indicate that this form is an abundant bird of passage in Arabia from the middle of March to the first week of May (Meinertzhagen, 1954). At the southern coast of the Caspian Sea *feldegg* arrives from the
middle of March (Schüiz, 1956). Both regions mentioned are partly situated within the breeding range of this subspecies.

*M. f. lutea* occurs north and northeast of the area occupied by *M. f. feldegg*. Populations of these two races, according to Smith (1950), overlap in a transitional zone, and while Meinertzhagen (1954) does not mention any intergradation between the two forms, he does speak of an intergradation between *M. f. lutea* and *M. f. flava*.

**Table 1.—Percentage of Different Races of Motacilla flava with Enlarged Gonads**

<table>
<thead>
<tr>
<th>Month</th>
<th>JAN.</th>
<th>FEB.</th>
<th>MAR.</th>
<th>APR.</th>
<th>MAY</th>
<th>JUNE</th>
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<tbody>
<tr>
<td>Year</td>
<td>No. %</td>
<td>No. %</td>
<td>No. %</td>
<td>No. %</td>
<td>No. %</td>
<td>No. %</td>
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**SUBSPECIES**

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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>feldegg</em></td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>lutea</em></td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>50</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>flava</em></td>
<td>2</td>
<td>0</td>
<td>13</td>
<td>7</td>
<td>15</td>
<td>69</td>
<td>-</td>
</tr>
<tr>
<td><em>thunbergi</em></td>
<td>8</td>
<td>0</td>
<td>43</td>
<td>8</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>flavissima</em></td>
<td>3</td>
<td>0</td>
<td>20</td>
<td>16</td>
<td>16</td>
<td>81</td>
<td>54</td>
</tr>
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**WHERE COLLECTED**

<table>
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<tr>
<th>Location</th>
<th>1952</th>
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<th>1960</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>21</td>
<td>54</td>
<td>229</td>
</tr>
<tr>
<td>Camargue</td>
<td>-</td>
<td>-</td>
<td>93</td>
</tr>
<tr>
<td>Swedish Lapland</td>
<td>5</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td></td>
<td>54</td>
<td>52</td>
<td></td>
</tr>
</tbody>
</table>

*All collected in Camargue.*

In the Congo we noted *M. f. lutea* in 1952 until 7 March and in 1959 until 17 March. The majority of the collected *lutea* had enlarged gonads; birds in such a stage secured in March represented 69 percent. This subspecies appears on migration south of the Caspian Sea at the beginning of April (Schüiz, 1956).

Individuals of *M. f. flavissima* were obtained between 13 March and 27 April 1952 and between 3 March and 17 March 1959, but birds were observed until 14 April 1959. The specimen collected on 27 April (1952) was a female, whose ovarian follicles did not show any sign of development.

This was also the case with the gonads of all individuals of *flavissima* obtained in March during two different years. Thus, birds of this subspecies differ in this respect in a striking way from the four other races checked in the Congo.

Arrivals of the British *M. f. flavissima* on its breeding area are well known. Data collected by Smith (1950, 1956) show that the main part of the popula-
tion comes to Britain between the second fortnight of April and the first week of May. Although essentially a migrant to tropical west Africa, individuals of this subspecies occurred regularly in the eastern Congo, but they represented a pronounced minority in comparison with *M. f. flava* and *M. f. thunbergi*. The collected material of *M. f. flavissima* consists of 23 specimens, of which 22 were obtained in March 1952 and 1959. The number of measured individuals may be considered to be sufficiently high to give significant data, but it is difficult to understand why *M. f. flavissima* should have another pattern of gonadal development than the other subspecies sharing its winter habitats in tropical Africa. As far as the molt is concerned, there is no deviation in *flavissima* from the general pattern of the other four races, but fat deposition in both sexes of *flavissima* shows peculiar features which vary in a remarkable way from the pattern in *M. f. flava* and *M. f. thunbergi* (cf. above).

Because of the wide distribution of *M. f. flava* in the Palaearctic, the timetable of its departure from the winter quarters in the Congo varies more than that of other subspecies. Also, the breeding range of *M. f. thunbergi* in northern Eurasia is enormous, but in this case the departure for migration takes place within a rather limited period in April and early May. This is probably due to the rather uniform climatic situation that prevails in its breeding area in early spring.

A feature of the development of the gonads in *M. f. flava* and *M. f. thunbergi* is that the gonads of the former race have reached a more advanced stage of growth at the departure from the Congo than is the case in *M. f. thunbergi* when this race begins its migration about a month later.

Although the periods of starting migration overlap in various races of *M. flava*, there is a pronounced periodicity for the majority of birds, as shown by our observations in the (Belgian) Congo. A southern race, such as *feldegg*, leaves its winter quarters in February, followed by the more northerly *lutea* in February–March, by *flava* and *flavissima* in March–April, and by *thunbergi* in April–May. Except for *flavissima*, this periodicity in the same races is also reflected in their passage in the Caspian region (cf. Schüz, 1956) and in their arrival on the breeding ranges.

No indications could be found that any external factors are involved in the regulation or initiation of the gonadal cycle during the stay of *M. flava* in its tropical winter areas. The role of long days or changing light intensities (photoperiods) in regulating the gonadal cycle can clearly be excluded during the period that the birds spend around the Equator. The preparatory phase of the reproductive cycle in *M. flava* does not seem to depend on conditions in the winter quarters. If there is a summation of external and hormonal factors involved as a timing regulator of the sexual and migratory cycle in *M. flava*, it seems to be ultimately related to conditions on the breeding grounds.

Detailed data on measurements of gonads, conditions of tubules contain-
ing spermatogonia, ovaries, and measurements of oocytes in different races of *M. flava* during the period from January to May in different years will be given in another paper. Here I will only mention that the schedule of gonadal growths in different races is subspecifically quite different. Of the five subspecies studied in the Congo the first to appear to be in a migratory readiness according to its gonadal state and behavior is *M. f. jeldegg* in February, followed by *M. f. lutea* in March, by *M. f. flava* in March and April, and by *M. f. thunbergi* in April and May. In *M. f. flavissima*, however, which apparently leaves the Congo in March and April, no correlation between gonadal development and departure on migration of these wagtails could be found.

The fact that Yellow Wagtails migrating during the spring from equatorial regions to Palearctic areas show a pronounced progressive phase of gonads, during which the birds attain complete spermatogenesis before or just when they arrive at their breeding grounds, may indicate a certain response to the longer days at higher latitudes, but apparently it is not necessary for either the initiation of gonadal growth or for the attainment of migratory readiness that these birds must previously be subjected to longer days.

Such an explanation does not prevent the material and the results obtained in the Congo in 1958–59 from confirming in most details and general features the main conclusions drawn after the expedition of 1951–52 (cf. Curry-Lindahl, 1953, 1958), e.g. that the internal cycle in *M. flava* seems to be genetically stabilized and functions in a rhythm that is synchronized with conditions in its breeding areas.

The wide scale of temporal range in the initiation and further development of gonadal growth, with all its reproductive processes, as well as of molt and fat deposition, indicates that each subspecies depends on different internal, rhythmical factors. These may be linked with external stimuli to which the birds are exposed when they are in their breeding range, or they may involve an internal timer, which is entirely innate from the very beginning of the birds' life, thus also in this case synchronized to the conditions at the breeding grounds (cf. Curry-Lindahl, 1953, 1958).

This view, that the sexual cycle and the time of migration in *M. flava* are governed by an endogenous rhythm of reproduction uninfluenced by any external stimulus in the tropics, is also shared by Marshall and Williams (1959). Marshall (1960) goes so far as to state that "the most important single—and only universal—factor in the regulation of avian breeding seasons, including migration, is the internal rhythm of reproduction that is normally and spontaneously renewed after a period of regeneration that follows each breeding season" (cf. also Marshall, 1961).

*M. flava* provides, in my opinion, striking evidence of the existence of an internal timer and an innate physiological rhythm in long-distance migratory birds. Most probably this is also the case in all Holarctic birds wintering around the Equator and south of it.
BEHAVIOR

Marshall and Williams (1959) noted behavioral changes in *Motacilla flava* in Uganda prior to its departure for the North. At the end of March a greater social cohesion was manifested. These premigratory changes in social organization were, according to Marshall and Williams (1959), expressed quantitatively in the collecting results: "... when a brightly plumaged bird was killed frequently another would fly up and inspect the cadaver."

During our collecting work in the Congo the same thing happened from time to time, but we failed to combine this behavior with any change of social relations between individuals belonging to a flock of Yellow Wagtails, because in the Congo the described behavior occurred during the whole period from December to April (1951–52, 1958–59). No distinct behavioral changes at all could be observed by us. The flocks kept steadily together in December as well as in April, and the intraspecific and intrasubspecific relations, as well as individual behavior, did not seem to undergo any modifications.

ACKNOWLEDGMENTS

The author is indebted to the Institut pour la Recherche Scientifique en Afrique Centrale (I.R.S.A.C.), the Institut des Parcs Nationaux du Congo Belge (I.P.N.C.B.), the Swedish Natural Science Research Council, and the Royal Swedish Academy of Science for facilities and grants that made possible the expeditions to the Congo in 1951–52 and 1958–59, as well as collecting activities in Camargue, France, and in Swedish Lapland.

I must especially thank Luc Hoffman, Station Biologique de la Tour du Valat, for his help in collecting Yellow Wagtails in Camargue over a 3-year period.

SUMMARY

Different subspecies of the Yellow Wagtail (*Motacilla flava*) leave the wintering grounds in tropical Africa in a certain order and without any relation to changes in local weather conditions. The first to leave in spring is the southerly race, *M. f. feldegg*, members of *M. f. lutea* are next to take off, followed by *M. f. flava* and *M. f. flavissima*, while the last to leave its winter quarters is the northernmost *M. f. thunbergi*.

Physiological phenomena, molt, fat deposition, and gonadal development as well as departures on migration in these races (populations) of *M. flava* follow different patterns, in spite of the fact that the birds are wintering together in uniform external conditions.

The normal sequence of physiological events while the Yellow Wagtails are to be found in tropical Africa is approximately as follows. Molt occurs in December–April, fat deposition in January–April, gonadal growth in February–May, and spring migration also in February–May. The molt may be terminated before or after migration, while deposition of fat and initiation of growth of gonads precede the vernal flight. Prior to the onset
of spring migration, the swelling gonads are still small and only slightly advanced beyond the condition that is found during the previous months. Arrival at the breeding areas occurs for different races in March–June. In *M. f. flava* and *M. f. thunbergi* the gonads increase tremendously in size during the migratory flight. Reproduction can generally start immediately after the arrival of these races at their breeding grounds.

The wide scale of temporal range in the initiation and further development of gonadal growth, with all its reproductive processes, as well as of molt and fat deposition, indicates that each subspecies depends on different internal, rhythmical factors. These may be linked with external stimuli to which the birds are exposed when they are in their breeding range, or they may involve an internal timer, which is entirely innate from the very beginning of the birds' life, thus also in this case synchronized to the conditions at the breeding grounds.

**LITERATURE CITED**


Pancreatic Islets and Annual Cycle in Some Avian Species

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The purpose of this paper is to summarize the results of previous investigations on the behavior of the pancreatic islets in some species of small birds and to discuss their relation to temporary adiposity.

It is an astonishing fact that there exist almost no publications on seasonal changes in the endocrine pancreas of birds, although its histology proves to be a very useful tool for this purpose. Contrary to the situation in other vertebrates, A- and B-tissue are widely separated into different islets, and the large A-islets allow a profound study of their cellular components (Clara, 1924a, 1924b; Nagelschmidt, 1939; van Campenhout and Cornelis, 1954). While in lower vertebrates the ratio of A- to B-tissue is about 1 : 1 (Ito et al., 1960) and in mammals about 1 : 4 (Ferner, 1952), we find in birds nearly the reverse situation of the latter and a corresponding increased glucagon content (Vuylsteke and de Duve, 1953; Weitzel et al., 1956; Al-Gauhari, 1960). The physiological significance of this high glucagon content of the bird pancreas seems to be still unknown. Mialhe (1958) has shown in a series of excellent experiments on the domestic duck that both insulin and glucagon are indispensable for maintenance of normoglycemia in this species. Ablation of the pancreas results in hypoglycemia due to loss of glucagon. The cellular composition of the A-islets in birds (Müller et al., 1956; Hellman and Hellerström, 1960; Epple, 1961) led to the question of whether this tissue is the source of more than one hormone (Epple, 1962). Hormone-like acting substances of the pancreas not identical with insulin or glucagon have been described, but there is no general agreement about their physiological role (lit. in Noel et al., 1958).

The studies referred to below began in 1956 at the suggestion of my teacher F. W. Merkel and have been carried out partly in collaboration with D. S. Farner, J. R. King, and F. W. Merkel. Involving small Oscines (Turdus merula, Erithacus rubecula, Sylvia communis, S. borin, and Zonotrichia leucophrys gambelii), these studies concerned mainly the following problems:

1) Is there an annual cycle of the endocrine pancreas in these species?
2) If so, is there increased insulin output during invernal and/or premigratory fattening?
3) Does an antagonism exist in the annual cycle between insulin and glucagon production?
4) Could such an antagonism explain the genesis of the winter and/or premigratory adiposity in these species?

The first attempt to clarify these questions was a study on the annual cycle of the islets of Langerhans in the European Blackbird (*Turdus merula*), a partially migrating thrush (Drost, 1930) with a marked fat deposition in midwinter. The results of this investigation (Epple, 1961) may be summarized as follows:

1) There exists a pronounced annual cycle of islet activity with a peak in summer after breeding and preceding the molt, and a trough in winter nearly at the time of fat deposition.

2) A- and B-tissue are almost always in parallel activity.

3) The D-cells of the A-islets behave throughout like A-cells. In a later publication they are considered as a third, hormone-producing form of islet cell (Epple, 1962).

In a second still-unpublished investigation in collaboration with F. W. Merkel on a great number of *Erithacus rubecula* and *Sylvia communis* kept for different periods under various artificial photoperiods, it was found that A- and B-tissue were generally at an equal level of activity, and there was often high islet activity but no correlation with the state of obesity.

In another unpublished experiment in collaboration with D. S. Farner and J. R. King on *Zonotrichia leucophrys gambelii*, we tried to answer the question: Is the rapid premigratory fattening in this species (Farner, 1961; King, 1961a and 1961b) correlated with changes in the islet activity? The experiment was performed by artificial photostimulation which induces fat deposition probably identical to the premigratory obesity found in spring under natural conditions (Odum and Major, 1956). The result was the same as in the investigations of *Erithacus rubecula* and *Sylvia communis*.

Two *S. borin* killed during fall migration on Heligoland showed highly active islets with some degenerating elements. It cannot yet be decided if this indicates the beginning of regression after the annual peak of activity, but even in these animals both components of islet tissue were at the same level of activity. The results of these investigations demonstrate that: (1) Premigratory hyperphagia in spring and obesity in midwinter are not caused by antagonism between insulin and glucagon; (2) invernai fat deposition in *Turdus merula* occurs under diminished islet activity; and (3) in light-induced fat deposition, which is very similar to premigratory fattening, there is no significant difference in islet activity as compared with control animals.

From these findings three questions in particular arise:

1) How do winter and premigratory fattening occur without increased insulin output?

2) How are the cyclic changes in the pancreatic islets in *Turdus merula* to be explained?

3) What is the significance of the corresponding activity in A- and B-tissue?
FAT DEPOSITION IN BIRDS

To answer the first question, some examples might be recalled which indicate that fattening might take place even in the absence of insulin and that enhanced food intake is not necessarily followed by an increase in islet volume. Gassner et al. (1958) describe how stilbenes cause fattening in the absence of the pancreas. Koch (1955) found that B-cells atrophy in obese animals of various species following stilbene treatment, and Hausberger (1958, 1959) mentions that hypothalamic obese rats show hyperphagia and concomitant fat deposition without islet hypertrophy.

The factors that might play a role in fat deposition in birds could be classified as metabolic and regulative. The former include lowered standard metabolic rate, slight hypoglycemia, enhanced lipophilia, and endocrine shifts. The latter include encephalic hyperphagia, improved insulation by feathers or fat storage, and diminished motor activity.

Metabolic Factors

Lowered Standard Metabolic Rate.—This might be involved in invernal fattening, yet data in the literature are conflicting (see Merkel, 1958; King and Farner, 1961).

Hypothermia and Hypoglycemia.—The former was found in invernal and premigratory fattening (Merkel, 1958). The latter was shown in the domestic duck by Mialhe (1954). In small birds, great fluctuations in the daily cycle of blood sugar during migration might favor anabolic processes (Merkel, 1958).

Enhanced Lipophilia.—In the tissues of birds during premigratory fattening, this causes increased fat accumulation while glycogen content is reduced (Farner et al., 1961). Of course, this temporary phenomenon must be governed either by increased food intake itself (perhaps “exercise” of tissues leading to a shift in enzyme pattern) or by humoral or nervous signals.

Endocrine Shifts.—As there is no evidence for a specific hormone associated with fat storage in tissues, the main endocrine factor allowing accumulation of the fat stores in midwinter might be relative inactivity of insulin antagonists.

It seems that, during this time in all birds of the North Temperate Zone investigated so far, the entire endocrine system is inactivated except for the thyroid, which offers such conflicting pictures that evaluation of its annual cycle is at present impossible (lit. in Wilson and Farner, 1960). But a trough in activity is exhibited in the diencephalic neurosecretory system (lit. in Laws, 1961), anterior pituitary (Wolfson, 1945), adrenals (Burger, 1938; Höhn, 1961; Bouman, to be published), gonads (see Aschoff, 1955; Farner, 1961; Threadgold, 1960), and parathyroid (vide Höhn, 1961).

Premigratory fattening in spring occurs apparently under progressive activity of all endocrines (lit. cited above). During this period, additional gonadotrophins, testosterone, and thyroxin enhance body weight in finches
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(Schildmacher and Steubing, 1952; Schildmacher and Rautenberg, 1952). If this proves to be a specific and perhaps only temporary effect of these hormones, it would be very desirable to know how they work, e.g. via encephalic feeding centers, or by exerting a “conditioning effect” (Ingle), i.e. by enhancing the action of factors that promote hyperphagia and obesity. In the latter case their interference with insulin could not be excluded by our findings in Zootheria leucophrys gambelli, Erithacus rubecula, Sylvia communis, and S. borin.

Regulative Factors

Encephalic Hyperphagia.—The literature on the neural regulation of food intake has been reviewed by Brobeck (1955). Since there is a lack of a specific hyperphagia-stimulatory hormone—it seems very doubtful that insulin acts this way under physiological conditions (lit. in Conn, 1944)—and since hyperphagia occurs apparently very rapidly under various hormonal constellations in fall (Merkel, 1958), winter (Kendeigh et al., 1960), and spring (lit. in Farner, 1961; King, 1961a, 1961b; Odum, 1960; and Wolfson, 1959), the findings advocate a primary nervous regulation of this increased food intake triggered by photic and maybe other stimuli which might be supported by regulative and metabolic factors.

Other Factors.—In winter fattening, improved insulation by feathers or fat deposition might be accessory factors, at least in some species (e.g. see Wallgren, 1954), and diminished motility seems to play an important role in midwinter obesity in Sylvia communis (Merkel, 1956, 1958).

ANNUAL PERIODICITY OF ISLETS IN THE BLACKBIRD

The second question concerned the meaning of the annual periodicity of the islets in Turdus merula. Here, the trough of islet activity at the peak of invernal fat deposition is accompanied by inactivation of insulin antagonists (see Fig. 1) and a continual food intake during daylight (Peters, pers. comm.; see also Peters, 1961). About blood sugar and metabolic processes there exist almost no data, presumably because of difficulties in keeping and handling this highly excitable bird, but it is very striking that the seasonal changes of blood sugar in the domestic duck (Mialhe, 1954) closely parallel the islet activity in T. merula. Moreover, invernal fat deposition in both species occurs at the same time, and the drakes begin their sexual display in the fall when—judging from the onset of autumnal song—the refractory phase in T. merula is finished (Epple, 1962). As in T. merula and all species investigated so far, the adrenals of the Mallard (Anas platyrhynchos) are inactive in winter (Höh, 1947), and despite their phylogenetic distance and different molting times (two molts in the Mallard according to Höhn, 1949) both species resemble one another more in their periodicity than Turdus merula and the more closely related Erithacus rubecula or Sylvia communis (data on the latter two species in Merkel, 1956, 1958, and 1960).
I think that the blood-sugar curve in the duck and the adrenal-cortex activity in all comparable species give, together with the continual food intake during the winter days, some hints for the interpretation of the annual islet periodicity.

When food intake in winter leads to alimentary hyperglycemia, increased output of insulin is not necessary because of diminished secretion of antagonistic hormones, which inhibit the glucose penetration into cells. This latter effect is well known from glucocorticoids and prolactin and has been demonstrated in birds (Mialhe, 1958). In winter, therefore, a basic insulin output might be sufficient for all processes influenced by this hormone. Additionally, a lowered basic-blood-sugar level—which is in balance with cell sugar—could enhance the glucose penetration into cells during alimentary hyperglycemia, since glucose uptake of tissues is influenced by the difference in its concentration in blood and tissues. Thus (e.g. following Kühnau, 1958), the hyperglycemia in Diabetes mellitus may be considered as a compensation for the lack of the uptake-furthering action of insulin.

In summer, the reverse situation is true. There is high activity of the adrenal cortex which apparently is closely correlated with gonadal development (in the Mallard: Höhn, 1947; in Turdus merula: see Fig. 1). During breeding, increased secretion of prolactin might also raise the blood sugar,
thus causing enhanced activity of the B-cells. Other hormones may also interfere. Progesterone, found in regressive gonads (Lofts and Marshall, 1959), might stimulate the B-tissue of the islets (Kerr et al., 1952), and it must be mentioned that thyroxine is able to further insulin destruction in tissues (Elgee and Williams, 1955a, 1955b). The behavior of the islets of Langerhans in some forms of obesity described particularly by Hausberger (1958, 1959, and 1961) is very interesting. Here, islet hypertrophy is caused by hyperadrenocorticism which, on the other hand, seems to be stimulated by deficiency of gonadal hormones. Regardless of the concomitant fat deposition, this sequence resembles the order of events in the annual cycle of the endocrines in *Turdus merula* (Fig. 1). Perhaps here we have a key to its understanding.

**ACTIVITY IN A- AND B-TISSUE**

What is the significance of the corresponding activity in A- and B-tissue? As the present state of knowledge of the physiological role of glucagon is very poor and statements in the literature are very conflicting (see Lukens, 1959; Berthet, 1961; Weinges, 1961; Glasser and Izzo, 1962), it seems too early to discuss this problem. Yet the parallel activity in almost all animals under a wide variety of environmental conditions indicates clearly that both components of the pancreatic islets work as a functional unit which is not split off by pronounced alterations of the endocrine system caused by seasonal or artificial photostimulation.

**ACKNOWLEDGMENTS**

I wish to express my most sincere thanks to the Committee on Travel and Subsistence Grants of the XIII International Ornithological Congress for a travel subsidy. The investigations were partially made possible by a scholarship of the Deutsche Forschungsgemeinschaft. I have to thank the Vogelwarte Helgoland for help in providing the specimens of *Sylvia borin*.

**SUMMARY**

In this review of literature on the behavior of the pancreatic islets in some small-bird species, the relation of the islets to temporary adiposity is discussed and a working hypothesis is elaborated to explain the cyclical changes of the islets in *Turdus merula*. Diminished islet activity during invernal fattening in this species is suggested as an adaptation to the lowered secretion of insulin-antagonistic hormones of the adrenal cortex and perhaps of other endocrines (e.g. prolactin). Generally low basic-blood-sugar level at the same time might favor the penetration of glucose into the cells during alimentary hyperglycemia. Increased insulin output therefore appears unnecessary. In summer, the situation is reversed: Increased activity of the adrenal cortex—which apparently is closely correlated to gonadal development—and probably other insulin antagonists raise the blood-sugar level, thus causing enhanced insulin output.
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Annual Physiological Cycles in Captive Birds of Differing Migratory Habits

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Study of the annual cycle in captive birds in outdoor aviaries provides much useful information. The observed seasonal and daily changes in physiology and behavior demonstrate what the influence of caging per se has on the natural cycle; this provides a standard of reference for indoor experiments where unnatural photoperiods, lighting conditions, temperatures, and other factors may influence the birds in ways that would otherwise go undetected. If the birds are held at a locality within the breeding or wintering range, the observed cycles, allowing for the influence of caging, may be compared directly with those of wild birds during the appropriate seasons. During the remainder of the year, of course, it must be assumed that the environmental conditions are different from those encountered by the wild birds, but even this situation may provide valuable information on the influence of these conditions, if differences between the cycles of the captive and wild birds are revealed.

Regardless of whether or not the cycles in captive birds are exactly comparable to those in wild birds, such investigations provide the opportunity to study in detail the cycles in individual birds, including such aspects as the temporal relationships between different events, the influence of one event upon another, and the day-to-day influence of weather. These seldom can be studied adequately in wild birds.

The present paper describes and compares certain aspects of the annual cycle in captive birds of six species: Hermit Thrush (Hylocichla guttata), Slate-colored Junco (Junco hyemalis), White-crowned Sparrow (Zonotrichia l. leucophrys), White-throated Sparrow (Zonotrichia albicollis), Fox Sparrow (Passerella iliaca), and Swamp Sparrow (Melospiza georgiana). These birds were held in individual activity-registering cages in aviaries where they were exposed to outdoor conditions of daylength, light intensity, temperature, humidity, etc. They were, however, partly protected from full sunlight and wind. Weekly observations were made on body weight, fat class, molt, and overt reproductive features such as cloacal protuberance and incubation patch. Activity was recorded continuously for the study of Zugunruhe (nightly unrest) and the hour-to-hour pattern of daylight activity. This paper will be concerned only with the cycles of body weight and Zugunruhe. Details of the methods used have been published earlier (Weise, 1956). Additional information will be supplied where necessary below.

This work was supported by National Science Foundation Grants G-4435

and G-18546 and by grants from the University of Wisconsin Research Committee. I wish to acknowledge the invaluable aid of Raymond Stefanski.

**WHITE-THROATED SPARROW CYCLES IN ILLINOIS**

In an earlier study (Weise, 1956), 12 White-throated Sparrows were held in captivity at Champaign, Illinois. The cycles of body weight and fat were briefly as follows. In midwinter there was a fairly high peak with week-to-week fluctuations correlated inversely with temperature, as found in wild birds by others (Odum, 1949; Helms and Drury, 1960). In late winter and early spring, weight and fat declined, reaching a low point in late March at the time of the partial prenuptial molt. As the molt diminished in mid-April, there was a sudden and rapid period of fat deposition and weight increase culminating in early May (at the peak of the natural migration period). In middle and late May the weight and fat dropped abruptly to a somewhat lower level, then declined more slowly through June and early July, reaching a second low point for the year at the onset of the complete postnuptial molt. The picture in the autumn was not so clear. Two of three birds deposited fat and gained weight in September and October while the other did not. In any event, fat and weight in late November and December began to increase toward the midwinter peak.

In regard to Zugunruhe, there was none during the winter or early spring. In late April, some days after the onset of fat deposition, Zugunruhe appeared rather abruptly. At first, however, there were many nights of slight or no activity interspersed among nights of intense activity; these differences in intensity were correlated with air temperatures and weather conditions. In late May and June the birds were intensely active nearly every night; but in late June and early July, nights of reduced activity or inactivity again appeared, and Zugunruhe ceased completely at about the onset of the postnuptial molt. Zugunruhe reappeared in September after the molt, reached a peak in October, and gradually declined and disappeared in November or early December.

It was concluded that: (1) From late November to mid-April the weight and fat cycles of the captive birds corresponded closely with those of wild birds on the wintering grounds, as described by Odum (1949) and Odum and Perkinson (1951); (2) during the migration periods the birds were capable of rapid fat deposition but this fat was not utilized or depleted in a normal fashion due to the conditions of captivity; (3) Zugunruhe was a reliable indication of the "urge" to migrate; and (4) during the natural breeding period the migratory condition persisted in the captive birds, superimposed on the reproductive condition, again as a result of the conditions of captivity.

**WHITE-THROATED SPARROW CYCLES IN WISCONSIN**

Since the Illinois study left a number of questions unanswered, I decided to repeat the experiment. Accordingly, 7 male and 8 female White-throated Sparrows have been studied in an outdoor aviary in Milwaukee, Wisconsin, between October 1959 and June 1962, individual birds being kept under observation for periods ranging from 6 to 31 months. Periodically new birds have been added to replace old birds killed for autopsy, so that in each migration season both old and new birds have been represented. Conditions in the aviary are essentially similar to those in the Illinois experiment, and the methods and types of observation are similar.

The results are shown in Fig. 1. In this figure, body weights are expressed in terms of percentage above lean weight in order to compare birds of different sizes. In computing this the minimum observed weight of each bird, while in fat class 0 (no observable fat), was used as the lean weight. Thus, "lean weight" here is not strictly comparable to the "lean weight" or "fat-free weight" determined by lipid-extraction techniques (Odum and Perkinson, 1951; Connell, Odum, and Kale, 1960; King and Farner, 1959).
In these graphs data for males and females are combined, since close examination of the cycles of all the individual birds has revealed no sexual differences in the amplitude of the cycles.

*Zugunruhe* is measured by an index determined by dividing each hour of the night into 20 equal intervals, and counting the number of intervals on

![Chart](image)

**Fig. 1.** Body weight and *Zugunruhe* cycles in the White-throated Sparrow in Milwaukee, Wisconsin, from October 1959 to June 1962. Based on 15 birds as follows: 8 from October 1959 to July 1960; 11 to December 1960; 7 to July 1961; 5 to June 1962. Sexes combined. See text for further explanation.

the activity recording chart in which one or more activity marks occurred. Therefore, an activity unit is defined as a 3-minute interval in which locomotor activity took place.

The activity cages used here were constructed and adjusted in such a way as to minimize error due to differences in exercise patterns of the birds or to unequal sensitivity of the cages (Weise, 1962). A very high proportion of the changes of position of each bird was recorded. Therefore, I believe it feasible to compare quantitatively the activity of different individuals and different species, recognizing of course that the method of record-chart analysis imposes upper limits on the activity scale. In practice, these upper limits have never been attained in any bird.
The cycles in the Wisconsin birds were similar to those in the Illinois birds in most respects. Aside from minor differences in timing and amplitude, there was a high degree of uniformity in the responses of the individual birds. The prenuptial molt and its associated weight-fat minimum were slightly later in the Wisconsin birds, in early April rather than late March, but the spring fat deposition took place at about the same time. The timing of this fat deposition and the subsequent peak was nearly identical in the three springs of 1960, 1961, and 1962. Weather conditions and mean weekly temperatures during late April and May were very similar in these three years.

The Wisconsin birds failed to corroborate the presumed autumn fat deposition and weight gain. Although most individuals deposited some fat during the fall, it was a gradual process, irregular in timing and extent. Of 11 birds in the fall of 1960 and 5 in 1961, only 3 deposited fat at a rate and to an extent approaching that in the spring. One of these gained 4.4 g in 3 weeks (20 September to 13 October), with a maximum weekly gain of 1.5 g as compared with a maximum of 3.1 in the spring; another gained 3.6 g between 13 September and 18 October, with a maximum weekly gain of 2.5 g compared with 3.2 in the spring; the third gained 5.8 g between 17 August and 29 September, with a maximum weekly gain of 1.4 g compared with 2.7 in the spring. The remaining birds showed much slower and less extensive weight gains.

The net effect of these irregularities in timing and extent was that the average weights, as shown in Fig. 1, simply increased gradually and slowly throughout the fall, from the low point at the time of the postnuptial molt toward the midwinter peak in January.

The Wisconsin White-throated Sparrows exhibited a Zugunruhe cycle very much like that seen in the Illinois birds. The onset in the spring was temporally very precise, the average dates of first nightly activity for the 3 years being 27 April, 26 April, and 28 April. Although the levels of intensity in the autumn were considerably lower than in late May and June, they were about the same as in the actual spring migration period in late April and May. During the entire autumn period of Zugunruhe, each individual exhibited an alternation of periods of intense nightly activity and periods of reduced activity or none. The influence of weather in this respect has not yet been analyzed. In the autumn, Zugunruhe occurred in all of the birds, regardless of the individual differences in body weight and fat.

SLATE-COLORED JUNCO CYCLES IN WISCONSIN

For comparative purposes, the Slate-colored Junco has been included in the study since its inception in 1959. This species is an earlier migrant in the spring than the White-throated Sparrow; its migrations appear to be more greatly influenced by weather, and its wintering range lies farther north and includes southern Wisconsin. Eight individuals have been used, 3 males and 5 females.
Several differences between the two species are apparent in the body-weight cycle (Fig. 2). In the Juncos the midwinter weight levels were somewhat lower, and there was little or no tendency for a late-winter decline. This is almost certainly correlated with the fact that the prenuptial molt in this species was very slight, almost nonexistent, involving only some small interramal feathers.

The timing of the spring period of fat deposition varied more than it did in the White-throated Sparrow, being conspicuously later in 1960 than in 1961 and 1962. This may be connected with the weather in the immediately preceding weeks. March of 1960 was colder than usual, the ground remaining snow-covered until the end of the month. Not only was the fat deposition in the captive birds delayed, but the first marked influx of wild migrant Juncos in Milwaukee was also very late (27 March 1960, as compared to 12 March 1961 and 17 March 1962).

In any case the body-weight increase and its subsequent peak averaged 2–3 weeks earlier in the Juncos than in the White-throated Sparrows. Imme-
diately after this peak, as in the White-throated Sparrows, there was a rather abrupt decrease in weight. Then followed a long steady decline, extending through the postnuptial molt period until early October when there was evidence, both in 1960 and 1961, of fairly rapid although not very extensive fat deposition.

Zugunruhe in this species was similar to that in the White-throated Sparrow, except for differences in timing. The average date of first Zugunruhe over the 3-year period was 14 April (19 records) for the Junco, 27 April (20 records) for the White-throated Sparrow. A distinct difference is seen between the two species in the relationship between the onset of Zugunruhe in the captive birds and the migratory movements of the wild birds. In the White-throated Sparrow, both in Illinois and Wisconsin, Zugunruhe was first noticed near the beginning of the natural migratory period for the species, just slightly later than the appearance of the first influx of migrants in the area. In the Junco, however, Zugunruhe did not begin until past the peak of the natural migratory period, at a time when departures of wild birds far outbalanced influxes.

The postnuptial molt in this species was somewhat later than in the White-throated Sparrow; and this, coupled with the earlier onset of Zugunruhe, resulted in a longer spring period of Zugunruhe. In September most of the Juncos were occasionally active at night, but the peak of autumn nightly unrest came in late October and November. The average intensity of Zugunruhe in the autumn was conspicuously less than in the White-throated Sparrow, possibly connected with the fact that southern Wisconsin is within the wintering range of the species.

COMPARISON WITH OTHER SPECIES

The observed differences between the White-throated Sparrow and Slate-colored Junco raised the question of whether there were interspecific differences in the amplitude of the weight and Zugunruhe cycles that might be correlated with the length of the migration route, or with the geographical or latitudinal location of the breeding and wintering ranges in relation to Milwaukee.

Accordingly, birds of four additional species were added to the aviary in the fall of 1960 and spring and fall of 1961: 6 Hermit Thrushes, 7 White-crowned Sparrows, 8 Fox Sparrows, and 5 Swamp Sparrows. Late-summer and fall observations on these species are not yet extensive enough for firm conclusions, although there are sufficient data for the winter and spring to warrant confidence. The results obtained so far are shown in Fig. 3 and 4. The species have been arranged in two groups according to the time of spring migration. Table 1 summarizes the locations of the main breeding and wintering ranges and the approximate lengths of the migration routes.

Among the early spring migrants the Fox Sparrow and Junco generally pass through Milwaukee from mid-March to late April, while the Hermit
Fig. 3. Comparison of body weight and Zugunruhe cycles in three species of early spring migrants. Number of birds as follows: *J. hyemalis* as described for Fig. 2; *P. iliaca*, 2 from November 1960 to November 1961, 8 to June 1962; *H. guttata*, 1 from February 1961 to August 1961, 1 from October 1961 to January 1962, 5 to June 1962. Data for both sexes and all years combined.

Table 1.—Estimated Migratory Distances for the Six Species Studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Breeding Range</th>
<th>Wintering Range</th>
<th>Minimum Length of Migratory Route (miles)</th>
<th>Distance from Milwaukee (miles)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>EARLY-SPRING MIGRANTS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. iliaca</em></td>
<td><strong>57°–52°</strong></td>
<td><strong>40°–30°</strong></td>
<td><strong>830</strong></td>
<td><strong>620</strong></td>
</tr>
<tr>
<td><em>H. guttata</em></td>
<td><strong>53°–45°</strong></td>
<td><strong>40°–30°</strong></td>
<td><strong>350</strong></td>
<td><strong>140</strong></td>
</tr>
<tr>
<td><em>J. hyemalis</em></td>
<td><strong>55°–45°</strong></td>
<td><strong>45°–32°</strong></td>
<td><strong>0</strong></td>
<td><strong>140</strong></td>
</tr>
<tr>
<td><strong>LATE-SPRING MIGRANTS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Z. l. leucophrys</em></td>
<td><strong>58°–50°</strong></td>
<td><strong>38°–32°</strong></td>
<td><strong>830</strong></td>
<td><strong>480</strong></td>
</tr>
<tr>
<td><em>Z. albicollis</em></td>
<td><strong>55°–45°</strong></td>
<td><strong>38°–30°</strong></td>
<td><strong>490</strong></td>
<td><strong>140</strong></td>
</tr>
<tr>
<td><em>M. georgiana</em></td>
<td><strong>55°–40°</strong></td>
<td><strong>40°–30°</strong></td>
<td><strong>0</strong></td>
<td><strong>0</strong></td>
</tr>
</tbody>
</table>

* a Range boundaries are estimated from the 1957 American Ornithologists' Union Check-List, and from Audubon Field Notes Christmas Counts. Boundaries and other data apply only to the approximate longitude of Milwaukee. It is assumed that the majority of birds of these species migrate more or less directly north and south.
Fig. 4. Comparison of body weight and Zugunruhe cycles in three species of late spring migrants. Number of birds as follows: Z. albicollis as described for Fig. 1; Z. leucophrys, 2 from November 1960 to January 1962, 7 to June 1962; M. georgiana, 1 from May 1960 to November 1960, 2 to July 1961, 5 to June 1962. Data for both sexes and all years combined.

Thrush is somewhat later, from early April to early May. These periods were not accurately reflected by either the fat deposition or the onset of Zugunruhe in the captive birds of these species. As was true of the Juncos, the Fox Sparrows and Hermit Thrushes did not attain the migratory condition until toward the end of the natural migration period. The Hermit Thrushes were particularly late. Aside from its intrinsic interest as a species from a far-distant taxonomic group, the Hermit Thrush was probably a poor choice for comparison with the emberizines. This species was much more adversely influenced by extremes of cold during the winter as attested by very pronounced weight fluctuations. Moreover, in late winter there was a marked weight decline in all of the six thrushes and a definite, although not extensive, pre-nuptial molt in two of them. In these respects, as well as in the timing of fat deposition and Zugunruhe, the Hermit Thrushes more nearly resembled the White-throated Sparrows.
Although the Fox Sparrows uniformly reached fat class 4 (very heavy fat) in the spring, as did the other species, the percentage of weight gain was notably lower, 26.3 percent, as compared with 35.3 percent in the Juncos. This difference was significant at the 95 percent level.

During the postnuptial molt and in the autumn, the weight curves for these three species were quite similar.

In regard to Zugunruhe the Fox Sparrows, with the longest migration route, were most intense, but not significantly so. In the autumn there were some apparent differences, with both the Fox Sparrows and Hermit Thrush (only one bird) exhibiting much more Zugunruhe than the Juncos.

In the group of later spring migrants, the Swamp Sparrow is earliest, arriving in the Milwaukee area before the middle of April; however, probably the bulk of the migrants pass through in late April and early May. Possible differences in migratory habits between the two races of the Swamp Sparrow, *M. g. georgiana* (which breeds in Wisconsin) and *M. g. ericrypta* are not known. The Swamp Sparrows used in this study were believed to be transients in the Milwaukee area rather than local breeding birds; however, it is not known to which subspecies they belonged. (A group of Swamp Sparrows collected from local breeding populations is now under investigation; these appear to differ importantly from the transients discussed in the present paper.)

White-throated Sparrows pass through the Milwaukee area with great regularity in late April and early May, while White-crowned Sparrows are definitely later, migrating through from early to late May.

These migration periods were reflected quite accurately by the spring fat deposition and the onset of Zugunruhe in the captive birds of this group. As far as amplitude is concerned, there were no species differences in the extent of the spring-weight gain, although the White-crowned Sparrows were less fat during the winter. In the autumn both the Swamp Sparrows and White-crowned Sparrows exhibited some fairly rapid weight gains after the postnuptial molt which terminated in late September in the former and in late August in the latter.

The White-crowned Sparrows developed somewhat more intense Zugunruhe in the spring than did the White-throated and Swamp sparrows. In the autumn, however, there were strong differences, representing a gradient that might be expected from the lengths of the migration routes—White-crowned Sparrows greatest, White-throated Sparrows next, Swamp Sparrows least.

In the White-crowned Sparrows, as in the Fox Sparrows, the timing of the fall period of Zugunruhe was not in correspondence with the natural migration period. The onset of Zugunruhe was very early, as soon as the molt (which itself was very early) neared completion in August. It is quite possible that in these two species all the events at this time of year were abnormal since the birds were being held at photoperiods and temperatures far different from those on their subarctic breeding grounds. The other four
species, being on or relatively near their breeding ranges, were probably encountering near-normal photoperiods and temperatures.

**SIGNIFICANCE OF THE CYCLES IN CAPTIVE BIRDS**

The experimental work on Wisconsin White-throated Sparrows reported here has confirmed the cycles observed in the earlier study in Illinois, except in the matter of autumnal fat deposition. It is now apparent that, under these conditions (which are not far different from those on the breeding grounds), the White-throated Sparrow does not exhibit a uniform period of rapid and extensive fat deposition in the fall. On the other hand Zugunruhe, indicating migratory readiness, does occur in all birds, is quite uniform in timing, and reaches about the same intensity as in spring. These results are in agreement with the findings of Millar (1960), who made an intensive study of White-throated Sparrows migrating through Madison, Wisconsin. On the basis of a large number of weight and fat records, not only of newly captured birds but also of repeats during stopovers, he concluded that this species accomplishes its autumnal migration in the absence of extensive fat reserves. I believe that this is the correct explanation for the low lipid index values found by Odum (1960) in White-throated Sparrows killed at a TV tower during autumnal migration in Georgia.

This leads to the further possibility that the extensive fat deposition in the spring, in this and similar overland migrants, is not so much an adaptation for performing long migratory flights as it is for withstanding unfavorable weather, possible food scarcity, and/or restricted opportunity for securing food, as the birds fly into an increasingly more hostile climate on the way north.

Although none of the six species used here can be considered really a long-range migrant, the differences in the lengths of their routes and in the locations of their ranges, as shown in Table 1, are sufficient to lead one to expect some differences in the migratory condition in terms of fat reserves and the intensity of the urge to migrate. However, in the spring, all of the species exhibited extensive fat deposition and very intense Zugunruhe, regardless of how near or far they were from their respective wintering and breeding ranges. Apparently the ability to migrate and the readiness or urge to migrate are at a maximum in all of these species in the spring.

In the fall, however, some differences occurred, although these need to be confirmed by further observations. The two species with the longest routes and with the most northerly breeding ranges exhibited much more intense Zugunruhe than the other species, and one, the White-crowned Sparrow, also possibly developed greater fat deposits. The two species with the shortest routes, the Swamp Sparrow and Slate-colored Junco, on the other hand exhibited relatively little Zugunruhe, perhaps indicating only an occasional or a weak urge to migrate. It is not possible at present to say whether these differences in the intensity of the migratory urge are adaptations for the
length of the journey, or for moving away from an unfavorable environment, since the species with the longest routes also had the most northerly breeding ranges, which would be most adverse in winter.

SUMMARY

Since 1959 certain features of the annual cycle have been studied in captive birds in an outdoor aviary. Three species that migrate early in the spring, the Slate-colored Junco, Fox Sparrow, and Hermit Thrush, have been compared with three species that migrate later, the Swamp Sparrow, White-throated Sparrow, and White-crowned Sparrow. The form of the body-weight cycle was basically alike during the first half of the year in all six species, with a moderate midwinter peak, a late-winter depression, and a rapid increase to a maximum in April or May. The timing of this increase corresponded well with the natural time of migration in the group of late migrants, but was relatively late in the group of early migrants. During the second half of the year the weight in all species declined and reached a minimum at the time of the annual molt. In the fall, weight increases again occurred but were much more variable in timing, rate, and extent than in the spring. It is suggested that in these overland migrants the vernal premigratory-fat deposition is an adaptation for moving into a more hostile climate, rather than for making long migratory flights. Zugunruhe, indicating the urge to migrate, appeared in the spring in all species toward the end of the rapid weight increase, and remained intense throughout what would normally be the migration and breeding periods. It declined at the time of the annual molt and reappeared in the fall, when species differences were apparent. The two species with the longest migration routes (and most northerly breeding ranges) exhibited the greatest Zugunruhe, while the two with the shortest routes exhibited the least.

REFERENCES CITED


In recent years, knowledge and understanding have increased about the physiological conditions that promote or permit behavior patterns. In one direction studies of the brain have shown that certain areas control particular patterns. In another direction studies of endocrines reveal that certain hormones stimulate or inhibit particular patterns. The present paper will trace historically the changes in interpretation of aggressive behavior in birds and describe our current understanding of the role of hormones. Purely endocrine features will be omitted. A major task is to clarify the relation of territorial and courtship behavior to each other. Another objective is to suggest areas for further work.

THE EARLY VIEWPOINT

When ornithologists first became aware of territorial behavior, it was considered to be part of courtship. Howard (1920) studied migratory species almost entirely and naturally noted that defense of territory and courtship began almost simultaneously. He stated:

Securing a territory is then part of a process which has for its goal the successful rearing of offspring. In this process the functioning of the primary impulse, the acquirement of a place suitable for breeding purposes, the advent of a female, the discharge of the sexual function, the construction of the nest, and the rearing of offspring follow one another in orderly sequence. But since we know so little of the organic changes which determine sexual behaviour, and have no means of ascertaining the nature of the impulse which is first aroused, we can only deal with the situation from the point at which the internal organic changes reflect themselves in the behaviour to a degree which is visible to an external observer.

Thus, defense of territory is a part of the sexual sequence.

The function of song further confused the situation. Howard (1920) described the value of song in attracting the female:

So that just at the moment when the sexual impulse of the female is most susceptible to stimulation, the males are betraying their positions and are thus a guide to her movements. Nevertheless, even though she may have discovered a male ready to breed, success is not necessarily assured to her; for with multitudes of individuals striving to procreate their kind, it would be surprising if there were no clashing of interests, if no two females were ever to meet in the same occupied territory.

Based on these observations, territorial behavior, including song, was considered to be part of the sexual sequence. Other early workers (Altum, see Mayr, 1935; Nice, 1933) ignored or neglected the problem.

These early observations were conducted in the field without knowledge of research carried on in poultry and zoological laboratories concerning endocrines and developmental aspects. Furthermore, the early field investi-
igators of territorial behavior were unaware of the work on social rank. The lack of communication perhaps set the stage for the claim that territorial and courtship behavior were a physiologically unified process (reviewed in Allee et al., 1939). For example, several workers confirmed the observation that androgens produced aggressive behavior, certain courtship patterns, and crowing in male or female chicks, in capons, and in hens. The tacit assumption was made that the aggressive behavior seen in social-rank situations and the territorial behavior seen in wild birds were essentially the same. The demonstration that androgens produced song, even in females (Shoemaker, 1939), added further conviction. Most of this information has become common knowledge (see Guhl, 1961). Thus, it seemed clear that two basic patterns—territory and courtship—were controlled in the male by androgens.

FIELD OBSERVATIONS

The study of aggressive behavior now shifts to a new generation of field workers who began to notice situations that did not confirm the earlier concepts. Items here and there in Tinbergen's work on Snow Buntings (Plectrophenax nivalis) and Northern Phalaropes (Lobipes lobatus), in Nice's work on Song Sparrows (Melospiza melodia), in Sherman's work on Flickers (Colaptes auratus), and in many other reports had cast doubt on the concept that aggressive behavior and courtship were under the same hormonal control. An early example was Laskey's (1935) brilliant study of Mockingbirds (Mimus polyglottos). Males and females each defend separate territories during winter, but the female abandons hers at nesting time. Another example was Davis' (1942) study of the Crotaphaginae showing the phylogeny of change from defense of territory by a pair to the development of group territory, each separate from courtship. A complication arises here historically in the meaning of the term "sexual fighting" (Tinbergen, 1936), which refers to competition for the female. It consists of aggressive behavior between males in direct reference to the female rather than to the territory. Courtship, in contrast, includes the mutual stimulation preparatory to forming a pair bond. I have suggested (Davis, 1942) that these three patterns are clearly separable and that other types of aggressive behavior (e.g. protection) occur:

It is becoming clear that the separation of the elements of territorial defense and sexual fighting should have been recognized earlier. The behavior of other species shows clearly that there are several causes of fighting among birds. For success in reproduction there are three principal reasons for defending the nest site: (1) predators must be driven off; (2) a sex-partner must be secured and defended against other members of the species which attempt to obtain the partner; (3) a spot suitable for pairing, for placing the eggs, and for raising the young must be secured. It is proposed to restrict the term territorialism to the last-mentioned type of fighting. The most important separation is the distinction between fighting over the piece of land and fighting in relation to the sex-partner.

Nowadays the term sexual fighting is rarely used. It seems apparent that much behavior once called sexual fighting was really territorial or perhaps
social rank in nature. In other cases, errors of observations occurred. However, some cases of sexual fighting do exist (Tinbergen, 1936).

Observations suggesting that territorial and courtship behavior were separate continued to accumulate. Lack (1943) showed that European Robins (Erithacus rubecula) defend territory in the fall; Davis (1941) showed that Kingbirds (Tyrannus tyrannus) court and pair before defending a territory; a more recent study (Lind, 1955) showed that the Blackbird (Turdus merula), which does not migrate in Denmark, defends its territory in the fall and winter; observations of flocks of sandpipers (Hamilton, 1959) showed that the individuals were very aggressive during migration. Innumerable recent studies indicate that territorial behavior occurs at times and under conditions different from courtship behavior.

It is desirable to comment on the role of song and certain displays. Song clearly serves to advertise the existence of a male. Thus, in most species it is a repellant to an intruding male and an attractant to a female. In addition to song, other features such as brilliant colors or special displays serve the same function. Note that there is only one function, advertising; the reaction to these several displays is different in a male and in a female. Some species have separate advertising displays for each sex. Thus, the male Starling (Sturnus vulgaris) (Davis, 1959) advertises his presence in his territory (near nest hole) by certain chuckles and movements of throat feathers. He advertises to a female by a “scream” and vigorous wing flapping. The first occurs all year (except summer); the second only in the spring (and occasionally in a warm fall).

**HORMONAL CONDITIONS**

The early field observer noted the correlation between the increase in territorial behavior and the increase in the size of the gonads. In laboratory experiments, injection of androgens into domestic fowl resulted in fighting and courtship. The conclusion naturally was that androgens controlled aggressive behavior and courtship, although the levels of concentration might differ. But as indicated above, observations of behavior in nature disagreed with this generalization. In particular, Davis (1959) confirmed Kessel’s (1957) observation that Starlings vigorously defend a nest hole in the fall when, of course, the gonads are small. A series of endocrine experiments was planned to clarify these disagreements.

First, laboratory tests demonstrated (Davis, 1957) that testosterone had no effect on social rank or defense of a nest box. Some additional unpublished data are presented here. The methods used were much the same as those described (Davis, 1957). The design followed the idea of Allee et al. (1939). The injection of hormone into low-ranking birds should result in a rise in rank if the hormone is effective. Five Starlings, castrated 6 weeks previously, were placed together in a large cage. The birds remained together for 2 weeks and established a social hierarchy. At that time, one
A 20-mg pellet of testosterone propionate was implanted into the pectoral muscles of each of the fourth- and fifth-ranking birds, and the effects on behavior of the group were observed for a period of two more weeks. The 20-mg pellets undoubtedly constituted a massive dose for the Starling, since 1 mg testosterone propionate administered to a chick resulted in an almost fivefold increase in comb weight. (No indication of anesthetic effect was present.)

The general level of activity of this group of birds was high. Implantation of testosterone pellets into the two lowest-ranking birds (Yellow and Red) had no appreciable effect (Table 1) either on the total amount of their fighting or on the social rank of the other birds in the group. Actually, the two birds receiving testosterone reversed ranks, although there was very little difference in their fighting success. The total number of fights in the total group per observation period decreased slightly from 11.6 to 10.2 after the two birds received testosterone. These results showed that, contrary to the results in domestic fowl, an established rank was not upset by injection of androgen into low-ranking birds. The possibility that learning or habit was significant was recognized and has not yet been excluded.

The second aspect to consider is courtship. Unfortunately, Starlings do not show courtship under these particular conditions of captivity, so that this aspect was not examined experimentally. However, I obtained some information by consideration of the relation of the wing-waving performance to the size of the testes. Testes are usually small during fall (Hilton, 1961). But in two different years a small increase occurred and at these times males mildly performed the wing-waving display. In addition, indirect evidence suggested that testosterone was not released as much in the fall as in the spring (Hilton, 1961). Thus, it seems clear that a correlation exists between the advertising display of Starlings (wing-waving and “screaming”) and the increase of androgens. An experimental test of this relation will have to await methods to persuade Starlings to perform in captivity.
The next approach was to consider other hormones, since androgens seemed to be unlikely candidates. Luteinizing hormone (LH) seemed to be the most likely candidate. The logic was simply that the agent must be a reproductive hormone and it could not be follicle-stimulating hormone (FSH) because the testes were small; therefore it had to be LH. The work, reported very briefly (Mathewson, 1961), showed that luteinizing hormone affected rank. Some unpublished details follow. To determine the effects of LH before and after castration, five adult male Starlings were placed together. The birds were observed (through a 1-way mirror) for 5-minute periods several times a week for 6 weeks. Observations were always made just after the birds were fed, because aggressive encounters were more frequent at that time. The social rank of each bird was determined by the number of times he won or lost aggressive encounters with the other birds. A “win” was defined as a physical threat to another bird (that is, flapping of the wings, or striking with the feet or bill) that resulted in retreat of the threatened bird. A “loss” was defined as a retreat from a threat or a fight.

After a social rank had been clearly established, 200 µg of Armour LH was injected into the third- and fourth-ranking birds in the hierarchy for 6 days. Saline was injected into the others. Observations of aggressive behavior were made as before. Then all five birds were castrated and behavioral observations immediately resumed. After 2 weeks of recovery, Green and Red-White were again given 200 µg Armour LH daily for 2 weeks.

Results of this experiment (Table 2) show that before the birds received

<table>
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<th>INJECTED</th>
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<td>3</td>
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<td>0.86</td>
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<td>17</td>
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<td>5</td>
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<td>0</td>
<td>4-5</td>
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* Injected.
any treatment, they had established a very clear-cut social rank, with Yellow the most dominant and Red-White the most subordinate. When Red-White and Green were given LH injections, the rank of Green (third) was unchanged, but Red-White had more fights per observation period (2.14 as compared with 0.43 before injection) and rose in rank from fifth to fourth. During this time, Yellow, although he was not injected, also had more fights per observation period. Examination of the raw data indicated that the increase in fights was due almost entirely to encounters with the two birds that were receiving luteinizing hormone, Green and Red-White. These two birds increased fighting only with Yellow; they did not fight the other birds in the group any more than before they were injected. Green and Red-White each won more fights with Yellow than previously, but they also lost more. Nevertheless, the increase was enough to raise Red-White's rank. Because of the activities of Green, Red-White, and Yellow, there were more total fights in the whole group per observation period (10.56 fights per 5 minutes as compared with the previous 7.42 fights).

Two weeks after the birds had been castrated, they had again established a stable social rank. Although the resulting order of individuals was different from the original, Yellow remained dominant. There was a slight increase in the total number of fights observed per 5-minute period after the birds were castrated when compared with the observations of the noncastrated, uninjected birds (8.77 fights were recorded per 5 minutes as compared with the previous 7.42). When Green and Red-White were again injected with Armour LH, there were no apparent changes in the rank order of the group, but the general level of activity decreased. Total fights per observation period decreased to a low of 4.66.

These results were equivocal, but it was apparent that learning may have played a part in obscuring the effects of gonadotrophic hormones on social rank. Therefore, another experimental procedure was designed to minimize its effects. Pairs of birds that had never been in the same cage (although their home cages were in the same room) were placed together in an observation cage. A single perch was placed in the cage, and the birds fought vigorously for possession of it. The criterion of dominance was control of this perch. Usually, dominance was clearly established within 5–10 minutes after the birds had been placed in the cage. As soon as dominance of one of the birds was evident, the birds were replaced in their home cages. Later, the subordinate bird was given an intraperitoneal injection of commercial luteinizing hormone and immediately placed in the observation cage with his previously dominant partner (which received saline). Changes in behavior, if they occurred, were usually evident in the first 5–10 minutes after injection.

For purposes of presentation, letters are used to designate castrated birds, numerals to designate intact birds. The notation A/1 indicates that castrated A dominated noncastrated bird 1, and so forth. The first tests of behavior of paired birds were done from July through October 1958. In these experi-
ments, castrated males were always paired with intact males. In six such pairs, the castrate dominated the intact bird in five cases (A/1, C/3, C/4, D/5, D/6), while the intact bird was dominant in only one case (2/B). (Note that some birds were used in more than one pair.) The subordinate, intact birds 1, 4, and 6 were then given various doses of Armour LH in saline. Upon injection of 250 μg LH, 1 assumed dominance over A. Bird 6 was given a total dose of almost 3,000 μg LH but remained subordinate to C. One other subordinate bird (5) was given a total of 2,000 μg testosterone propionate but did not assume dominance over D.

In August and September 1959, another behavior experiment was conducted. Four castrates and four intact birds were used. Out of twelve pairs, the castrate dominated the intact bird 11 times (A/1, A/2, A/3, B/1, B/2, B/3, B/4, C/2, C/3, C/4, D/4) and was defeated only once (4/A). When intact birds 1, 2, and 3 were given Armour LH (a dose of 500 μg was arbitrarily chosen, based on the results of the previous experiment), there were clear-cut reversals of dominance in six out of eight pairs in which birds 1, 2, and 3 were used. The six reversals were 1/A, 1/B, 2/A, 2/B, 2/C, and 3/A. In only two cases did an injected bird remain subordinate to his castrated partners (B/3, C/3).

A third experiment was run in March 1960, using two castrates and two intact birds. In this experiment, each bird was paired with every other bird, a total of six pairs. The results before injection were as follows: A/B, A/1, 1/B, 2/A, 2/B, 2/1. In contrast to the previous experiments, an intact bird was the most dominant and a castrate the most subordinate. After the relationship of each bird to every other bird in the group had been separately established, castrate B was given 1,000 μg of Armour LH. He then dominated A and 1, to whom he had previously been subordinate, but remained subordinate to 2, the most dominant bird in the group. The intact bird 1 was given 1 mg of Armour LH, whereupon he dominated castrate A and intact bird 2. He also continued to dominate castrate B, although B had also been given LH.

These data indicate that castrated birds nearly always dominated their intact partners. In the first experiment, castrates dominated in 5 out of 6 cases and, in the second experiment, in 11 out of 12 cases. Current experiments (Vandenbergh, unpublished) show that intact Starlings on short days dominate intact Starlings on long days. Castrates on short days dominate castrates on long days, but castrates on long days are an even match for intact birds on short days.

Although evidence is not available from the present program of research, there is ample evidence from other sources that pituitaries of castrated animals contain more gonadotrophin than do those of intact animals. The aggressive behavior of castrated Starlings is considered to be strong evidence that the hormonal control of aggressive behavior differs from that reported for some other animals. An important implication (although not tested ex-
Hormonal Control of Aggressive Behavior

Evolution of Hormonal Control

The information now available about hormonal basis is meager. Only a few species have been examined, but perhaps some speculation will stimulate research and suggest problems to explore. Animals have a propensity for utilizing hormones to perform new functions. Among mammals, numerous cases indicate that the animal took advantage of an endocrine and put it to work. It is no surprise, then, that birds have used two hormones for aggressive behavior. Perhaps further research will reveal others. Conversely, it is not unexpected that one hormone controls several behavior patterns. The imaginative problem is how did these changes occur. We can make the assumption (which, of course, may be wrong) that the pituitary hormones are more primitive and that the gonadal hormones developed later and came under control of the gonadotrophins. On this basis, aggressive behavior (territorial) was controlled by LH, and courtship behavior was unregulated. However, secondary sex characters soon developed, and courtship behavior came under the control of gonadal hormones due to the increased efficiency of breeding. In specialized species (domestic fowl), the control of aggressive behavior (social rank) has shifted to androgens but in less specialized species (Starlings) gonadotrophins still control aggressive behavior.

An item of value for promotion of the species is the increased efficiency attained if the hormone that stimulates courtship inhibits aggressive behavior to the other sex. Exactly this situation occurs in Starlings. Androgens and estrogens inhibit the production of LH in mammals and birds. Castrated Starlings dominate intact birds. Presumably as the level of androgens rises, the production of LH is inhibited. The bird thus becomes less aggressive. Since the territory has already been staked out, generally no disadvantage results from some loss of aggressiveness. In contrast, a disadvantage of aggressiveness is apparent in hens, since the dominant hens produce fewer eggs and chicks.

How should the above speculations be tested? An obvious step is to examine certain passerine birds that show unusual behavioral relations. Certainly the English Robin and the Mockingbird should be tested to determine what hormones control territorial behavior. Highly specialized birds, such as loons or grebes, should also be studied. Naturally, some ratites could be included. From the viewpoint of hormones, obviously one should also determine the role of follicle-stimulating hormone (FSH) in aggressive behavior. No such experiments have been published.

Song

The function of song was early recognized to advertise the availability of a male (Howard, 1920, and many others). This function is another device...
that helps the female find a male and that increases efficiency of reproduction. However, I suppose that song should be considered merely another attribute of a suitable habitat. Thus, the female chooses (perhaps through imprinting) a suitable area for nesting that includes such items as certain types of plants, intensity of sunlight, range of temperature, and also song. Song to the female is just another feature of the habitat. Once located in a suitable habitat, the next stage is courtship, which ensures fertilization. Thus, the reproductive sequence is a chain of discrete activities that individually serve to promote reproductive efficiency. Each one may be independently controlled by different hormones, or several may be controlled by the same (some, of course, may have no hormonal control). On this basis, song is another discrete aspect of avian reproduction that fits into a chain of actions. The major links are: (1) isolation (protection from interference); (2) discovery by female (song, conspicuous behavior); and (3) fertilization (tuned by courtship). Hormones facilitate these aspects in many species.

SUMMARY

The physiological basis of aggressive behavior has received increased attention in recent years. The early viewpoint was that territorial defense and courtship were a unified pattern, presumably under unified control. However, certain field observations indicated that the two patterns might be separate. Experiments with Starlings (Sturnus vulgaris) showed that, contrary to its effect in chickens, testosterone did not result in an increase in rank. It was further shown that luteinizing hormone (LH) resulted in dominance (if the rank were not previously established). Some speculations about the evolution of hormonal control suggest the possibility that LH originally controlled aggressive behavior, but that in some species control has passed to the gonadal hormones.

LITERATURE CITED


Hormonal Control of Mullerian Duct Differentiation
in the Chick Embryo

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INTRODUCTION

For many years biologists have devoted much time to thought and experimentation on the general problem of the developmental mechanisms responsible for urogenital differentiation in the avian embryo. Although its designation as the representative bird embryo may be questioned, the chick embryo (Gallus sp.) has been a standard experimental organism for such studies, and it is common knowledge that in this organism the urogenital

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1 Publication of this paper was in part financed by a research grant from the National Institutes of Health, U.S. Public Health Service.

system of the sexes passes in embryogenesis through an early, "neutral" stage to the sexually differentiated condition. There is now good evidence that embryonic hormones or modifiers play important roles in mediating such developmental alterations of the previously formed, "paired" components of the urogenital system (see Fig. 1). From an epigenetic point of view, genetic factors are, of course, ultimately responsible for these differentiations, but, because of limitations currently enforced by available experimental techniques and the lack of a plausible model explaining at the molecular level the mechanism(s) through which embryonic hormones induce or bring about their characteristic effects, experimentation in this area is at the present restricted for the most part to studies of results of injections of steroid hormones and attempts to correlate differentiational changes in tissues with associated biochemical shifts.

This approach to causal analysis of developmental systems is not necessarily the most rewarding, and an overall conclusion to the present discussion might be stated in this manner: Future progress in the area of the physiology of urogenital differentiation in the chick embryo depends upon (1) the isolation and chemical identification of the embryonic hormones or modifiers and (2) the discovery of the biochemical steps through which, say, gene products, or results of protein synthesis, initiate chemodifferentiation of specific tissues—thus resulting in the respective morphological changes of the various components of the urogenital system during embryogenesis.

In the present paper, the chief concern is with the causal basis of sexual differentiation of Mullerian ducts in the chick embryo. The major aims of the present report are threefold, and are listed as follows:

1) To review briefly the previous literature that relates to experimentation concerning the factors regulating urogenital differentiation, thus setting the stage for consideration of two problems still unresolved: (a) what is the chemical nature of the embryonic hormone responsible for the "death" or involution of Mullerian ducts in male embryos and (b) through what biochemical or physiological steps do exogenous and endogenous hormones lead to inception of the "death" process (i.e. physiological autolysis), which in turn leads to involution of these ducts;

2) To describe some recent work in the writer's laboratory, and that of F. L. Hisaw at Harvard, which deals with enzymatic and nucleic acid correlates of involution or stabilization of the ducts;

3) To outline, on the basis of knowledge now available, several alternative hypotheses that as a first approximation are useful, for model purposes preliminary to experimentation, in attempting to explain (a) the specificity of various hormones insofar as they influence the differentiation of Mullerian ducts in different ways and (b) the sexual and positional specificities of these ducts as they apparently seem capable of differentiating differently in response to the same hormonal stimulus.
THE EVIDENCE FOR A HORMONAL BASIS FOR UROGENITAL DIFFERENTIATION

To set the stage for the following considerations, it is necessary to review the evidence for the statement that in this organism embryonic hormones—produced apparently by the gonads—arrive at a given period of development at the sites of various components of the urogenital system, and there modify, initiate, or induce their characteristic differentiations. As stated above, the study of the effects of hormones on embryonic differentiation of the urogenital system is an old problem about which much has been written. No attempt will be made here to gather together all of this information. Instead, a review will be made only of those studies that, prior to 1958, deal with the delimitation of factors controlling, affecting, or modifying the differentiation of the urogenital system of the chick embryo. Primarily, the matter of hormonal control of involution or retention of Mullerian ducts will be considered, along with necessary considerations of the differentiation of the Wolffian ducts and gonads.

For more extensive and detailed accounts of such problems in this and other vertebrate representatives, the reader is referred to the reviews of Witschi (1939), Moore (1944, 1947), Jost (1948, 1953, 1960), Willier (1939), Wolff (1953, 1959), Romanoff (1960), Dodd (1960), and others cited by these reviewers.

Of historical interest are the observations and conclusions of Lillie (1916, 1917) concerning the “freemartin” in cattle. This worker notes for the cow that fusion of foetal membranes may occur in case of twins, resulting in reciprocal blood exchange. If the twins are of opposite sex, the female may be modified to an “intersex” and born a sterile freemartin. The explanation for this phenomenon is obvious: viz. male hormones from the male foetus, carried by the blood, reach the female foetus at a period when her urogenital apparatus is susceptible to hormone influence, and bring about so-called “masculine” modifications. The freemartin interpretation thus predicts that the foetus secretes androgens or androgen-like hormones and that the embryonic urogenital system can respond to steroid hormones (cf. Bouin and Ancel, 1903). Recent avian studies in this area have mostly confirmed the hormone theory for urogenital differentiation. However, as Moore (1944) and others have noted, the freemartin effect is a rare event among twin-bearing placentals, and there is no experimental proof that the embryonic hormones are steroidal in structure.

Normal Pattern of Urogenital Differentiation

The normal differentiation pattern for the chick urogenital system is demonstrated in Fig. 1. At periods of 5–6 days of incubation, both male and female embryos possess undifferentiated pairs of gonads, Mullerian ducts, and Wolffian (i.e. mesonephric) ducts. In the male embryo, by the fourteenth day, the Mullerian ducts have involuted and disappeared. The Wolffian ducts remain and are functional. These are the vas deferens of
the male bird. The gonads have lost their cortical elements, and the medullary elements have developed into two grossly similar embryonic testes.

In the female embryo, by the fourteenth day the right Mullerian duct is undergoing, relative to involution of the ducts of the male, a slow anterior-to-posterior involution. The left duct (the functional oviduct of the mature female) has grown in thickness, and has a slight expansion (the shell gland) at its junction with the cloaca. The Wolffian ducts are still present, but are destined to disappear shortly after hatching in the female. The female gonads are now different in shape and composition: the right gonad (ovotestis) is reduced, containing fragments of both cortical and medullary elements, and the left gonad has undergone hypertrophy favoring cortical elements, thus forming what is clearly an embryonic ovary (cf. Romanoff, 1960).

It will be observed from the above account and from Fig. 1 that male and female embryos possess, during the "neutral" period, equivalent, paired components of the urogenital system—at least at the level of gross morphology. During differentiation, then, the earlier-formed series of paired organs are differentiated in different ways for the respective urogenital systems of the adult male and female.

Experimental Studies on the Differentiation of the Urogenital System

Results of Steroid Injections.—Beginning in 1935, several groups of workers (e.g. Breneman, 1935; Dantchakoff, 1935a, 1935b; Willier, 1935; Wolff
and Ginglinger, 1935) reported on the effects of injections of sex hormones into the chick embryo immediately prior to the period of sex differentiation. The studies of these workers indicate that injected estrogenic steroids result in the atypical retention of Mullerian ducts ("feminization") in the male embryo, and that androgenic steroids are capable of inhibiting development of the left Mullerian duct ("masculinization") in the female embryo. Androsterones, however, demonstrate an "estrogenic effect" by causing retention of Mullerian ducts in male embryos. The Wolffian ducts show no response to androgens or estrogens in terms of retention or involution, although they hypertrophy under androgen (testosterone and androsterone) stimulation. Male embryos receiving estrogen or androsterone are "feminized" by modification of their gonads—the left gonad being ovary-like, demonstrating emphasis of cortical elements. Correspondingly, female embryos, "masculinized" by testosterone, develop testis-like gonads.

Subsequent studies (e.g. Willier, 1937; Wolff, 1937; Gaarenstroom, 1939; Wolff et al., 1948; Snedecor, 1949; Stoll, 1951; Hamilton, 1961) of the influences of injected steroids on urogenital differentiation in the chick embryo have been for the most part in general accord with the findings of workers in 1935. Raynaud (1940), Stoll (1951), and Hamilton (1962) have studied the interactions of steroid hormones by observing the effects of injections of combined doses of some androgens and estrogens on the differentiation of Mullerian ducts. Their findings indicate that the responsiveness of male Mullerian ducts to estrogens may be greater than to androgens. Hamilton (1962), working with only naturally occurring steroids (testosterone and estradiol-17b), observed that in male embryos injections of 10 μg of estradiol can override, or inhibit, the effects of 1,000 μg of co-injected testosterone—thus permitting Mullerian ducts of this sex to "live" and grow beyond the period during which they would be expected to "die" as a result of the operation of either endogenous hormones or exogenous testosterone.

**Results of Transplants and in vitro Experiments.**—Transplantation experiments on undifferentiated gonads, Mullerian ducts, and Wolffian ducts have been conducted mostly by Wolff and associated workers at Strasbourg, and more recently, at Paris. Before the technical advancement of organ-culture techniques, such experiments were restricted mainly to transplantation of embryonic organs to the chorioallantoic membrane of chick embryos at various stages of development. Most of these experiments involved gonad transplants (e.g. Minoura, 1921; Greenwood, 1925; Willier, 1927; Willier and Yuh, 1928), and failed to reveal marked, induced alterations of the urogenital system of hosts. However, after these workers' experiments, Bradley (1941) and Wolff (1947) successfully introduced gonad grafts into the coelomic region of hosts, and found evidence (e.g. modified gonads of the host) of modifications of the normal differentiation process. Wolff also reported (1947) that grafts of gonads differentiated in the normal direction when transplanted to hosts of the opposite sex (cf. Dennis, 1936).
Wolff's 1947 experiments are extensive and merit some consideration here. For coelomic grafts of gonads, he found that if undifferentiated male gonads (of 6–10 days' incubation) were grafted into undifferentiated female hosts (2–3 days' incubation), the host Mullerian ducts disappeared, and the host gonads were essentially unchanged. The reverse experiment, in which female gonads were grafted into a male host, resulted in "feminization" (i.e. retention of cortical elements) of the left gonad of the host, as well as "partial maintenance" of the Mullerian ducts. Wolff and Haffen (1951, 1952) have brought together, in in vitro parabiosis, undifferentiated male and female gonads of the duck, and they find that the female gonads exert a "feminizing influence" on the male gonads by causing them to develop a cortical layer.

Another set of experiments involves the in vitro study of the effects of steroid hormones on Mullerian and Wolffian ducts. Briefly, it has been found (Wolff, 1953, 1959) that male Mullerian ducts, excised after the differentiation of the gonads, undergo involution in vitro; Mullerian ducts excised before gonad differentiation, however, do not undergo involution in vitro. If the Mullerian ducts are taken at the earlier stage, and are cultured along with Wolffian ducts in the presence of water-soluble androgens, the Mullerian ducts—but not the Wolffian ducts—undergo degeneration. From such in vitro studies, it has been concluded for in vivo differentiation that male hormones arrive at the site of the Mullerian ducts and there cause the formation of a proteolytic enzyme which initiates involution of the Mullerian ducts by autolysis (see Wolff, 1953, 1959). This conclusion is discussed in greater detail below.

Results of Embryonic Castration.—Wolff and Wolff (1951) have successfully X-irradiated that region of the embryo (25–35 somite area) which gives rise to the gonads. They find that total castration (where both gonads failed to originate or organize) resulted in the retention of the Mullerian ducts in both genetic males and genetic females. This is further evidence (cf. Salzgeber, 1950) that embryonic gonads in the chick embryo actually secrete or liberate the substance that initiates regression of the Mullerian ducts.

In the female embryo, destruction of either the right or the left gonad is said to result in the normal female pattern of Mullerian ducts. Thus, from the studies of Wolff, it seems for the female embryo that either the right "ovotestis" or the left ovary can liberate the substance that initiates the regression of the right Mullerian duct. This conclusion is not completely substantiated by the findings of Huijbers (1951), as cited by Romanoff (1960). Romanoff reports that Huijbers found that hemicastration of female embryos results in the normal involution of the right Mullerian duct if the left gonad is absent and that atypical retention of the right duct results if the right gonad is absent. However, the more recent findings of this worker (Groenendijk-Huijbers, 1962), discussed in greater detail later in this paper,
support Wolff's conclusion that either the right or the left embryonic gonad of the female produces a hormone (androgenic or only androgenic-like in operation?) that diffuses through or across adjacent tissues to induce involution of the right Mullerian duct.

In another study, Lutz and Lutz-Ostertag (1956) demonstrate that high-frequency sound waves can destroy the presumptive gonad tissue and thereby permit the maintenance of Mullerian ducts—an observation that also substantiates Wolff's conclusions from studies of X-ray castration of chick embryos. Incidentally, the studies cited contradict Gaarenstroom's theories (1939) concerning the origin of the asymmetry of the Mullerian duct system in the female chick embryo. He discussed involution in terms of induction and effectiveness varying with distance from the left gonad, and hypothesized that the reduced right gonad (ovotestis) was associated with the atrophy of the right Mullerian duct and that the normal left ovary permitted retention of the left Mullerian duct.

Effects of Hypophysectomy and Some Other Factors.—Fugo and Witschi (1938) and Fugo (1940) have reported on the effects of hypophysectomy—i.e. ligation and removal of the presumptive hypophyseal region on the second or third day of incubation. Their results, recently confirmed by Kenyon and Watterson (1958), indicate that pituitary removal has no noticeable effect on the pattern of urogenital formation and differentiation. From this, it appears that urogenital development and differentiation is independent of the pituitary. For the chick embryo, the development of the reciprocal, hormonal relation between the pituitary and the gonads remains to be described (for such problems in the rat or rabbit embryo, see Pfeiffer, 1936; Wells, 1951; and Lisk, 1961).

Concerning the influence of extraneous factors on the process of urogenital differentiation, it has long been known that various factors (e.g. humidity, temperature, surgical alterations; see Willier and Yuh, 1928) may exert an influence on the normal pattern of urogenital formation and differentiation in the chick embryo (cf. Gaarenstroom, 1939; Romanoff, 1960). Gaarenstroom (1939) has found that if injections are made prior (on 0–2 days of incubation) to the period of Mullerian duct formation, 1-mg doses of androsterone prevent the formation of the ducts in both sexes. This, however, may represent a pharmacological or nonphysiological action and is here considered to have little relation to the normal process of embryonic Mullerian duct formation. Also, spontaneous modifications or anomalies have been described for the chick urogenital system (see review of Lutz and Lutz-Ostertag, 1959).

Finally, Stoll (1951) and Salzgeber (1955) have demonstrated that increased incubation temperature from the second to the eighth day of incubation will often result in the maintenance of the Mullerian ducts in both sexes. In interpreting experiments concerned with X-irradiation, high-frequency sound wave, or surgical castration of embryos, the possibility that
such “shock” treatments artificially induce atypical maintenance of Mullerian ducts should not be ruled out unequivocally.

Preliminary Conclusions

Involution of Mullerian Ducts in the Male Embryo.—In the male chick embryo, following the formation of the Mullerian ducts, there is a “neutral” period between 6–8 days of incubation, during which the ducts have the physiological competence to respond to either endogenous or injected steroid hormones (Hamilton, 1962). In the normal male embryo, the embryonic gonads (early in the “neutral” period) differentiate into testes (cortical components disappear and medullary components develop). These embryonic testes in turn liberate some substance (referred to by various authors as androgen, testosterone, “masculinizing hormone,” etc.) that passes via diffusion (Wolff and Wolff, 1951) to the Mullerian ducts, and there brings about the involution of the ducts. This substance is defined as a “male” hormone by virtue of its influence on the ducts. Its chemical structure is unknown. By the twelfth day of incubation the ducts have, or have almost, disappeared from the embryo.

The conclusion that an embryonic hormone or modifier is responsible for the “death” of male Mullerian ducts is supported by evidence mainly from classical endocrinological techniques, e.g. in vivo organ transplantation, embryonic castration, injections of hormones. Most recent workers argue that involution of these ducts is a result of hormone action, not hormone interaction. As a result of injections of estrogens into embryos of this sex, retention of Mullerian ducts has been commonly observed, and Wolff (1956) and Stoll (1951) have argued that these injections result in their effects only indirectly via suppression of production of androgen by the males’ embryonic testes. On the other hand, Hamilton (1961) and Groenendijk-Huijbers (1962) have presented evidence for the thesis that exogenous estrogen can prevent, in the male embryo, exogenous androgen or the endogenous “masculinizing” hormone from exerting the “death” influence at the cellular level of the Mullerian duct.

Stabilization and Involution of Left and Right Mullerian Ducts in the Female Embryo.—In the female embryo there is also a “neutral” period during which both Mullerian ducts are responsive to endogenous or exogenous hormones. In the normal female the gonads differentiate into a small right ovotestis and a left embryonic ovary which shows development of cortical components. Both the right and left gonads of the female embryo seem capable of liberating substances that cause, in some unknown manner, the anterior to posterior involution of only the right Mullerian duct. This conclusion is based on results from experiments concerned with castration and either dextral or sinistral hemicastration of female embryos. Attempts to interpret these results have been usually in the context of the results from injections of steroid hormones into otherwise normal embryos (e.g. androgens
inhibit stabilization of the left female Mullerian duct, and estrogens permit maintenance of the two male ducts and reduce the degree of involution of the right female duct). Wolff (1953, 1959) and co-workers have thus concluded for differentiation of the Mullerian ducts in this sex that a hormone produced by the ovaries or ovotestes is responsible for involution of the right Mullerian duct.

This conclusion leaves unanswered the question of why the left female Mullerian duct is not also so affected by the male hormone. Groenendijk-Huijbers (1962) explains this in terms of embryonic secretions of female hormone protecting the left, but not the right, duct from the male hormone. She thus attributes the asymmetrical nature of the differentiation of female Mullerian ducts to a result of each duct possessing a different, embryonic hormonal environment. In contrast, Hamilton (1961, 1962) emphasizes the possibility that the two female Mullerian ducts possess different physiological competences for response to male hormone (or to ratios of combined male and female hormones?).

SOME ENZYMATIC AND NUCLEIC ACID CORRELATES OF INVOLUTION OR STABILIZATION

The evidence reviewed above, and the resulting conclusions, indicate, as Wolff has continually stressed, that the differentiation of Mullerian ducts in the chick embryo is regulated by embryonic hormones. The ducts of the two sexes appear to have different physiological competences for responding to either endogenous hormone secretions or to injected steroid hormones. The same may be valid for the right and left duct of the female. For the female embryo, the involution of the right Mullerian duct suggests that only the right duct responds (by “death”) to the secretions of the embryonic gonads. In the idiom of present-day developmental physiology, the two Mullerian ducts of the female may be considered different in physiological competence (i.e. they possess different biochemical systems). Although this is speculation, this difference may be derived from (1) intrinsic factors such as genetic differences inherent to the tissues themselves, and/or (2) extrinsic factors, such as biochemical stimuli arriving from other embryonic regions at certain stages of development.

One problem in determining how hormones control the differentiation of the Mullerian ducts lies in finding either the enzyme or other biochemical substrate through which endogenous hormones operate. Several difficulties must be recognized.

First, the in vivo results of studies of injections of steroid hormones tell little about the process of normal differentiation. Some difficulties here are as follows: (a) Injected steroid hormones are usually applied to a physiological environment in which endogenous hormones occur and may be co-acting with the injected hormones in ways that are unaccountable; and (b) the metabolic steps are for the most part unknown between the injection of
steroid hormones into the embryo and the observed resulting morphological and biochemical modifications.

Second, the conclusions of *in vitro* analysis cannot be considered conclusive because of the contradictions with *in vivo* results. For example, androsterone treatments, *in vivo*, result in retention of Mullerian ducts in male embryos; certain androsterones, *in vitro*, cause autolysis of Mullerian ducts (Wolff, 1953). Again, injections of estrogen, *in vivo*, tend to permit complete maintenance of Mullerian ducts in males, but, *in vitro*, permit only partial stabilization of the ducts (Wolff, 1953). As a third example, estrogens, *in vivo*, will prevent regression of both Mullerian ducts in the male embryo; however, in the female embryo estrogen injections cannot prevent some involution of the right Mullerian duct—even though studies of experimental castration of embryos (cited above) reveal what (from published reports) appears to be complete retention of both ducts in female as well as in male castrates.

About all that rigorously can be concluded from the *in vivo* and *in vitro* experiments is that exogenous androgens seem to be associated with atrophy of Mullerian ducts, and estrogens with stabilization of the ducts. Studies of combined injections of estrogens and androgens (Hamilton, 1962) suggest that estrogens inhibit action of androgens at the cellular level of the Mullerian ducts. While intracoelomic transplantations of medullary and/or cortical elements of embryonic gonads provide evidence for formation of “intersexes” (e.g. Wolff, 1947; Mintz and Wolff, 1954); such experiments do not provide information about the structure of embryonic hormones.

Wolff and associates—on the basis of experiments described above—postulate that an androgen-like substance activates a proteolytic enzyme in Mullerian ducts, which in turn initiates their involution. They conclude that this mechanism for the induction of involution of Mullerian ducts in the male embryo is the same for induction of involution of the right Mullerian duct in the female embryo. The problem of asymmetrical differentiation in the female, however, is not discussed fully in their papers (see below). The only other experiments having a bearing on this subject are those of Brachet et al., who demonstrated (1958) that there are higher concentrations of certain proteolytic and hydrolytic enzymes in the Mullerian ducts which normally atrophy than in the normally stabilized left female duct. superficially, such results support Wolff's theory that involution of these ducts is a result of androgen-induced activation of a proteolytic enzyme. However, such increases of active catabolic enzymes may simply be the normal result of physiological autolysis, which happens because of other unknown biochemical events occurring in response to embryonic or injected hormones.

**Experiments Correlating Levels of Enzymes and Nucleic Acids with Stabilization or Involution**

**Methods.**—Mullerian ducts at various stages of differentiation were excised from White Leghorn embryos and quick-frozen on aluminum
planchets (preweighed) resting on dry ice. Plates and tissues were then quickly weighed (Sartorius balance). Tissues were then analyzed or stored in a deep freezer for later analysis. By this method, tissue enzyme activity or nucleic acid concentration could be expressed on a per-unit wet-weight basis.

In ribonuclease determinations, a modification of the method of Anfinsen et al. (1954) was used. Briefly stated, 1.0 ml of 1.0 percent yeast ribonucleic acid (Schwarz; purified) in 0.1 M acetate buffer (pH 5.2) was combined with 0.5 ml of the buffer and 10 ml of the enzyme (extract or standard). After incubation at 25° C for 25 minutes, the reaction was stopped with 0.5 ml of 0.75 percent uranyl acetate in 25 percent perchloric acid. After 5 minutes, precipitated substrate was removed by centrifugation at 3,000 rev/min (International centrifuge) for 10 minutes. Then a 0.2 ml aliquot of supernatant was added to 6.0 ml H₂O. This was then examined for optical density at 260 mµ.

Tissue samples were homogenated in 0.1 M acetate buffer (pH 5.2) at 25° C and centrifuged for 25 minutes at 3,000 rev/min. The supernatant (cytoplasmic fraction) was removed and tested. Each original supernatant or extract was divided in two equal portions, and each was either tested immediately by the technique cited above, or tested after dialysis against 4 M urea (12 hours) and then against 0.1 M acetate buffer (pH 5.2; 12 hours). By this method, the ribonuclease content of the cytoplasmic fraction of a particular duct could be tested either for the lyo (active or soluble) state in initial extracts or for the desmo (insoluble or bound) state in extracts dialyzed against urea.

It must be kept in mind that the ribonuclease activity reported later in this paper in Fig. 3 and 4 as "Anfinsen units" represents measurement of an enzyme that splits purified ribonucleic acid (Schwarz) into nucleotides. It appears to be a ribonuclease; verification remains to be completed. Mullerian duct ribonuclease was estimated by comparing the influence of sample extracts on purified ribonucleic acid with the influence of a standard (purified pancreatic ribonuclease) on the same preparation of nucleic acid substrate (see Fig. 2). Thus, the activity of an unknown is tested (method of Anfinsen et al., 1954) and then expressed as "Anfinsen units" equivalent to micrograms of purified ribonuclease required to give, when similarly tested, the same optical density.

For determination of desoxyribonucleic and ribonucleic acids, the methods of Ceriotti (1952) and Ogur and Rosen (1950) were exactly followed.

1) Developmental changes in levels and activity of ribonuclease.—It was decided to check for differences in total cytoplasmic ribonuclease of individual ducts before and during involution. Also, determinations were concurrently made for the states of activity (lyo or desmo) of the ribonuclease. The desmo or insoluble state represents the enzyme in the bound or masked condition (see Hannibal and Nachlas, 1959). For a discussion of lysosomes, an
apparently new category for cytoplasmic particles, the reader is referred to de Duve (1959). When necessary, as at early stages of incubation, corresponding ducts were pooled for amounts of tissue necessary for analysis. Since Brachet et al. (1958) reported values only for ducts at 9–11 days of incubation, it seemed necessary to find the level of ribonuclide of each duct as early as 7.5 days of incubation in order to determine if the ducts possess at

Fig. 2. Influence, as measured by differing optical densities at 260 μm, of purified pancreatic ribonuclease on purified yeast ribonucleic acid (Anfinsen et al. technique, see text). Straight line, fitted by eye, represents standard to which ribonuclease extracts from pooled, "yet uninvoluted" Mullerian ducts are compared (see text).

that time (prior to the arrival of endogenous hormone?) differences in amounts of total ribonuclease.

If Wolff’s theory that an androgen-activated proteolytic enzyme is responsible for the onset of involution is true, then higher amounts of ribonuclease would be expected in those ducts that normally regress, than in the left female duct which normally does not undergo involution. The possibility here is that the ducts that atrophy would have sufficient levels of proteolytic enzyme to respond to endogenous hormones. However, if the atrophy of Mullerian ducts is only an indirect response to hormone action, equal amounts of proteolytic enzyme in the ducts prior to the period of differentiation might be expected. For example, Moog (1952), in a study of the change (from 1 to 7 days of incubation) of alkaline phosphatase in various embryonic organs of the chick, found equal amounts of the enzyme in various undifferentiated tissues. Then, as the various tissues began to differen-
icate, the enzymatic levels changed in the direction (high, low, intermediate) of the levels to be found later in their differentiated counterparts.

Ribonuclease determinations on the basis of activity per 2 mg of tissue were made for Mullerian ducts; these results are summarized in Fig. 3 and 4. It will be seen from these findings that the ribonuclease levels are approximately equal at 7 days of incubation for the right and left duct of each sex. Then, by the ninth day of incubation, the ribonuclease of the male Mullerian ducts and the right Mullerian duct of the female is about three times as great as that of the left female Mullerian duct (Fig. 3). For the three Mullerian ducts which normally degenerate, the total ribonuclease (of "yet uninvolved" tissue) after the ninth day appears to remain the same, although there is a progressive increase in the lyo (and a decrease in the desmo) fraction during the process of involution. For the male Mullerian ducts and the right Mullerian duct of the female, these changes appear identical, except that in the case of the latter the desmo-to-lyo shift is slower or delayed (Fig. 4).

2) Changes in levels of ribonucleic and desoxyribonucleic acids associated with involution or stabilization.—This experiment represents a measurement of the obvious. If Mullerian ducts are undergoing involution as a result of autolysis and necrosis, then it is to be expected that as a result of intracellular digestion (de Duve has aptly referred to lysosomes as representing "suicide sacs") nuclear as well as cytoplasmic materials will be hydrolyzed.

![Fig. 3. Changes in levels of total fractions (bound and soluble fractions) of ribonuclease for Mullerian ducts undergoing either involution (the two male ducts and the right female duct) or stabilization (the left female duct); to show the tissue rise in total amount of ribonuclease for Mullerian ducts "destined to die and in the process of dying," and the absence of such rises for the "living" left duct of the female.](image-url)
Ribonucleic and deoxyribonucleic acid levels have been determined at different periods of incubation for the left duct of the male, prior to and during involution, and for the left duct of the female during its normal "stabilized" development (Fig. 5 and 6).

From determinations of ribonucleic acid and deoxyribonucleic acid in the left duct of the female embryo, it is evident that from the ninth to the sixteenth day there is a small, but consistent, increase in ribonucleic acid, with deoxyribonucleic acid remaining roughly the same per-unit wet weight. For the involuting left duct of the male, declines in the levels of ribonucleic acid and deoxyribonucleic acid are as expected. Determination methods, as here used for these nucleic acids, are too variable to allow more quantitative conclusions. As to the systemic fates of by-products of this intracellular digestion of cells of Mullerian ducts, little is known (are these by-products "resorbed," and do macrophages exert a cleaning influence?).

In any event, these data, along with developmental shifts in levels and activity of ribonuclease (Fig. 3 and 4), serve as a reminder that for sexual differentiation of Mullerian ducts two processes are occurring more or less simultaneously: physiological autolysis of male ducts and the right female duct and normal growth of the left female duct. In addition, it may be that the "caudal" portion of the right female Mullerian duct is growing in a
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Fig. 5. Developmental changes in the tissue levels of ribonucleic acid associated with stabilization (A) or involution (B) of Mullerian ducts. This and Fig. 6 are based on analyses of samples of “yet-uninvoluted” fragments of the ducts (see text for relation between Fig. 3 and 4 and between Fig. 5 and 6). Numbers refer to repeats of the experiment for different samples of the same duct. To show the progressive disappearance of ribonucleic acid in Mullerian ducts undergoing autolysis and involution.

Fig. 6. Developmental changes in tissue levels of desoxyribonucleic acid associated with stabilization (A) or involution (B) of Mullerian ducts. Numbers refer to repeats of the experiment for different samples of the same duct. To show the progressive disappearance of DNA in Mullerian ducts undergoing autolysis and involution.
normal manner simultaneously with the anterioposterior involution of the "cephalic" region. If one measures the length of the right Mullerian duct for female embryos at different stages of development, it becomes clear that the duct regresses in linear dimension from the ninth to about the fifteenth day, and that thereafter the duct increases in length. This increase represents normal overall growth of the cloacal remnant in what appears to be expansion equivalently synchronized with such for the stabilized left female Mullerian duct. It is uncertain, however, whether tissue of the right duct, continuous to the cloaca, is increasing in linear dimension at, say, the eleventh day when the more anterior regions of the duct are well advanced in physiological autolysis (see following experiment).

3) Determination for Mullerian ducts of onset and spread of autolysis.—This experiment was designed to test for the right male and right female duct whether the rises in ribonuclease and soluble ribonuclease fraction are autolytic processes which the various parts of a duct exhibit simultaneously or sequentially.

The right female Mullerian duct, involuting from the anterior to the posterior, and involuting more slowly than its counterpart in the male, is remarkably suited for such experimental analysis of the spread or onset of physiological autolysis. Normal involution of the right (and left) duct of the male embryo is sometimes stated to be posterioanterior, although others (e.g. Gaarenstroom, 1939) have reported a uniform collapse of all parts of the ducts, followed by disappearance spreading away from the middle of the ducts. My observations support those of Gaarenstroom, although anterior remnants of the male ducts persist (12–24 hours) longer than posterior remnants (some aspects of the so-called "male type" of involution are discussed below).

At 9 days of incubation, right female ducts (minus cloacal regions) were excised, quick-frozen on dry ice, cut in half, and the same was done for right male Mullerian ducts. Then, for each sex separately, the anterior and posterior halves were respectively pooled and analyzed for ribonuclease activity. From Table 1 it is apparent that the anterior and posterior halves of the male ducts are roughly equivalent at the same time period in ribonuclease content—both for total and for soluble ribonuclease. Results from analysis of right female ducts, however, demonstrate that—by this time period—the posterior half contains smaller amounts of ribonuclease in the soluble state, but essentially the same amount of total ribonuclease when compared to the anterior half.

Thus, it would seem that during autolysis of the right Mullerian duct of the female, there occurs throughout the duct a uniform rise in total ribonuclease (in the bound or desmo state), and that during involution there is for this enzyme a progressive shift to the soluble state, associated with the anterioposterior involution of the duct. For the Mullerian ducts of the male embryo, such changes seem uniform throughout their tissues.
Preliminary Conclusions on Some Autolytic Aspects of Involution

These findings confirm the work of Brachet et al. (1958) on differences in hydrolytic enzymes of right and left Mullerian ducts of male and female chick embryos differentiating or involuting in the normal manner. On the seventh day of incubation, Mullerian ducts possess approximately the same amounts of cytoplasmic ribonuclease on the basis of unit weight of tissue. During the next 2 days of incubation, the ducts that normally regress (the two of the male and the right of the female) show approximately a threefold increase in total ribonuclease—approximately 90 percent of which is in a bound or unsoluble state. Following this, in male ducts, there is a rapid shift of the ribonuclease from the bound to the lyo or soluble state—correlated with the rapid involution and disappearance of the ducts. In the female embryo the same rise in total ribonuclease is demonstrated only by the right Mullerian duct. The involution, however, of the right female duct is a slower process than in the male, with actual autolysis (release of ribonuclease to the soluble state) originating anteriorly. In this case, the shift of the ribonuclease to the soluble state seems to proceed posteriorly down the duct, followed by actual morphologic involution. In association with this increase in activity of ribonuclease, there is a decrease in ribonucleic acid. The decrease in desoxyribonucleic acid is presumably a result of increased desoxyribo-ribo-ribonuclease activity (cf. de Duve, 1959).

Table 1.—Activity of Ribonuclease Extracted on the Ninth Day of Incubation from Anterior and Posterior Halves of Right Mullerian Ducts of Male and Female Embryos

<table>
<thead>
<tr>
<th>Source of Tissue</th>
<th>&quot;Anfinsen Units&quot; of Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trial No. 1</td>
</tr>
<tr>
<td><strong>RIGHT FEMALE DUCT</strong></td>
<td></td>
</tr>
<tr>
<td>Anterior halves</td>
<td>9.3 (15%)</td>
</tr>
<tr>
<td>Posterior halves</td>
<td>7.8 (6%)</td>
</tr>
<tr>
<td><strong>RIGHT MALE DUCT</strong></td>
<td></td>
</tr>
<tr>
<td>Anterior halves</td>
<td>8.6 (14%)</td>
</tr>
<tr>
<td>Posterior halves</td>
<td>9.9 (17%)</td>
</tr>
</tbody>
</table>

*Explanation: To demonstrate the different, soluble enzymic compositions (in terms of percent of "Anfinsen units" of ribonuclease) of the anterior and posterior halves of the right Mullerian duct of the female embryo. In parentheses is given the percentage of the total activity which is found in the soluble state upon initial extraction. Note the absence of such differences in soluble ribonuclease for anterior and posterior halves of the right male Mullerian duct (see text).*

As mentioned above, progress in research on the mechanism of differentiation of Mullerian ducts in the chick embryo is impeded because of lack of information concerning (a) the chemical nature of the embryonic hormones...
and (b) the biochemical steps through which such endogenous hormones exert their characteristic influences in initiation of, and/or (?) participation in, chemodifferentiation. Below—in a rather pedantic manner—an effort is made to examine the bearing on (a) and (b) of some recent studies, most of which have appeared since 1958. This examination is presented in the form of alternate hypotheses that seemingly satisfy pre-existing data.

The Chemical Nature of the Embryonic Hormones

About this topic, nothing as yet can be said with confidence, and the same seems to hold for related problems in the amphibian or mammalian embryo (cf. Dodd, 1960; Gallien, 1962; Jost, 1960; Price and Pannabecker, 1959; Witschi and Dale, 1962). If it is assumed that the gonads of the chick embryo produce in embryogenesis a hormone that passes through adjacent tissues to the Mullerian ducts—and this is a standard conclusion—then it appears that the hormone concerned is a “diffusion” substance and not an inductor in the classical sense. For the chick embryo, much of the thinking on this topic has been overly influenced by results of injections of steroid hormones into embryos and by studies of gonad transplantations (in vivo and in vitro). Such studies per se do not provide evidence that embryonic hormones are steroidal in structure. The same may be said of studies demonstrating embryonic secretions or presences of steroid hormones (Dale, 1962; Hamilton and Botticelli, 1963). I have recently concluded (Hamilton, 1961: 272) that these embryonic hormones or modifiers may be “estrogenic or androgenic only in the sense that their effect is normal male and female differentiation of Mullerian ducts. . . .”

From an empirical point of view, such a “diffusion” embryonic hormone is expected to be in structure either (a) a steroid, (b) a steroid–protein complex, or (c) a protein. To this list should be added (d) nucleoprotein. This addition is here made not so much on the grounds of supporting experimental evidence as on the basis that such macromolecules provide a rich setting for information-transfer processes in the regulation of metabolic activities at the intracellular level, and thus would help to account (and the same, of course, may be said for proteins) for the apparent varying specificities of different embryonic hormones influencing different, but contiguous, embryonic tissues.

Although no firm stand is here taken, my present tentative view is that the hormones initiating differentiation of Mullerian ducts of the chick embryo are protein or nucleoprotein complexes, and not simple molecules as thought by some workers. This has been argued elsewhere (Hamilton, 1962) on the basis of the following points: (a) The dose levels of injected steroid hormone required (Hamilton, 1962) for “intersex” modifications in urogenital differentiation are usually far greater than is expected for normal physiological operations of these hormones; (b) in gonad transplantation studies, gonadal substances seem to fail to pass from the chorioallantoic membrane to the host urogenital system (Willier, 1927), while in the case of intra-
coelomic grafts of gonadal tissue (Wolff, 1947) the host urogenital system is frequently modified in embryogenesis; (c) from analysis of problems concerned with induction (sensu stricto), the inductors are generally considered to be macromolecules (Grobstein, 1956, 1957). To this list, another point, related to (c), may now be added: (d) Witschi and Dale (1962:360) have raised the possibility—only, however, for sexual, gonadal differentiation—that “antibody-like substances . . . antagonize or completely suppress the development of gonadal structures of opposite sex.” The reaction system these writers consider is a “short distance” one of tissue or cellular contacts involved in induction. In any event, their speculations involve macromolecules of the size order, at least, of proteins, and such conceivably might be involved in the “long distance” problem of the hypothesized, gonad-produced hormone which apparently diffuses to the site of the Mullerian ducts.

Only experimentation can now test the validity of these (a–d) and other possibilities for the structure of the Mullerian duct hormone in the chick embryo. There still remains the problem of whether or not there is more than one such embryonic hormone (see below). There now is a need for screening of extracts—of different molecular components of embryonic gonads—for their in vivo and in vitro influences on the process of Mullerian duct differentiation.

Factors Regulating Sexual Patterns of Differentiation of Mullerian Ducts

This problem relates to the larger one of the factors responsible for the so-called asymmetry of the avian urogenital system (see e.g. Domm, 1924, 1927, 1955; Witschi, 1935, 1939; Willier, 1939; Burns, 1949; Wolff, 1953, 1956). For the Mullerian ducts, the problem is still unresolved, and, considering the multiplicity of factors involved, this is not surprising. To account for sexual and positional differences in the differentiation of these ducts (involution of male ducts, anterio-posterior involution of the right female duct, and stabilization of the left female duct), various workers have sought causal explanations that resort to hypotheses concerned with differences (a) in the hormones or hormone combinations produced by each sex, and (b) in the physiological competences of ducts for different responses to the same hormonal stimulus.

Before discussing three accounts purporting to explain the control of sexual pattern of differentiation of Mullerian ducts, it is useful to examine one theoretical aspect that some workers seem to have forgotten: In interpretation of experimental studies dealing with the matter, the concepts of varying specificities for tissue responses to hormone and varying specificities for hormonal influences on tissues need not be considered as mutually exclusive. Thus, there is no reason, a priori, to demand on general theoretical grounds that either hypothesis (a) or (b) account completely for the pattern of differentiation in both sexes. One or the other—or a combination of the two—might also hold true for one sex and not for the other.
Fig. 7. Photograph of the urogenital system of a genetic male chick embryo (at 18 days of incubation) treated with 100 µg of estradiol on the 5–6 day of incubation. Note the retention of both Mullerian ducts (MD) and the "feminization" of the gonads, and, in particular, the ovary-like, feminized left testes (FT).

Furthermore, if evidence can be found that specific Mullerian ducts have different responses to the same hormones, and if it can be demonstrated that such ducts also are capable of responding differently to different hormones (i.e. evidence for a combination of hypotheses a and b), then the theory may be advanced that within the cells of the Mullerian ducts there occurs a hormone-receptor apparatus demonstrating the potentiality for a "range of responses" (see Witschi and Dale, 1962). This concept or theory has antecedents in the elective theory proposed by Burnet, Lederberg, and Medawar (see e.g. Medawar, 1960). The observation (Fig. 7) that injections of estradiol in male embryos give their Mullerian ducts "a release from the results of evolution and a new lease on life" (i.e. the chance to grow in a manner that only the ancestors of male birds were allowed untold thousands of years in the past) provides some evidence for application of the elective theory in
interpretation of the responses of these ducts to embryonic hormones in embryogenesis.

**Wolff's Interpretation.**—In brief, Wolff (1953, 1956, 1959) believes that a male hormone, one of the androgenic series of steroids, reaches both Mullerian ducts in the male, and there induces degeneration of such ducts. He cites X-irradiation castration and hemicastration studies to show that in the female either the right or the left gonad is capable of producing the hormone responsible for involution of the right duct. He fails to discuss explicitly (as noted by Groenendijk-Huijbers, 1962) the matter of why the left female duct is not also "destroyed" by the hormone so influencing the left duct. In his 1953 review, Wolff's diagram (p. 132) indicates "estrogen" as affecting (by induction of stabilization) the left female duct at a period of time after male hormone has exerted its influence on Mullerian ducts. He favors the idea that Mullerian ducts develop and stabilize (initially at least) in the absence of male and female hormones, and that male hormone is responsible for the involution of the two ducts in the male embryo (and the right duct in the female embryo? See Wolff and Wolff, 1951). Thus, he considers the sexual pattern of differentiation of Mullerian ducts to be a result of single-hormone action on Mullerian ducts of equivalent physiological competence (hypothesis a).

**Groenendijk-Huijbers' Interpretation.**—This worker (1962), concluding mostly from results of surgical castration experiments, takes an approach different from that of Wolff. She states that there are two kinds of involution for Mullerian ducts: a "male-type" involving posterior-anterior regression, and a "female-type" which is anterior-posterior in direction. Reporting that (a) hemicastration and subtotal castration of male embryos result in male-type and female-type regression as well as complete preservation of the ducts, and that (b) estrogen-treated males and left-castrated females show similar female-type patterns of regression, she states that in the female embryo a masculinizing hormone determines the anterioposterior involution of the right duct, while in addition a feminizing hormone protects both the right and the left female ducts from posterior-anterior (male-type) involution. Without discussing in detail how the feminizing hormone can protect (by stabilization) the left duct and not also so affect the right duct, she concludes (1962:13–14) that a "correct balance between the masculinizing and feminizing hormone insures the phenotypic appearance of the female Mullerian ducts."

Concluding, apparently according to hypothesis a, Groenendijk-Huijbers (1962) presents as original her view that the masculinizing hormone is responsible for involution of the right female Mullerian duct. She states (p. 11) that Wolff considers the feminizing hormone to be the reducing agent in this case. However, she cites only his 1950 and 1951 papers, and fails to note his more recent reviews of 1953, 1956, and 1959, wherein he concludes, on the basis of the castration and in vitro experiments, that a hormone
(nature unspecified) of either the right or left gonad is responsible for involution of the right female duct. Implicit in Wolff's 1959 paper is the idea that male hormone is responsible for involution of the right female Mullerian duct.

Groenendijk-Huijbers thus considers the sexual pattern of differentiation of Mullerian ducts to be a result of sexual differences in embryonic hormone combinations, and that appropriate balances or ratios of feminizing-to-masculinizing hormones regulate posterioanterior involution of ducts in the male and anterioposterior involution of the right duct in the female. Her interpretation differs from that of Wolff by (a) the postulation of a role for two, not one, embryonic hormones and by (b) the belief that direction of involution is determined by hormone interaction (i.e. male-type when masculinizing hormone is predominant in amount to feminizing hormone and female-type when such levels are reversed).

Hamilton's Interpretation.—The writer's view (Fig. 8) of the controlling, sexual mechanisms for differentiation of Mullerian ducts has been expressed in previous publications (Hamilton, 1961, 1962) and may be stated in very simple terms:

Since injections of estrogens into female embryos tend not to prevent some involution from the anterior of the right Mullerian duct, and since Wolff and others have found that in cases of embryonic hemicastrations of right or left gonad the right duct of the female will still undergo involution, there is some evidence that the right duct of the female has a lower threshold for response to the endogenous hormone (presumably the masculinizing hormone) than does the left duct. Wolff (1959) reports that male and female ducts, when excised before exposure to the endogenous hormones, are stable in an an hormonal in vitro environment for a period of time beyond that expected for their in vivo degeneration. Such findings suggest that the pattern of sexual differentiation of Mullerian ducts is a result of (a) embryonic hormone action, not interaction, of (b) different physiological competences between the right and left female ducts, and of (c) different physiological competences (in threshold of responses to the masculinizing hormone) between male ducts and the right female duct.

The latter point (c) requires further clarification. Although the absence of information on the structure, quantity, and timing of influence of the endogenous, masculinizing hormone (i.e. the Mullerian duct hormone or male hormone referred to earlier in the paper) demands tentative conclusions, results from quantitative studies of injections of steroid hormones reveal that a higher estrogen dose level is necessary for retardation of involution of the right female Mullerian duct than for complete preservation of the two ducts in the male embryo (see Hamilton, 1961). The dose of exogenous androgen required to induce atypical degeneration of the left female duct must be far greater in quantity than that of endogenous masculinizing hormone which apparently "kills" the ducts in the male. This is additional evidence for dif-
Fig. 8. Schematic diagram of factors that are thought to regulate sexual differentiation of Mullerian ducts (a modification of that used by Wolff, 1953, 1956). To show (a) the hypothesized development of androgen-inhibited hormone receptors in the two male and right female ducts; (b) the stabilization of the left female duct by means that seem independent of hormones; and (c) the rise and release of catabolic enzymes in the Mullerian ducts "destined to die." Arrows of broken lines denote for the female embryo possible actions of hormones which have yet to be proved or disproved by experimentation. Embryonic hormones (male, female) are defined on the basis of their operations, and thus their substantive properties are unknown.

It is obvious that a healthy state of disagreement exists. Wolff, in recent papers, emphasizes the "death-inducing" action of male hormone on male Mullerian ducts and the action of an unspecified, but presumably male hormone on the right female duct (viz. hypothesis a involving hormone action, not interaction). His concept may be criticized for lack of consideration of why the left female Mullerian duct is not also so influenced by the hormone
in operation on the right duct. Groenendijk-Huijbers places great weight on the possibility that direction of involution of Mullerian ducts is a result of specific balances of female and male hormones, and that a certain ratio of the two hormones results in the female phenotype for normal differentiated ducts (viz. hypothesis b involving hormone interaction). Her interpretation may be criticized for (a) failing to account for how the “proper” balance of the two hormones can protect the left female duct completely without also so protecting the anterior portions of the right duct and for (b) failing to consider that Wolff and co-workers have found that female as well as male ducts “stabilize” in a hormone-free environment (in vitro as well as in vivo).

My theory (1961 and 1962) notes the “range of hormone responses” inherent to Mullerian ducts, and emphasizes, for the male embryo, the “death-inducing” operation of the male hormone and, for the female embryo, the possibility of a differential in competence between the right and left duct for response (by “death”) to the gonadal hormone, which is presumably the same hormone produced by gonads in the male embryo. This represents hypothesis b with the assumption that induction of “death” and involution of Mullerian ducts is a result of hormone action, not interaction. It may be criticized on the grounds that the differential in competence for female Mullerian ducts is an inference based on results of injections of exogenous hormones. Certainty about this awaits either (a) experiments for otherwise normal females demonstrating that a hormone produced by the right and/or left gonad reaches the two Mullerian ducts and induces degeneration of only the right duct or (b) experiments for otherwise normal females showing that male and female hormones produced by the gonads reach both ducts (see Fig. 8). In this case, it would be evident that at the cellular level the female hormone can override the “death” influence of the male hormone for local reactions at the left, but not the right, Mullerian duct. Demonstration of the latter (b), while confirming my concept of different competences for right and left female Mullerian ducts, would negate—for the female embryo—my and Wolff’s contention that regulation of pattern of differentiation is initially a result of hormone action. It would thus support that part of Groenendijk-Huijbers’ thesis which states that stabilization of the Mullerian duct is due to hormone combination, but not the part which deals with direction of involution, or inception of involution of the right duct, being a function of hormone balance.

The Mechanism Whereby Hormones Bring about Involution or Stabilization: A Problem Still Unresolved

Attention is here directed to some alternate hypotheses concerned with the biochemical steps through which androgens or the embryonic hormones induce autolysis and involution of Mullerian ducts. This is mostly conjecture based on the little data relevant to, and available for, the problem. This is not to say, of course, that these are the only hypotheses now being consid-
tered. Rather, these represent ideas that can be experimentally tested, and such are now being attempted in my laboratory.

Conclusions from in vitro organ cultures.—In an attempt to determine the processes through which androgens initiate in vivo involution of Mullerian ducts, Wolff and associates (see Wolff, 1959, for details and other references) have demonstrated that undifferentiated Mullerian and Wolffian ducts, when maintained in vitro, will remain apparently normal and maintain their organization for about five or six days. If these ducts are cultured in the presence of androsterone, the Mullerian, but not the Wolffian, ducts undergo rapid autolysis and involution. These workers place much emphasis on the action that androgen exhibits in such cases, and argue for the hypothesis that endogenous male hormones, secreted by the gonads, activate or evoke a proteolytic enzyme in Mullerian ducts—an activation or evocation which thereby causes involution and degeneration of the ducts.

Two problems, however, are unsatisfied by this hypothesis. (a) While in vitro studies demonstrate that the undifferentiated Mullerian ducts are capable of responding (by degeneration) to androsterone, there is some evidence that estrogens will induce partial degeneration of Mullerian ducts (see Wolff, 1953:127). This suggests that the in vitro response of undifferentiated Mullerian ducts to steroids may not be completely specific, insofar as estrogenic and androgenic differences are concerned. Also, no one has yet studied the effects of steroids on the right Mullerian duct of the female when it is maintained in vitro immediately after the in vivo loss of competence to respond to androgenic stimulation. The degree to which such in vitro studies can be relied upon for giving information about in vivo metabolism remains to be established. (b) As stated previously in this paper, the cells of tissues undergoing autolysis and necrosis normally release hydrolytic and proteolytic enzymes. Therefore, the “activation” of a proteolytic enzyme by androgen, as postulated by Wolff and co-workers, may be only a result—not cause—of the degeneration of Mullerian ducts.

Conclusions from Studies on the So-called Mechanism of Steroid Hormone Action.—As to the specific enzymes through which hormones influence Mullerian duct differentiation, no conclusions of a positive nature can be made from data now available. However, some inferences can be drawn in the light of the findings of endocrinologists and biochemists attempting to correlate hormone action with either the mechanics of enzyme activity (see e.g. Pincus, 1955; Hechter, 1955; Hagerman and Villee, 1957; Jensen and Jacobson, 1962) or the synthesis of rate-limiting enzymes (see Mueller, 1960).

It seems best to consider the hormonal control of urogenital differentiation not as a special problem, but rather as the old one of the role of enzymes and substrates involved in hormone action. Many of the in vitro studies of the effects of hormones on tissue slices or homogenates have demonstrated that both androgens and estrogens may act to inhibit respiratory processes
Recently, Yielding and Tomkins (1959) have demonstrated enzyme preparations that facilitate the oxidation of reduced diphosphopyridine nucleotide (DPNH) and are inhibited almost completely by minute amounts of many steroids (including androgens, estrogens, and diethylstilbestrol). Their studies on dehydrogenase activity are of interest in comparison to those of Villee and Talalay and their respective associates (for references, see Hagerman and Villee, 1957), who have found mammalian dehydrogenases (extracted from placental tissue) which—in affecting hydrogen transfer between reduced triphosphopyridine nucleotide (TPNH) and DPN—are accelerated by certain (but not all) hormones with estradiol-17β being the most effective. It would appear (see Hagerman and Villee, 1957: 321–324) that the estrogen-sensitive enzyme system of the placenta is one which transfers hydrogen ions and electrons from reduced TPN to DPN. Such conclusions have been extended, analogously, by Baron et al. (1960) to the study of androgenic stimulation of the prostate gland; they find that there is an androgen-activated transhydrogenase present in rat and human prostatic tissue that promotes oxidation of DPNH. The prostate transhydrogenase was quite specific, with the rate of transfer being increased twofold by androsterone and unaffected by estradiol.

Yielding and Tomkins (1959) studied enzyme extracts taken from a variety of tissues, none of which are normally stimulated to growth by the action of steroids. In contrast, the studies of Villee, Talalay, Baron, and their co-workers involved the use—in each case—of enzyme extract from tissues which normally show marked growth responses as a result of steroid stimulation. Pincus has also reviewed (1955:676) some in vitro studies of the effects of steroids on respiration and enzymes; in most cases of either inhibitory actions or lack of effect, the tissue being examined was one that normally does not show a specific growth response to steroid stimulation. Thus, a wide array of de- or transhydrogenases—apparently of varying specificities—occur in tissues, and these may be important factors controlling tissue responses to either different or comparable hormones. For tissues that normally show specific growth responses to steroid stimulation, then, steroid-influenced de- or transhydrogenases may be expected, and this provides a precedent for the idea (see below) that Mullerian ducts contain an unknown, androgen-inhibited, estrogen-stimulated hormone receptor.

Speculations about Steroid Hormone Influences on Mullerian Ducts.—Lacking knowledge of the chemical structures and concentrations of the endogenous hormones responsible for differentiation of Mullerian ducts, the following hypothesis is offered for what it is worth in consideration of how injected steroid hormones influence the developmental fates of Mullerian ducts by "activating" or "inhibiting" a hypothetical intracellular receptor. It is hoped that this may represent an approach which will serve analogously for future work on the mechanism of operation of the endogenous hormones.

1) Since estradiol promotes the maintenance and growth of Mullerian...
ducts in male embryos, the presence of an estrogen-activated steroid receptor may be postulated for the undifferentiated ducts of the male and the left duct of the female embryo. The fact that estrogen injected into female embryos normally does not prevent some involution of the right Mullerian duct indicates the possibility for this duct that the threshold for activation of the estrogen receptor is relatively high or that the estrogen receptor is lacking. Either of the latter possibilities, if true, would help to explain why a hormone produced by the female gonads could induce degeneration of the right (but not the left) Mullerian duct in the presence of another hormone promoting maintenance of the left duct.

2) Since male Mullerian ducts respond to an embryonic hormone by undergoing autolysis and involution, one may postulate the presence of a steroid receptor that is inhibited by androgens. Since the left Mullerian duct of the female embryo will undergo degeneration only after androgen treatment of relatively large doses, its steroid receptor can be considered to have a high threshold for inhibition by androgen. The right Mullerian duct of the female, being less estrogen-sensitive or more androgen-sensitive, can then be thought to have a low threshold for androgenic inhibition of the steroid receptor.

3) Thus, on an empirical basis, the Mullerian ducts of the chick can be envisioned as possessing—at the intracellular level—a steroid receptor or substrate that determines the particular responses of Mullerian ducts to steroid hormones. In general, the receptor would appear to be androgen-inhibited and estrogen-activated. Although specific Mullerian ducts seem to react to hormones in ways that differ in degree but not kind of response, this does not detract, at a first order of explanation, from the concept of the steroid-sensitive receptor—if it is postulated that varying specificities (viz. varying organizations at the molecular level) for the receptor account for the influences that are exerted on it by various concentrations of injected androgens and/or estrogens.

4) For experimental purposes, it is necessary that such a model account for (a) the various effects that injected steroid hormones have on the differentiation of Mullerian ducts and (b) the differential responses of Mullerian ducts to the same hormones or hormone combinations. About the first requirement (a), it can be said that most estrogens tested to date result in male embryos in retention of Mullerian ducts, and that most androgens, while inducing degeneration of the left female Mullerian duct, do not interfere with involution of these ducts in male embryos. Exceptional, however, is the androsterone class of steroids. While inducing degeneration of the left female Mullerian duct, these steroids are remarkable in that, for results of injections of large doses in male embryos, they resemble estrogens by “permitting” atypical retention of Mullerian ducts. Some workers have attributed this to a male–female differential in response to a particular androgenic configuration. This seems unlikely since Wolff (1959) notes that androste-
rone has an \textit{in vitro} influence on Mullerian ducts comparable to that of testosterone in \textit{in vivo} responses (i.e. induction in the ducts of autolysis and involution). Furthermore, I have found (1961) that extremely large doses of injected androsterone are necessary for such “feminizations” of male embryos. This, of course, raises the possibility that the male embryo has the capacity (in the liver where other steroid conversions are known to occur?) to convert small amounts of the exogenous androsterone to the estrogenic, phenolic series of steroids. If this reaction occurs, it means that small amounts of estrogens can “stabilize” Mullerian ducts at their cellular levels by overriding or suppressing the operation of endogenous male hormone as well as the operation of a large concentration of exogenous androsterone. This point has previously been concluded from results of injections of combinations of large doses of androgen and small doses of estrogen (Hamilton, 1961).

Concerning the second requirement (b), there is at present no certain means of detecting differences (or similarities) between Mullerian ducts (e.g. the right and left duct of the female embryo) for hormone responses of their respective steroid receptors. A good inference for a differential in steroid-receptor specificity (restated: a differential in physiological competence for response to embryonic hormones) can, however, be taken from the studies of Morgan and Greb (1958). These workers have found, via inbreeding experiments in chickens, evidence for genetic control of degree of involution, i.e. they have found a genotype or mutant which in some way lengthens the right Mullerian duct of the female. The inference, however, must be ruled out if it is subsequently shown that such morphologic adjustments to shift in genotype represent increased growth of the cloacal remnant (see Fig. 1), and not a decrease in the competence or ability of the duct to respond (by “death”) to the embryonic hormones. In any event, the hypothesis of a genetic control for specificity of the steroid receptor provides a means for explaining both sexual and positional differences in competence for response to hormones.

5) The suggestion has been made (Wolff, 1953) that androgen or male hormone either activates or evokes a proteolytic hormone which then causes regression of the ducts. In 1959, Wolff modified this by suggesting that the male hormone (a) induces necrosis of Mullerian ducts and, at the same time (b) “determines the formation” of a proteolytic enzyme which carries out a rapid autolysis of the duct. The data presented previously in this paper provide evidence for a rise in inactive ribonuclease between the seventh and ninth day of incubation. \textit{Presumably}, this represents protein synthesis induced by the male hormone. This is not certain since as yet there is no evidence to show that Mullerian ducts in an \textit{in vitro}, hormone-free environment fail to exhibit a rise in inactive or bound catabolic enzymes, such as ribonuclease.

As to the inceptive means whereby androgens induce autolysis and necrosis of Mullerian ducts, several alternate possibilities exist:
a) Androgens may exert a "toxical" influence on the ducts (Wolff, 1953);
b) Androgens may suppress respiration via interference of the oxidative enzymes associated with the Kreb's cycle and the cytochrome system (see Hamilton, 1962, and below); or
c) Androgens may inhibit protein synthesis.

Each of these possibilities would lead to autolysis and release of proteolytic and hydrolytic enzymes, and experiments are now needed that can test the respective validities of these possibilities. Incidentally, if it is assumed that steroid hormones simply simulate some of the effects of the endogenous hormones, and if it is assumed that the latter are macromolecules of the order of proteins, then there is a possibility that the "controlled" sexual and positional (for the female) degenerations of Mullerian ducts represent (d) the operation of "antibody-like mechanisms" in a manner comparable to that hypothesized by Witschi and Dale (1962) for gonad differentiation.

As to the mechanisms whereby estrogens, in vivo, induce stabilization of Mullerian ducts, hypothetical counterparts to the above may be listed:
a) Estrogens may present "toxical" influences;
b) Estrogens may promote respiration by stimulatory influences on oxidative enzymes and substrates;
c) Estrogens may stimulate protein synthesis; or
d) Estrogens may suppress "antibody-like" mechanisms which otherwise would lead to degeneration.

6) Finally, it is useful to remark, for model purposes at least, that the hypothesis of an androgen-inhibited, estrogen-stimulated steroid receptor for Mullerian ducts provides an explanation for the various effects of hormones on these tissues as well as for the various responses of tissues to hormones. Whether the steroid receptor represents a particular unit of protein synthesis or a regulatory enzyme complex (e.g. steroid trans- or dehydrogenase complexes), genetic control of its "specificity" is conceivable, and comparable considerations may be useful if it is soon found that the embryonic hormones operate directly or indirectly via influences on nucleic acids.

CONCLUSIONS ON THE HORMONAL CONTROL OF SEXUAL DIFFERENTIATION

In the chick embryo, beginning about the ninth day of incubation, sexual differentiation of Mullerian ducts begins—insofar as morphological changes are concerned. These sexual differentiations involve the degeneration and involution of the two ducts of the male embryo, and of the right duct of the female embryo. The left female duct is stabilized as the organ that will be the functional oviduct in the adult bird.

Such sexual differentiations are initiated by embryonic hormones produced earlier by the gonads. The exact time of arrival of these hormones at the
sites of the Mullerian ducts is uncertain, but between the seventh (while these ducts are still in process of formation!) and the ninth day is the expected range of this time period. The male and female ducts "destined to die" show, prior to the ninth day of incubation, a marked rise in proteolytic and hydrolytic enzymes. These may represent the lysosomes or "suicide sacs" as described by de Duve, Brachet, and others. For ribonuclease, there is evidence that the initial rise represents an increase of the enzyme in the bound or inactive state (see above). During the process of degeneration and involution of these ducts, these tissues show for this hydrolytic enzyme a progressive release from the inactive to the active state. Associated with this release is a progressive decline in tissue levels of ribonucleic and desoxyribonucleic acids. The systemic fates of the by-products of such autolytic processes are unknown.

Undescribed embryonic hormones or androgens seem to initiate these initial rises in levels of inactive proteolytic and hydrolytic enzymes (cf. Brachet et al., 1958). Since such rises begin shortly after the seventh day, and since it is thought by some workers that embryonic hormones initiate their "death" influences about the ninth day (time of onset of morphologic involution), the possibility cannot be ruled out that these ducts autodifferentiate, or differentiate under influence of some other intrinsic factor prior to the arrival of the embryonic hormone responsible for induction of autolysis and degeneration. If this is true, then the initial rises in inactive, catabolic enzyme may be considered as "metabolic preparation for death," and examples of pre-functional shifts in levels of tissue enzymes are not unknown for the chick embryo (see discussion above of the work by Moog, 1952).

The causes of the sexual patterns of Mullerian duct differentiation are still not certain. For the male embryo, one hormone (the male or "masculinizing" hormone) seems responsible for their normal involutions, and in the female embryo, either one or two hormones may be exerting influences. However, since Wolff has evidence suggesting that Mullerian ducts stabilize in a hormone-free, in vitro environment, the role of one hormone is sufficient to explain the initiation of involution of these ducts. Hamilton (1961) and Groenendijk-Huijbers (1962) attribute involution of the right Mullerian duct of the female embryo to the influence of the same hormone that is correspondingly operative (i.e. the male hormone) in the male embryo. The former worker emphasizes differences in physiological competences of right and left ducts, and the latter emphasizes different combinations of male and female hormones, for explanation of the asymmetrical differentiations of Mullerian ducts in the female embryo.

Evidence for a differential in competence for response to the same hormone (or hormone combination!) by female Mullerian ducts may be found in the genetical conclusions of Morgan and Greb (1958). Such evidence, although still not precise (see above), is useful in explaining the "range of responses" to hormones which Mullerian ducts exhibit. It is remarkable that
these ducts in the male embryo can respond to exogenous estrogen or androgen, or appropriate combinations of the two, by "living" or "dying." Empirically, there is evidence of an estrogen-stimulated, androgen-inhibited steroid receptor in the cells of Mullerian ducts, and the concept of genetic control of the specificity of this hypothesized receptor is useful to explain for these ducts sexual and positional differences in physiological competences, as manifested by different responses to injected hormones.

The nature of the intracellular interaction between receptor and hormone is unknown, as is, of course, the receptor itself. While a variety of possibilities has yet to be ruled out by experimentation, there is some support from theoretical endocrinology for the idea that the hormones influencing the differentiation of Mullerian ducts exert their characteristic influences via stimulations and inhibitions of either (a) oxidative enzyme mechanics or (b) synthesis of key enzymes controlling normal cellular activities. The latter, of course, refers to influences on sites of protein synthesis or to influences on genetic factors (cf. Clever and Karlson, 1960) which, in turn, then regulate or modify protein synthesis.

In any event, either of the above speculations (a, b), or those cited earlier in the paper might conceivably lead—in the case of inhibitory actions—to physiological autolysis of Mullerian ducts, to a critical lowering of intracellular pH values, and, thus, to the expected release of hydrolytic and proteolytic enzymes. Whether androgen or the male hormone directly (Wolff, 1959) or indirectly (Hamilton, 1962) promotes the shift of catabolic enzymes from the inactive (bound) to the active (soluble) state is still uncertain.

From these conclusions, it seems safe to generalize that morphologic involution (and stabilization?) of Mullerian ducts in the chick embryo is a result of preceding chemodifferentiational processes initiated by the influence of hormones produced by the embryonic gonads. Sexual differences in the pattern of such differentiations (chemical as well as morphological) may be attributed to different genetically controlled competences for responses to hormone as well as for sexually different "urogenital environments" of concentrations of hormone and/or (?) hormone combinations. While a little is known of the roles of exogenous or extrinsic hormones for such differentiations, and something is known of the physiological results of these differentiations, almost nothing is known of the important intermediate step concerned with the mechanism of hormone—intracellular receptor interaction responsible for the inception of chemodifferentiation. Future progress on this problem awaits description of the chemical nature of the embryonic hormones and of the intracellular substrates or receptors of Mullerian ducts which apparently have "built in" a variety of responses to extrinsic hormonal stimuli. Only then can efforts—other than speculations as here presented—be made to theorize rigorously on the ways genetic factors can control specificity of such cellular responses to hormones.
ACKNOWLEDGMENTS

I wish to express my gratitude to Ernst Mayr and Frederick L. Hisaw. These critics and scientific logicians have extended to me the particular kinds of assistances and inspirations for which they are well known. In addition, I acknowledge my intellectual debt to the studies and writings of Étienne Wolff. My query of certain conclusions by Wolff (e.g. whether androgen leads to release of catabolic enzymes in Mullerian ducts by indirect rather than by direct means, see text) represents, for the most part, emphasis of different, but alternate hypotheses, and as such is presented in the vein of delightful scientific disagreement.

Thanks are also due to many others, among who only a few are: C. Botticelli, P. F. Spahr, John Enders, R. H. Barth, Jr., Mrs. M. Williams, W. J. Bock, Mrs. Pauline West, and Mrs. Joyce Todd.

This study was supported by R.G. 8871 of the Division of General Medical Sciences, National Institutes of Health, U.S. Public Health Service, and represents part IV in a series of studies dealing with the physiology of urogenital differentiation in the chick embryo.

SUMMARY

A review is made of the evidence (results from injections of steroid hormones, in vivo and in vitro transplantations, embryonic castrations, and so forth) which supports the conclusion that in the chick embryo hormones produced by the gonads are responsible for initiation of sexual differentiation of Mullerian ducts. The chemical structure of these embryonic hormones is still uncertain. While it is usually thought that such embryonic hormones are steroidal in structure, some evidence points to the conclusion that they are macromolecules of a size greater than that of steroids. The possibility is emphasized that injected steroid hormones simply "mimic" or simulate the actions of the endogenous hormones. Among others, one point supporting this conclusion is the observation that large, nonphysiological doses of steroid hormones must be injected for modification of normal patterns of differentiation.

For explanation of the asymmetrical nature of the female Mullerian duct system, the hypothesis is favored which suggests that the right female Mullerian duct is suppressed by male hormone produced by either gonad, and that the left duct initially stabilizes in a manner that is initially independent of embryonic hormones. Mullerian ducts (and particularly those of the male embryo) appear to have "built in" (genetically presumably) a "range of responses" to hormones. Thus, male ducts either "die" under influence of androgen or male hormone, or "live" under influence of estrogen, and it is remarkable that such tissues can show such a marked range of activities (involving catabolic or anabolic processes) simply as a result of response to different steroid configurations.

Starting with the assumption that knowledge of the mechanism of steroid
actions and interactions on these tissues may prove useful in understanding the process of chemodifferentiation of Mullerian ducts, an intracellular steroid receptor is hypothesized. This may represent an influence on either molecular activity or synthesis. One possibility for the latter involves specific influences on nucleic acids which in turn control protein synthesis. The receptor is considered to be androgen-inhibited and estrogen-stimulated. Varying specificities of the receptor are thought to account for the different thresholds of specific Mullerian ducts to particular hormones and hormone combinations. Thus, for the female embryo, the right duct (which normally atrophies) appears to have a low threshold for androgen inhibition and a high threshold for estrogen stimulation, while the left duct seems to have a low threshold for estrogen stimulation and a high threshold for androgen inhibition.

Evidence is presented that in the Mullerian ducts "destined to die" there is a pre-involution rise in the hydrolytic enzyme ribonuclease (presumably true for some other catabolic enzymes). The initial enzyme rise in the two male and right female ducts (from 7-9 days of incubation) is approximately 300 percent over that of enzyme levels in the left stabilizing duct of the female. This "new" enzyme is mostly (about 90 percent) in the inactive or bound state. It is uncertain whether the protein synthesis of these enzymes contained in "suicide sacs" is induced by the male hormone or by other factors either intrinsic or extrinsic to the ducts. Following the rise in inactive enzyme, physiological autolysis occurs in the "ill-fated" ducts. Morphologic involution of the ducts occurs, and associated with its onset is a progressive shift in catabolic enzyme from the inactive to the active state. Data are presented to indicate that during autolysis and involution of the ducts, levels of ribonucleic acid and desoxyribonucleic acids decline on a basis of per-unit weight of "yet uninvoluted" tissue. Ribonuclease and desoxyribonuclease are apparently responsible for this, and is further evidence that for these ducts chemodifferentiation precedes morphologic differentiation.

Evidence is presented that for the right Mullerian duct of the female (which normally undergoes anterioposterior involution) the initial rise in active ribonuclease occurs throughout the length of that duct (except for the region contiguous with the cloaca), and that the progressive shift to the active state begins at the anterior end and passes, during a period of several days, posteriorly in what appears to be a "wave" of increased rupturing of lysosome membranes. This is interpreted as further support for the theory that, for the two male and right female Mullerian ducts, the factors bringing about metabolic preparation for autolysis (rise in levels of inactive catabolic enzyme) may precede (and be independent of?) the factors that initiate the onset of autolysis.

It is thus concluded that sexual differentiation of Mullerian ducts in the chick embryo proceeds through a series of genetically determined stages during which competence to hormones is acquired or is lacking depending upon
the specificity of the intracellular hormone receptor. In terms of a "range of responses," discovery of the structure of this receptor—which seems capable of giving life or death to tissues depending upon slight differences in molecular structure of steroid hormones—may provide valuable information on basic mechanisms involved in the chemodifferentiation of embryonic tissues.

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The Physiology of the Avian Interrenal Gland: A Review

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The literature concerning the avian adrenal gland has been reviewed by Hartman and Brownell (1949), Sturkie (1954), and Chester Jones (1957). The objective of this review is to present the current status of our knowledge concerning the avian adrenal (interrenal) gland by reference to some of the earlier papers that have significantly advanced our understanding of this endocrine organ, and by reference to many of the reports that have appeared since the publication of the monograph on the adrenal cortex by Chester Jones (1957).

ADRENAL HISTOLOGY AND HISTOCHEMISTRY

Detailed studies of the anatomy and histology of the avian adrenal include those of Uotila (1939) and Kar (1947a, 1947b) concerning the domestic chicken (Gallus domesticus) and Miller and Riddle (1942) on the domestic pigeon (Columba livia). Hartman and his co-workers (Hartman, 1946; Hartman et al., 1947; Hartman and Brownell, 1949; Knouff and Hartman, 1951; Hartman and Albertin, 1951) described the adrenals of over 400 wild avian species. The adrenals of birds are encapsulated organs located medially and dorsally against the cephalic pole of the kidney and immediately posterior to the lungs. The gonads are ventral to, and largely obscure, the adrenals in gross dissection. The adrenals are generally separate, but in some species, for example the American Stork (Euxenura manguari) and the Bald Eagle (Haliaeetus leucocephalus), they are fused to a greater or lesser degree; within other species, for example the Herring Gull (Larus argentatus), Hairy Woodpecker (Dryobates villosus), and California Quail (Lophortyx californicus), both conditions prevail (Hartman and Brownell, 1949; Flickinger, 1959).

The avian adrenal gland is not organized into a defined cortex and medulla as is characteristic of the eutherian mammal; rather the interrenal (cortical) and chromaffin (medullary) tissues are intermingled throughout the gland. The amount and pattern of distribution of the two tissue types vary with the species and do not appear to bear a consistent relationship. In species with a high proportion of interrenal tissue, such as the Brown Pelican (Pelecanus occidentalis), the chromaffin tissue is represented as islets of various sizes scattered throughout the interrenal tissue; in species with a high ratio of chromaffin to interrenal tissue, such as the Black-throated Green Warbler (Dendroica virens), the chromaffin tissue is present as an interconnecting meshwork within the interrenal tissue, extending to the periphery of the gland (Hartman and Brownell, 1949).

1 The survey of literature pertaining to this review was concluded in June 1962.

Proc. XIII Intern. Ornithol. Congr.: 1041–1058. 1963
The interrenal tissue is organized into solid cylinders which appear in cross section as oval structures composed of closely packed prismatic cells. In longitudinal section, the tissue appears as cords of cells, each cord composed of a double row of tall columnar cells, the long axis of which lies perpendicular to the cord. The nucleus of each cord cell is displaced toward the end of the cell adjacent to the center of the cord. This results in the nuclei being arranged as a double row along the center of the interrenal cord. The end of each cell borders on a blood sinus. The interrenal cords are most commonly arranged as a meshwork of anastomosing cords in the central region; the cords radiate out to loop under the capsule. This arrangement gives the appearance of a central network and a peripheral looped (subcapsular) region. In the subcapsular region, the cells are large, oval or round in shape, present in masses, and possess considerable cytoplasm, with the nuclei having diffuse chromatin. In the central region, the cells are smaller and elongate, and the nuclei are smaller and have more compact chromatin.

The adrenal glands are heavily vascularized with sinusoids occurring extensively between the interrenal cords and between the interrenal cords and the chromaffin tissue. Large blood sinuses are commonly found in the central region of the gland, but may be present peripherally, particularly in the subcapsular region. Electron-microscope examination of the chicken adrenal has revealed a perisinusoidal space between the basement membrane of the endothelial cell and the interrenal cell (Fujita, 1961). An interparenchymal space also exists, particularly between the interrenal and chromaffin cells. Substances secreted by the adrenal may first enter these spaces and then pass to the vascular system.

The mode of cell replacement and perpetuation of the interrenal tissue of birds remains questionable and has not been investigated extensively. The “escalator” theory proposed for the origin and perpetuation of mammalian cortical cells (cf. Chester Jones, 1957) similarly was believed applicable to the pigeon (Miller and Riddle, 1942). In the Brown Pelican, the cords immediately beneath the capsule are expanded, and these expansions often bend inward between other radiating cords, suggesting to Hartman and Brownell (1949) a method of formation of additional cords. The recent work of Miller (1961) only partially supported this view of peripheral cell replacement and suggested instead that the potential for division resides in all of the interrenal cells. Stimulation of the interrenal with formaldehyde or insulin resulted in hypertrophy and hyperplasia which were confined to the peripheral ends of the cords; however, in glands stimulated to a greater degree, the hypertrophy and hyperplasia were general throughout the gland.

Histological zonation of the interrenal, characteristic of eutherian mammals, is absent from the avian adrenal. The single exception is represented by the Brown Pelican wherein, according to Knouff and Hartman (1951), the interrenal tissue shows zonation similar in position and appearance to the zona glomerulosa, zona fasciculata, and zona reticularis of mammals; how-
ever, the relative proportions differ with the zona fasciculata being reduced or absent in the pelican.

Recent histochemical studies of the interrenal tissue of the domestic pigeon by Sinha and Ghosh (1961) demonstrated a distinct cytochemical zonation within the interrenal tissue. Neutral lipids are most abundant in the subcapsular region and moderately abundant in the central region. Cholesterol, ascorbic acid, alkaline phosphatase, and "corticoids" show a reverse zonation with respect to the neutral lipids, these being more abundant in the central region. Sinha and Ghosh emphasize that caution need be applied to the cytochemical demonstration of "corticoids" until such time as the specificity of the ferric chloride Schiff method (Khanolkar et al., 1958) is established. A similar distribution of neutral lipids was reported for the domestic chicken and the duck (Anas boschas) (Arvy, 1961). These observations have been extended to compare the distribution and concentration of sudanophilic lipids, cholesterol, and alkaline phosphatase in the subcapsular and central regions in 11 species of birds from 8 orders (Ghosh, 1962). The cytochemical zonation demonstrable in the pigeon occurred in some species, in others it was only partially differentiated, and in some species no zonation was evident. Fayez and Rappay (1961a, 1961b) have also demonstrated the presence of neutral lipids, cholesterol, and phospholipids by cytochemical methods in the interrenal of the domestic chicken and the domestic pigeon. Both Sinha and Ghosh (1961) and Fayez and Rappay (1961a, 1961b) were unable to demonstrate ketosteroids by cytochemical methods. As pointed out by these authors, the methods presently available employing the plasmal, pseudoplasmal, and 2,4-DNPH reactions are widely in dispute (Pearse, 1960).

The cytochemical demonstration of zonation and the histological appearance of a central and a subcapsular region in the avian interrenal lead to the speculation that different regions of the interrenal are functionally differentiated. The histological zonation demonstrable in most eutherian mammals has a functional correlation; in vitro experiments have demonstrated that the mineralocorticoid, aldosterone, is produced primarily by the cells of the zona glomerulosa in the ox (Ayres et al., 1956; Giroud et al., 1958) and the laboratory rat (Giroud et al., 1956). Recently C. deRoos and Bern (1961) have suggested functional zonation in the production of the glucocorticoids, cortisol and corticosterone, by the adrenal cortex of the California sea lion (Zalophus californianus). Cortisol appears to be produced primarily in the peripheral regions of the cortex, corticosterone in the inner cortical areas. No experimental evidence is presently available to suggest functional zonation within avian interrenal tissue. However, reports persist in the literature to the effect that following hypophysectomy of the pigeon and duck, the atrophic changes in the interrenal cords are more pronounced in the central portion of the gland; the cells at the periphery are not much affected initially, although the atrophy progresses peripherally with time (Chester Jones, 1957; Miller, 1961). These results are consistent with information from laboratory mam-
males wherein hypophysectomy results in an atrophy of the zona fasciculata and zona reticularis but the zona glomerulosa is little affected. Glucocorticoid production is markedly reduced following hypophysectomy in mammals; aldosterone production falls but is much less affected (cf. Fortier, 1962). Although inherently a more difficult problem in birds, attempts to demonstrate regional steroid production within the interrenal tissue would be of considerable value.

When the connective tissue capsule is cautiously removed from the mammalian adrenal, the zona glomerulosa adheres to the capsule with little contamination from the interior cortical regions. These "capsule strippings" have been instrumental in demonstrating the zona glomerulosa as the site of aldosterone production. Similar preparations of avian adrenals might well answer the question as to the physiological significance of the subcapsular and central regions which can be distinguished histologically.

AVIAN CORTICOID HORMONES

Only recently has interest centered on the hormones actually produced by avian interrenal tissue. The report by Phillips and Chester Jones (1957) represented the initial demonstration of corticoids in nonmammalian vertebrates. Included in their results were data on the caponized rooster. Corticosterone was found to be the major secretory product in adrenal venous effluent blood; cortisol, cortisone, and aldosterone were present in trace amounts. Newcomer (1959a) measured the free and bound Δ4-ketocorticoids in the blood and adrenal tissue of the chicken and definitively established the adrenal as a source of corticoids. Corticosterone levels have been measured in adrenal venous effluent and peripheral plasma in several species of gallinaceous birds including the chicken, turkey, and Ring-necked Pheasant (Brown, 1960; Urist and Deutsch, 1960a; Nagra et al., 1960). This steroid was not chemically characterized as corticosterone by these workers; recently, however, Brown (1961) identified corticosterone as the major secretory product in the turkey. Urist and Deutsch (1960a) reported cortisol to be present in the peripheral blood of the chicken; however, as with corticosterone, the steroid was not definitively identified.

The secretory pattern of the adrenal of five avian species from different taxonomic orders was investigated by deRoos (1961a, 1961b) employing the technique of in vitro incubation of adrenal tissue. Corticosterone was demonstrated to be the major secretory product of the adrenal glands of the domestic chicken (cockerels), the domestic pigeon, the domestic duck (Anas platyrhynchos), the Western Gull (Larus occidentalis), and the Brown Towhee (Pipilo fuscus). Aldosterone was also identified as a secretory product in these species. 11-Dehydrocorticosterone was tentatively identified in the gull and was probably a secretory product in all but the towhee, where it was not detected. Additional steroids, present in small amounts, were partially characterized but their identity remains unknown. Phillips (pers. comm.) has
confirmed the in vitro production of corticosterone and aldosterone by duck adrenals. Although several workers (Phillips and Chester Jones, 1957; Urist and Deutsch, 1960a) have reported cortisol and cortisone in chicken blood, deRoos (1961a) was unable to demonstrate either of these steroids in vitro. Nagra et al. (1960) were unable to demonstrate cortisol in samples of up to 50 ml of adrenal venous effluent from the chicken, pheasant, and turkey.

The similarity of the secretory pattern of the five avian species investigated thus far has led to the suggestion that birds may display homogeneity with regard to the secretion of corticosterone as the major steroid hormone (deRoos, 1961a). A diversity of secretory patterns has been shown in all other vertebrate classes with corticosterone, cortisol, or both secreted by different species within a given vertebrate class (Dorfman, 1959; Chester Jones et al., 1959; Phillips, 1959; Carstensen et al., 1961).

FUNCTIONS OF THE INTERRENAL

Adrenalectomy.—Information regarding the functions of the secretory products of avian interrenal tissue is not extensive. Few studies have been performed on the effects of adrenalectomy in birds, and these studies have been primarily concerned with the gross effects of the operation. In part, the lack of investigation may be attributed to the difficulty of the operation in birds. The adrenals lie close to the lungs, kidneys, and major blood vessels, and the gonads lie wholly or partly over the adrenals. The diffuse nature of the avian ovary and the large size of the testis of the sexually mature male have confined the investigations largely to the immature male. Adrenalectomy, as well as other studies on the avian adrenal, has dealt almost entirely with the domesticated chicken, pigeon, and duck.

Adrenalectomy was performed on the chicken by Parkins (1931). The removal of both glands was fatal within 38–146 hours, with a mean survival time of 80 hours. Blood uric acid increased and blood glucose decreased, particularly in advanced stages of adrenal insufficiency. The symptoms observed resembled those shown by the dog or cat, although they developed more rapidly in the chicken. Birds near coma could be restored to normal activity with mammalian cortical extract. A shorter survival time was found for the adrenalectomized chicken by Herrick and Torstveit (1938). The untreated adrenalectomized bird died within 6–15 hours; however, treatment with cortical extract and saline for 2 or 3 days, followed by saline alone, prolonged the survival time from a few days to as long as 82 days. The principal symptom of muscle fatigue appeared shortly before death. The effects of adrenalectomy in the chicken were investigated recently in more detail, and this new study has increased our information with regard to the symptoms of adrenal insufficiency in this species (Brown, Meyer, and Brown, 1958). The adrenalectomized bird died within 60 hours without treatment. Preceding death, there was a decreased excretion of sodium, uric acid, and total nitrogen, along with decreased water intake. Shortly before death,
blood glucose decreased and blood potassium increased. Operated birds given deoxycorticosterone acetate (DCA) (4 mg/kg/day) maintained a normal blood picture and normal water intake but sodium excretion remained low. The blood and excretory patterns remained normal when treatment consisted of cortisone acetate (15 mg/kg/day), although there was loss of weight. However, the interpretation of these results is complicated by the fact that birds treated with DCA or with cortisone acetate continued to live after treatment was discontinued; in all cases 2–5 mg of residual adrenal tissue were found to be present.

Similar results have been obtained from the adrenalectomized pigeon. If given gelatin capsules containing NaCl and NaHCO₃, pigeons could be maintained for an average of 9 days following adrenalectomy (Riddle et al., 1944). Cortical extracts or DCA returned the operated bird to normal food intake and growth (Miller and Riddle, 1943).

An early study concerning adrenalectomy in the domesticated duck by Parkes and Selye (1936) demonstrated that the operation is fatal within a short time in this species also. The removal of both adrenals resulted in death within 6–20 hours. The removal of one adrenal, or one adrenal and part of the other gland, did not result in ill effects, and the remaining interrenal tissue hypertrophied. According to Büllbring (1937a, 1937b, 1940), the survival time was prolonged by the administration of mammalian cortical extract or DCA; with DCA the birds could be maintained for as long as the treatment was continued. The doses necessary to maintain the operated birds increased during the breeding season. Leroy and Benoit (1954) did not find a short survival time for the adrenalectomized duck. Four untreated ducks survived 3 weeks to a month without any evident adrenal tissue. With reference to this report, Chester Jones (1957) quotes Büllbring (1940): “The removal of every trace of gland is not always easy and a piece no longer than a pinhead can prolong the survival time considerably.” In addition to the difficulty of removing the adrenal glands completely, the possibility of accessory adrenal tissue in avian species has not been generally acknowledged. The amount and distribution of accessory interrenal tissue remains uninvestigated. Accessory tissue might well be stimulated to function in the absence of the adrenals and thereby influence experimental results. Nevertheless, there is general agreement that the adrenalectomized bird dies within a brief period without replacement therapy and shortly before death shows symptoms resembling those of the mammal.

Most of the present information concerning the function of the avian adrenal gland preceded the isolation and identification of the steroid hormones secreted by the adrenals. The current concept of adrenal function is derived from observations on the symptoms of adrenal insufficiency and the ability of steroids, known to be produced by the mammalian adrenal cortex, to maintain adrenalectomized birds. The present evidence leaves little doubt that avian corticoids perform functions similar to mammals in the control of salt
and water metabolism and in carbohydrate metabolism (gluconeogenesis).

Corticoid Administration.—Only recently have investigations been completed that indicate specific functions of the steroid hormones secreted by the avian interrenal tissue. Greenman and Zarrow (1961) compared the effectiveness of various steroid hormones in promoting a rise in blood sugar and an increase in liver glycogen in the chicken. The steroids were injected in 4 divided doses at 2-hour intervals in the liver glycogen test; single daily injections for 14 days were given in the blood sugar test. Cortisol (2.5 mg/day) and corticosterone (5 mg/day) produced a significant rise in blood sugar; a slight elevation was produced by cortisone (40–50 mg/day) and deoxycorticosterone (40 mg/day) at high levels. Cortisol acetate (25 μg), corticosterone (200 μg), and 11-dehydrocorticosterone (4 mg) produced a significant rise in liver glycogen; cortisone acetate (16 mg) and 11-deoxy-17-hydroxycorticosterone (16 mg) were inactive. Cortisol, corticosterone, and cortisone caused a depression of body weight. These studies establish that corticosterone, the major corticoid of the birds investigated thus far, functions as a glucocorticoid in the chicken. 11-Dehydrocorticosterone, which is probably a secretory product (deRoos, 1961a), has glucocorticoid activity at high levels. Corticosterone and cortisol, in addition to their gluconeogenic activity, have been demonstrated to cause involution of lymphatic tissue (bursa of Fabricius) and atrophy of the adrenal in chickens (Zarrow et al., 1962).

Greenman and Zarrow (1961), as a result of their experiments, state that "the point many investigators have failed to note is the fact that cortisone is virtually inactive as a glucocorticoid in the bird." Stamler (1952) had reported some years earlier that cortisone failed to induce hyperglycemia in chicks at dosages wherein cortisol was effective. Both cortisone and cortisol were found by Mialhe (1958) to be inactive in promoting hyperglycemia in the duck. He suggested that corticosterone, or another corticosteroid, might be the principal glucocorticoid of this species. Corticosterone subsequently was demonstrated to be the major secretory product of the interrenal of the duck (deRoos, 1961a). When administered to chickens, cortisone does possess specific activities, among which are: decreased adrenal weight; involution of lymphatic tissue; decreased weight gain; increased excretion of sodium, potassium, total nitrogen, and uric acid; gonadal atrophy and hypercalcemia (Hublé, 1958; Brown, Brown, and Meyer, 1958; Newcomer and Connally, 1960; Urist and Deutsch, 1960b; Zarrow et al., 1962). However, on the basis of the present limited data, the dosages necessary to elucidate these responses are generally much greater than those required for cortisol or corticosterone and suggest a pharmacological rather than a physiological response.

Although cortisol generally elicits a response greater than corticosterone at similar doses in the chicken (Elton, 1958; Greenman and Zarrow, 1961; Zarrow et al., 1962), caution must be exercised in interpreting results obtained
with cortisol until this steroid is demonstrated to be a secretory product of the adrenal of avian species. It is by no means established that either cortisol or cortisone are secreted by avian adrenals; in fact, present evidence suggests that they are not (see above).

The administration of mammalian corticotropin to chickens has been shown to cause an increase in liver glycogen, hyperglycemia (Brown, Brown, and Meyer, 1958; Howard and Constable, 1958; Siegel and Beane, 1961; Bell, 1961), lymphatic tissue involution (Hublé, 1958), and acidophilia (Newcomer, 1959a). These effects may be attributed to an increased production of corticosterone, assuming the adrenal response to avian corticotropin will prove to be similar to that of mammalian corticotropin (see below).

Aldosterone probably has functions in birds similar to its functions in mammals, although experimental evidence is limited. Saline loading in the intact domestic duck results in an initial diuresis (Scothorne, 1959). Holmes, Phillips, and Butler (1961) administered aldosterone to salt-loaded ducks and noted that there was a marked reduction in the initial diuresis and a decline in renal sodium excretion with an increased concentration of urinary potassium; total potassium excretion was reduced.

The terms glucocorticoid (corticosterone and cortisol) and mineralocorticoid (aldosterone) are terms of convenience, and there is a great deal of overlap in the activities of these steroids (Chester Jones, 1957). Corticosterone has considerable activity in regulating electrolyte and water metabolism in mammals; cortisol has little such activity (Simpson and Tait, 1952; Selkurt, 1954; Chester Jones, 1957). It is not known if corticosterone possesses important sodium-retaining activity in birds. Aldosterone also possesses glucocorticoid activity in mammals, but it is not known whether the small amount of this steroid in blood has significant influence on carbohydrate metabolism.

Additional Actions of Corticoids.—Additional biological functions of adrenal steroids may yet be found. There is little doubt that corticoids are involved in the secretory function of the nasal (salt) glands of marine birds. The paired, supraorbital nasal glands are inactive in the absence of an osmotic load. In response to an osmotic load (i.e. ingestion of sea water), the glands secrete a concentrated solution of electrolytes, principally sodium chloride; the amounts of other ions and organic matter are low (Schmidt-Nielsen, 1960). Secretion can be induced by an osmotic load (sodium chloride or sucrose), by electrical stimulation of the secretory nerve, or by parasympathomimetic drugs (Fänge et al., 1958). The salt-loaded duck displays a characteristic response in which there is a prompt excretion of hypertonic urine followed by secretion from the nasal glands. The extrarenal phase commences as the renal phase ceases (Scothorne, 1959; Holmes, Phillips, and Butler, 1961).

In addition to the influence of the autonomic nervous system, Holmes,
Phillips, and Butler (1961) demonstrated that corticoids can influence the secretion of the nasal gland in the domestic duck. The injection of cortisol, deoxycorticosterone, aldosterone, or mammalian corticotropin resulted in an increase in the secretion of sodium and potassium by increasing the amount and rate of nasal-gland secretion. Aldosterone was the most effective steroid tested. Phillips et al. (1961) demonstrated that this response was abolished by bilateral adrenalectomy and reduced by subtotal adrenalectomy; cortisol restored this response. The intravenous infusion of a less concentrated sodium chloride solution than that used by Holmes, Phillips, and Butler (1961) caused nasal-gland secretion in ducks, but no urine was produced during the experimental period (Phillips and Bellamy, 1962). In this experiment the administration of aldosterone had no effect on nasal-gland secretion; cortisol, deoxycorticosterone, or corticotropin produced a rise in the average and maximum rate of secretion. They concluded that aldosterone is not essential for nasal-gland function in the duck, and the positive response noted by Holmes, Phillips, and Butler (1961) may have been an indirect response due to increased sodium retention by the kidney. If one extrapolates from the mammal, salt loading would be expected to decrease aldosterone secretion (Holmes, Butler, and Phillips, 1961). Thus, the glucocorticoids are believed to be involved in the control of the nasal glands (Phillips et al., 1961). Recently, Phillips and Bellamy (pers. comm.) were able to demonstrate a decrease in aldosterone and an increase in corticosterone production in vitro when the adrenals were obtained from salt-loaded ducks. Significantly, corticosterone, the major corticoid of the duck, is more effective than either cortisol or deoxycorticosterone in stimulating nasal-gland secretion (Phillips and Bellamy, pers. comm.).

The locus of action of the corticoids on nasal-gland secretion remains unknown. In addition, the role of the autonomic nervous system in nasal-gland secretion, demonstrated by Schmidt-Nielsen and his co-workers (Fänge et al., 1958; Schmidt-Nielsen, 1960) needs to be harmonized with the present evidence for adrenal control.

The relationship between the adrenal glands and the gonads in birds remains ill defined, although there is ample evidence that reciprocal influences exist (cf. Chester Jones, 1957). No direct evidence is available to demonstrate the production of androgens or estrogens by the avian interrenal.

CONTROL OF INTERRENAL SECRETION

Hypophysectomy.—Investigations concerning the effects of hypophysectomy in birds have demonstrated that the interrenal is dependent on the anterior pituitary for normal function; however, the extent of control remains controversial. In fact, many authors have suggested that the avian adrenal may possess a great deal of activity which is independent of the pituitary. Young or adult pigeons survived hypophysectomy for one or more years (Schooley, 1939). The effects of the operation on the adrenal of this
species were described in detail (Schooley, Riddle, and Bates, 1941; Miller and Riddle, 1942). There was a significant decrease in absolute adrenal weight and atrophic changes in the cortical cells. The interrenal cords were reduced, and individual cord cells were smaller and contained smaller hyperchromatic nuclei. Atrophic changes were more pronounced in the central portion of the gland; the cells at the periphery were usually not much affected. Similar changes in adrenal histology and weight were reported for hypophysectomized ducks (Chester Jones, 1957).

Chickens are less resistant to hypophysectomy, but this is dependent in part on the age of the operated bird. Mitchell (1929) found that hypophysectomized chickens died within 2 weeks. A survival time of 5 days has been reported for chicks (apparently under 7 days of age) by Bates et al. (1940). The majority of adults died within 48 hours of the removal of the pituitary (Hill and Parkes, 1934). However, chickens 40–50 days of age survived for months; some lived as long as a year without treatment (Nalbandov and Card, 1943). The operation resulted in the almost complete degeneration of the adrenals with a possible partial recovery. There was partial reorganization of the medullary tissue but no cord-like arrangement of the cortical tissue. Recent studies on young chickens have failed to reveal a significant decrease in adrenal weight, adrenal cholesterol, and Δ⁴-ketocorticoids, or the excretion of uric acid and total nitrogen following hypophysectomy (Baum and Meyer, 1956; Brown, Brown, and Meyer, 1958; Newcomer, 1959) and have contributed to the view that the avian adrenal possesses a high degree of autonomy.

This thesis received direct support from Brown (1960, 1961), who reported that corticosterone levels in peripheral blood of the turkey remained normal after hypophysectomy. Corticosterone levels did not increase following stress (cold and water deprivation) in operated birds, but rose significantly in sham-operated and control birds (Brown, 1961). Newcomer (1959a) found that plasma Δ⁴-ketocorticoids were little affected following hypophysectomy in the chicken. In contrast, Meyer (1962) found a marked reduction in corticosterone-like steroids in adrenal vein blood following hypophysectomy of the chicken and pheasant; adrenal weight remained unchanged. Thus, direct measurements of blood corticoid levels in hypophysectomized birds have failed thus far to determine the extent of adrenal autonomy.

Corticotropin Administration.—Conflicting reports surround the effects of mammalian corticotropin (ACTH) on the avian adrenal gland. ACTH preparations caused an increase in adrenal weight in both intact and hypophysectomized young chickens (Bates et al., 1940). Miller and Riddle (1942) confirmed the ability of corticotropin to increase the weight of the adrenal in hypophysectomized pigeons and also noted that histologically the adrenal was restored to normal. In contrast, Brown, Brown, and Meyer (1958) found a "surprisingly small" increase in adrenal weight of stressed and ACTH-treated
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(intact and hypophysectomized) young chickens. Their experiments on the effects of surgery and hormones (ACTH, deoxycorticosterone acetate, cortisone acetate) led to the conclusion that the adrenals of birds do not hypertrophy to any great extent in going from a relatively inactive state to a highly secretory one and that the adrenals of hypophysectomized birds function at a relatively high level.

Garren et al. (1961) reported that 10 units of ACTH administered in divided doses at 2-hour intervals resulted in a significant increase in adrenal weight and a decrease in both body weight and the weight of the bursa of Fabricius in chickens. A single daily injection of 2 units of ACTH for 8 days led to the same results, but without an increased adrenal weight. Garren concluded that adrenal activity can be increased extensively without a concurrent increase in adrenal weight. In contrast to mammals, ACTH suspended in saline was more effective than ACTH in gel, or with zinc, under similar conditions. Similar results were reported for saline-suspended ACTH by Zarrow et al. (1962); however, single daily injections of ACTH suspended in beeswax-oil gave a marked increase in adrenal weight. The conclusion drawn was that adrenal hypertrophy is dependent on a continuous release of ACTH. Zarrow also suggested the possibility that corticoid levels might increase in the absence of adrenal hypertrophy.

There is ample evidence that the administration of mammalian ACTH results in a significant increase in plasma corticosterone in turkeys (intact or hypophysectomized), chickens, and pheasants, despite the controversy over the functional significance of adrenal weight changes (Nagra et al., 1960; Urist and Deutsch, 1960a; Brown, 1960, 1961). An important finding is that increased corticosterone levels were not accompanied by a significant increase in adrenal weight, at least in the rooster (Urist and Deutsch, 1960a). According to Phillips and Chester Jones (1957), corticosterone output by the adrenal of the caponized rooster decreased following ACTH administration. This decrease has been interpreted as adrenocortical exhaustion (Holmes, Phillips, and Butler, 1961; Phillips et al., 1961). Caponization itself does not seem to be a factor, inasmuch as castration had no effect on corticosterone production in the pheasant (Nagra et al., 1960). The ability of ACTH to increase corticosterone production by avian adrenals in vitro (duck, pigeon, gull, towhee, chicken) has been shown by deRoos (1961a, 1961b). Aldosterone and the other trace steroids were not increased significantly.

Effects of Hormones and Stressors on the Adrenal.—Substances capable of producing adrenal enlargement in mammals fail to enlarge the adrenal of at least one avian species, the chicken (Bates et al., 1940). The substances tested were thyroxin, insulin, estrone, dihydroestrone, testosterone, deoxycorticosterone, formaldehyde, ammonia, casein, zinc and copper sulfates, and potassium chloride. Even though many of these substances were administered in nearly lethal doses, only formaldehyde produced a suggestion of
adrenal enlargement and stimulation (as evidenced by thymus atrophy), and even this could not be confirmed. Garren and Shaffner (1952, 1956) found that physical stressors, such as recurrent muscle fatigue, caused adrenal hypertrophy and a reduction in the weight of the thymus, spleen, and bursa of Fabricius. Restraint also has been shown to cause a marked acidophilia in the chicken (Newcomer, 1959a). Flickinger (1959), working with both wild and pen-raised California Quail, was unable to demonstrate significant changes in adrenal weight or histology in response to cage stress, cold stress, or treatment with cortisol or ACTH. The absence of adrenal hypertrophy in response to cold stress also has been shown in the pigeon (Munday and Blane, 1961). Flickinger, as well as Munday and Blane, concluded that the avian adrenal may be less subject to pituitary control in comparison to the adrenal of mammalian species.

In contrast, formaldehyde or insulin resulted in a significant hypertrophy of the adrenal in normal pigeons or in pigeons in which the adrenals had undergone atrophy following hypophysectomy (Miller and Riddle, 1942; Miller, 1961). Following hypophysectomy, “very large” lesions in the median eminence and ventral hypothalamus resulted in adrenal hypertrophy rather than atrophy; injections of formaldehyde and insulin caused even further hypertrophy (Miller, 1961). The increase in adrenal size histologically was shown to be primarily a hypertrophy and hyperplasia of the interrenal tissue. Epinephrine injection caused minimal enlargement. Hypophysectomy and denervation of the adrenal followed by formaldehyde injection also resulted in hypertrophy. Miller concluded that the adrenal is capable of responding to stress in the absence of both the pituitary and an intact hypothalamic–hypophyseal system; he believes the stimulus to be humoral. Unfortunately, plasma corticoid levels were not determined, nor were other indices of adrenal activation included in this report. Without additional information it cannot be concluded that this increase in adrenal size had functional significance. The significance of the hypertrophy of the adrenal, which occurred in the hypophysectomized pigeon following lesions in the median eminence, is not immediately evident. The extent of the lesions involving broad areas of the hypothalamus suggests to this reviewer that the birds suffered considerable brain damage and the effects noted may have represented an additional “stress” to that imposed by the injection of formaldehyde and insulin.

CORTICOTROPIN RELEASE AND ITS CONTROL

The possible hypothalamic control over anterior pituitary release of corticotropin, which has been demonstrated in mammals (cf. Fortier, 1962), is largely uninvestigated in birds. Assenmacher (1958) reported that the duck adrenal was not greatly affected by separation of the connections between the pituitary and hypothalamus, as judged by adrenal weight and adrenal histology, and the ability of insulin to promote blood sugar changes. The
operations performed were: lesions of the anterior hypothalamus, section of the portal veins, section of the median eminence, and hypophysectomy followed by pituitary grafts. The thyroids were partially dependent and the gonads totally dependent on intact hypothalamic–hypophyseal connections (Assenmacher, 1958; Benoît, 1962). The failure of hypothalamic lesions to cause adrenal atrophy is not surprising in view of the failure of hypophysectomy to produce consistently a decrease in adrenal weight. Measurements of plasma corticoid levels would be of considerable value, particularly in view of the lack of agreement concerning the effect of hypophysectomy on adrenal steroid hormone production.

Corticosterone and other adrenal steroids have been shown to cause a decrease in adrenal weight, and this response strongly suggests that a “feedback” mechanism exists between the level of circulating glucocorticoids and the synthesis or release of corticotropin from the pituitary (Zarrow et al., 1962). If, as has been suggested, the avian adrenal possesses a great deal of autonomous activity, this feedback mechanism must be qualitatively different from that of mammals. Experiments designed to determine the effects of exogenous corticoids on the adrenal secretory rate and the influence of adrenalectomy on the release of corticotropin from the pituitary are of obvious importance in defining the pituitary–adrenal axis as it exists in birds. It remains unknown whether corticoids suppress corticotropin release via a direct action on the pituitary, the hypothalamus, or both.

**ADRENAL ASCORBIC ACID DEPLETION**

Adrenal ascorbic acid depletion has been used widely in mammalian studies as an index of pituitary–adrenal activation. In contrast, avian species have not responded to ACTH administration with a depletion of adrenal ascorbic acid, and this again has been taken by some workers as an indication of adrenal activity which is independent of the pituitary. The chicken (Jailer and Boas, 1950; Elton et al., 1959), Bobwhite Quail (Zarrow and Baldini, 1952), and duck (Zarrow and Zarrow, 1950) did not show depletion of adrenal ascorbic acid following ACTH treatment, cold stress, or epinephrine administration. Howard and Constable (1958) confirmed the failure of ACTH to decrease ascorbic acid in the adrenal of the chicken, but found an increase in blood glucose and liver glycogen, and a decrease in adrenal cholesterol. Administration of ACTH for 8 days resulted in a decrease in adrenal cholesterol and an increase in adrenal weight. It was concluded that ACTH is capable of stimulating the production of hormones from the adrenal without affecting adrenal ascorbic acid. The concentrations of ascorbic acid, cholesterol, and Δ4-3-ketocorticoids in the adrenal glands of young chickens were not significantly changed following hypophysectomy, according to Newcomer (1959b). In addition, there was no change in adrenal weight. These results were taken to indicate a great deal of functional independence by the adrenal in this species. Recently, Perek and his co-workers (Perek et al.,
1959; Perek and Eckstein, 1959) showed that adrenal ascorbic acid depletion occurred following ACTH treatment of 1-year-old laying hens, and that the depletion was comparable in degree and time to that seen in mammals; however, 3-month-old pullets failed to show this response. Other workers have used birds under 3 months old. It appears that the bursa of Fabricius may be involved in preventing the release of ascorbic acid from the avian adrenal (Perek and Eilat, 1960). Recent evidence indicates that the bursa of Fabricius, a lymphatic structure present in young birds as a cloacal diverticulum, is involved in the development of immunological maturity (Glick et al., 1956; Glick and Sadler, 1961). Adrenal ascorbic acid depletion occurred in 3-week-old and 6-week-old chickens when ACTH was administered to "bursectomized" birds (Perek and Eilat, 1960). Involution of the bursa of Fabricius was noted in intact birds when long-acting ACTH was given. Recently, Nagra et al. (1960) demonstrated increased corticosterone levels in the blood of 10- to 20-week-old chickens following the administering of ACTH. Adrenals of cockerels as young as 4 weeks responded to ACTH in vitro with a significant increase in corticosterone output (deRoos, 1961a). Thus, adrenal ascorbic acid depletion and adrenal weight changes are not necessary concomitants of increased secretory rate of the avian interrenal.

SUMMARY AND CONCLUSIONS

This brief review has attempted to present the current status of our knowledge concerning the avian interrenal gland. The major corticoid hormones secreted by the interrenal of birds so far investigated are corticosterone and aldosterone. Corticosterone functions as a glucocorticoid in birds; in addition, present evidence suggests that corticosterone is involved also in the control of the nasal (salt) gland secretion in marine birds. The limited data concerning the function of aldosterone indicate that this steroid possesses mineralocorticoid activity. The terms glucocorticoid and mineralocorticoid should be employed cautiously when describing the secretory products of the interrenal as there is undoubtedly some overlap in the activities of the several hormones secreted.

Evidence indicates that the interrenal is dependent on the anterior pituitary for normal function; however, considerable controversy surrounds the degree of control exerted by the pituitary. It has been suggested that the interrenal functions at a relatively high level in the absence of the pituitary; however, direct measurements of circulating corticoid levels in hypophysectomized birds have failed to resolve the extent of pituitary control over interrenal function. A pituitary–interrenal axis regulating glucocorticoid (corticosterone) production seems to exist in birds, while the secretion of aldosterone appears to be relatively independent of pituitary control. The factor, or factors, regulating aldosterone secretion remains unknown. Whether or not the hypothalamus influences the interrenal via the regulation of the release of corticotropin from the adenohypophysis remains uninvestigated.
Future work on the avian interrenal must consider the present evidence that the criteria employed in the past as indices of adrenal activation may not be indicative of adrenal activity, particularly adrenal weight changes and adrenal ascorbic acid depletion. In addition, future work involving the administering of corticoids should employ the hormones known to be produced by the interrenal. Unfortunately, much of the present information concerning avian interrenal physiology is based on information derived from the use of cortisone in experimentation, a steroid that is probably not produced by the avian interrenal and that is virtually inactive except at pharmacological doses. Evidence presently available is adequate to demonstrate that age, sex, and species are parameters that need to be considered. It is unlikely that a purified preparation of avian corticotropin will be available in the near future, and a cautious approach to results obtained with mammalian corticotropin is necessary until purified avian corticotropin is available and its effects on interrenal steroidogenesis studied.

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ENDOCRINOLOGY, MORPHOLOGY, AND METABOLIC STUDIES


Morphological and Physiological Properties of the Auditory System in Birds

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We conclude from the behavior of birds that hearing plays an outstanding role in their lives. This sense is of greater importance only in those mammals that rely essentially upon echo-orientation. Consequently, the absolute sensitivity of the ear and the frequency-difference threshold are the same in birds and mammals (for lit., see Schwartzkopff, 1960). There are, however, differences, sometimes far reaching, in the morphology of the auditory organ and the adjoining nervous centers of the brain. Some special developmental trends can also be observed in birds, sometimes within one order, apparently adaptations for special functions. The working mechanism of the auditory apparatus can today be understood only incompletely. It is the purpose of this paper to report on recent morphological findings and related physiological problems.

Middle Ear.—The morphological differences between mammals and birds are especially impressive in the middle-ear region. Instead of the chain of auditory ossicles, birds possess only the columella. The functional similarity here is therefore the more surprising. In general terms, the middle ear has to match impedances for sound transfer from air to the fluids of the inner ear. This function depends upon the transformation quotient of eardrum to oval window (columella footplate) and upon lever movements of the ossicles, the latter being known only qualitatively in birds. The transformation quotients (area of the eardrum plane/area of the oval window) are almost of the same magnitude in birds and in mammals, being 24 for Mus, 27 for Homo, 29 for Cavia, and 34 for Felis, in contrast to 18 for Steatornis, 25 for Parus, 31 for Melopsittacus, and 40 for Asio. This confirms earlier physiological evidence that similar continuous-sound stimuli are treated with equal efficiency. The greater variation in the data for birds results from the more ample material studied (Schwartzkopff, 1957a). From these data I have selected representatives with characteristically different habits. The nocturnally active owls occupy the first places; they are followed by the Oscines, from which Athene noctua does not differ.

Inner Ear.—The elements of the inner ear of birds are, in contrast to the middle ear, homologous with those of the mammalian ear, if we prescind from the lagena, since its participation in hearing processes is dubious. The

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peri- and endolymphatic spaces, however, have developed in quite different ways in both groups. In birds, the space on the upper side of the basilar membrane is completely filled with the folds of the glandular tegmentum vasculosum, leaving no room for an open scala vestibuli (Fig. 1). Only peri¬lymphatic fissures are found between the tegmentum and the bony ceiling of the cochlea. These fissures become somewhat enlarged basally underneath the footplate, and apically at the border between cochlea and lagena. These enlargements communicate by different channels, the ductus brevis and the ductus scalae tympani, with the well-developed scala tympani. Older de-

![Fig. 1. Schematic longitudinal section through the inner ear of birds; from Schwartzkopff and Winter (1960).](image)

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>cartilage</td>
</tr>
<tr>
<td>Co</td>
<td>Columella</td>
</tr>
<tr>
<td>Csty</td>
<td>Cavum scalae tympani</td>
</tr>
<tr>
<td>Cstey</td>
<td>Cisterna scalae vestibuli</td>
</tr>
<tr>
<td>Db</td>
<td>Ductus brevis</td>
</tr>
<tr>
<td>Dc</td>
<td>Ductus cochlearis</td>
</tr>
<tr>
<td>Dre</td>
<td>Ductus reuniens</td>
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<tr>
<td>Dsty</td>
<td>Ductus scalae tympani</td>
</tr>
<tr>
<td>Fsve</td>
<td>Fossa scalae vestibuli</td>
</tr>
<tr>
<td>Fr</td>
<td>Fenestra rotunda</td>
</tr>
<tr>
<td>Fsve</td>
<td>Fossa scalae vestibuli</td>
</tr>
<tr>
<td>Kw</td>
<td>Bony wall</td>
</tr>
<tr>
<td>La</td>
<td>Lagena</td>
</tr>
<tr>
<td>Mb</td>
<td>Membrana basilaris</td>
</tr>
<tr>
<td>Rsty</td>
<td>Recessus scalae tympani</td>
</tr>
<tr>
<td>Sty</td>
<td>Scala tympani</td>
</tr>
<tr>
<td>Tv</td>
<td>Tegmentum vasculosum</td>
</tr>
</tbody>
</table>

scriptions of the scala vestibuli, based upon histologically treated material, have not been confirmed by studies of the inner ear in the natural state (Schwartzkopff, 1954; Schwartzkopff and Winter, 1960).

The sound waves transferred to the cochlea by the columella have to spread through the tegmentum in order to affect the basilar membrane. On their way they are probably damped more efficiently than in the mammalian ear. The damping enables the basilar membrane to change its pattern of movement within a very short time. This would correspond with recent results of song analysis (Borror and Reese, 1956), showing that the song of many birds contains such rapid sequences of notes that the human ear cannot follow them. The ear of a Mockingbird (*Mimus polyglottos*), however, can. Similar conclusions have been drawn from our electrophysiological studies of the auditory nerve and brain activity in birds (Fig. 2). We think that birds have developed a special ability for resolving phasic stimuli of very short intervals. Comparable measurements in mammals show that birds' nervous responses to very fast-changing stimuli are better separated than those of mammals (Schwartzkopff, 1957b).
The internal ear of owls differs from that of most birds by its unusually long and slender basilar membrane (Fig. 3). Moreover, we did not find a ductus brevis. Starting from the assumption that the length of the basilar membrane is related to the discrimination of frequency, we end up with the paradoxical result that owls should perform much better than songbirds and that songbirds do not differ greatly from other groups, e.g. the pigeon. The last assumption, at least, has been disproved by conditioning experiments (Wassiljew, 1933; Knecht, 1940). Songbirds and parakeets can discriminate
between tones differing by not more than 0.3 percent; pigeons, only by 5 percent. Until frequency discrimination in owls has been tested, the possibility cannot be ruled out that the length of the basilar membrane is involved in the differentiation of intensity steps, rather than of frequencies. At least it is reasonable to assume that both functions are linked together in a complex way, as Pumphrey (1961) has suggested.

Table 1.—Relation of Size of the Inner Ear and the Auditory Nerve in Birds of Different Weight

<table>
<thead>
<tr>
<th>(1) Body Weight (g)</th>
<th>(2) Length of Inner Ear (cm)</th>
<th>(3) Cells, Ggl. Cochleare + Lagenare</th>
<th>(3) ÷ [1,000 × (2)]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parus major</td>
<td>18</td>
<td>0.35</td>
<td>6,140</td>
</tr>
<tr>
<td>Sturnus vulgaris</td>
<td>80</td>
<td>0.43</td>
<td>7,420</td>
</tr>
<tr>
<td>“Normal”</td>
<td>100</td>
<td>0.43</td>
<td>7,500</td>
</tr>
<tr>
<td>Columba livia</td>
<td>330</td>
<td>0.57</td>
<td>11,550</td>
</tr>
<tr>
<td>Branta canadensis</td>
<td>4,000</td>
<td>0.63</td>
<td>11,720</td>
</tr>
<tr>
<td>Steatornis caripensis</td>
<td>450</td>
<td>0.75</td>
<td>9,980</td>
</tr>
<tr>
<td>Asio otus</td>
<td>280</td>
<td>0.85</td>
<td>15,400</td>
</tr>
<tr>
<td>Tyto alba</td>
<td>290</td>
<td>1.12</td>
<td>16,550</td>
</tr>
</tbody>
</table>

Nervous Pathway of Auditory Excitation.—The number of nerve cells or fibers transporting the excitation of the basilar membrane toward the brain is linearly correlated with the length of the membrane (Table 1). These measurements were made on the length of the cochlea and lagena together. Thus, we have introduced an error which is, however, systematic and therefore does not affect the conclusions. My co-worker, P. Winter, also counted the nerve cells of the ganglion cochleare and lagenare together, since they cannot be separated in adult birds. It is surprising that Steatornis caripensis does not possess more auditory neurons.

The relation between basilar membrane and number of nerve cells that process auditory information becomes more complicated when we study the next stations of the auditory pathway inside the brain. Little is known about the higher auditory centers in the midbrain and forebrain of birds. Winter has counted the auditory neurons in the different nuclei of the medulla. In order to show graphically the relation to the size of the species studied, the figures from these nuclei were summated for each bird (Fig. 4). If the number of cells is plotted logarithmically against body weight, a field of distribution results which follows approximately the equation

\[ N = c \cdot W^{0.15} \]

where \( N \) means number of cells, \( c \) a proportionality constant, \( W \) body weight in grams, and 0.15 the allometry exponent. This equation seems to be valid for all daytime or dawn-active birds studied so far and includes Oscines, Athene, Steatornis, waterfowl, and the Eagle Owl (Bubo bubo). The slope, as indicated by the allometry exponent of 0.15, is considerably smaller than
for the whole brain, where values of about 0.5 have been published by different authors (see Schwartzkopff, 1957a).

Assuming that the efficiency of processing auditory information depends upon the number of neurons involved, the rather unimpressive slope would lead us to think that the acoustic performance in large birds is not essentially superior to that of small ones. Students of visual acuity in birds are facing

![Fig. 4. Number of auditory neurons processing acoustic information in (one-half of) the medulla of different species of birds, underlining the singular position of those owls that hunt by ear; closed circles: Striges; open circles: other families. From P. Winter, unpublished.](image)

A related problem. In the eye, however, only the density of visual-receptor cells and neurons in the retina is known so far, not the number of information-processing neurons in the brain.

Those species of owls that hunt mainly at night and have developed asymmetric external ears (Tyto alba, Strix aluco, Asio otus) do not fit into the "frame" of the majority of birds. This exceptional group is supposed to localize its prey essentially by ear. Tyto alba, weighing less than 300 g, has 47,500 auditory neurons in one-half of the medulla. In the crow (Corvus corone), of double that weight, 13,500 auditory elements have been counted; and in the Eagle Owl, weighing 2,800 g, not more than 18,000 (Winter and Schwartzkopff, 1961). This increase far exceeds the increased length of the basilar membrane and the increased number of cells forming the auditory nerve, which in Tyto are only about double that of the "normal" bird. We must assume from these figures that the neural interaction and cooperation between the cells of the auditory brain centers is of special importance for the nocturnally active members of the Striges. Correspondingly, those cen-
Fig. 5. Binaural interaction in the medulla of Strix aluco, nucleus laminaris activated by both ears symmetrically. In each record, the upper line shows the round-window response (A, C from left, B, D from right ear); lower line shows the potential recorded by a microelectrode close to (A, B) and inside the nucleus laminaris (C, D) of the left half of the medulla. Records A and B demonstrate the afferent volley from left and right ear to be of similar amplitude; the turnover of polarity depends upon electrode position. In records C and D, the identical activation of the nuclear mass by both-ear stimulation is seen.

Neurophysiology.—We do not know very much about the features of interaction between auditory neurons in birds. Electrophysiological experiments have shown that the nucleus laminaris, the first center where binaural interaction can occur, is activated from both ears equally in Tyto and Strix (Fig. 5). In the pigeon, however, Erulkar (1955) was unable to establish the presence of contralateral influences. We have seen in Melopsittacus (Schwartzkopff, 1957b) and some Oscines that contralateral activation is always less pronounced than ipsilateral. Interaction, restricted to the neurons of one side of the brain, has been reported recently by Stopp and Whitfield (1961). Most of the auditory neurons studied by these authors could be inhibited by certain frequencies while activated by others. From similar results in mammals it was concluded that adjacent neurons affect each other,
Fig. 6. Tonal sensitivity of auditory neurons in the parakeet. Upper part shows frequency of occurrence of nerve cells representing special tone areas; lower part, response areas of single auditory neurons. From Schwartzkopff (1957b).

thus producing contrast phenomena through which frequency discrimination might be improved (Whitfield, 1957).

As a result of peripheral and central analyzing mechanisms, most auditory neurons found in the medulla of birds as well as of mammals manifest a special sensitivity toward a certain tonal area (Fig. 6). In contrast to the experiments on mammals, no nerve cells have been observed that were sensitive for tones above 4 kc. Although this negative result of our experiments on the parakeet has been corroborated recently by Stopp and Whitfield (1961) in the pigeon, I still believe that this deficiency has been induced methodically. In any event, the majority of frequency-representing neurons was found in an area above 1 kc, in which tone discrimination is supposed to be best (Knecht, 1940).

The owls are unusual not only for having so many auditory neurons in the
medulla and displaying more binaural interaction but also in showing extraordinarily strong auditory activation of the cerebellum. In this part of the brain, we have found auditory activation only exceptionally in parakeets, starlings, magpies, crows, and falcons. In Strix and Tyto, however, nerve cells responding to acoustic stimuli are not so rare. The neurons in the cerebellum differ from the medullary neurons in that they show no preference for any special tone. They respond best to short click signals or the onset of tones. The latency of most of the elements is 10–14 msec, which means that the excitation has passed through other centers, such as midbrain and possibly even the forebrain, before being processed in the cerebellum. In exceptional instances we have observed latencies as long as 35–40 msec and as short as 2.5 msec in the cerebellum. The latter finding is proof of a short pathway connecting medulla and cerebellum directly.

Generally speaking, the greater auditory activity in the cerebellum of owls is a sign of the more efficient participation of the ear in spatial orientation and coordination of movements.

Auditory Localization.—The outstanding role of auditory localization in certain owls is reflected also by the morphology of the external ear. The very large ear openings are of remarkable bilateral asymmetry in four genera of the Striges. Basing his arguments on acoustics, Pumphrey (1948) has shown that this asymmetry may improve directional hearing in space, presupposing that owls are able to distinguish tones efficiently and that the bilateral asymmetry produces different directional characteristics in the two ears from which in turn asymmetric differences in pitch perception must result.

We have recently measured the directionality of the ears of Asio otus by picking up the cochlea potentials from both round windows (Schwartzkopff, 1962). The anesthetized owls were placed in a nonechoing chamber and rotated so that the sound source changed its position with regard to the head either in the horizontal or in the vertical plane. While the sound signals remained constant, the amplitude of the cochlea potential varied with the direction. From this the sound intensity affecting each ear was calculated. When the anesthesia was light, we recorded unsystematic variation in the sensitivity, even before the owl was rotated. These changes depended upon movements of the ear flaps. When the animal was in deep sleep with its ears open, the expected asymmetric directionality did not appear (Fig. 7). The resulting diagrams indicate that in the horizontal plane the maximum of sensitivity is directed lateral–forward, in the vertical plane lateral–downward.

In spite of these findings, we still believe in the importance of the asymmetric structures for auditory localization, as pointed out in principle by Pumphrey (1948). However, it does not seem true that bilateral asymmetry of sensitivity results directly from morphology, as it were, by producing differential flexion of the sound waves. We think it to be more likely that
Fig. 7. Directionality diagrams for both ears of *Asio otus* in the horizontal and vertical plane; stimulus frequency 3,000 cycles/sec. Distance from center indicates size of cochlea potentials. Horizontal section through the head in the center. The diagrams of each side form nearly mirror images, which means that in the anesthetized animal the asymmetry of the external ear opening has no influence. From Schwartzkopff (1962).

These structures provide the morphological basis of dynamic asymmetries in the movements of the ear flaps by which indirectly the directionality of the ear is influenced. These movements we cannot thus far control experimentally. Before proceeding further electrophysiologically we need behavioral studies of the ear movements in undisturbed tame owls.

Besides the negative results, the experiments with *Asio otus* showed rather strong time differences originating between both ears. These cannot be influenced by the asymmetry. The time differences are more than double what is to be expected from the different distances from the ears to the source of sound. The unexplained component is based upon differences in latency between the ears stimulated with different intensity according to the directionality diagram. We have found in earlier behavioral experiments that owls can evaluate time differences between both ears, while small songbirds most likely cannot.

The auditory localization of prey being of preponderant importance for the nocturnal owls, apparently all physiological possibilities for improvement
are utilized. Although we cannot as yet describe the extent of owls' ability to locate an object in space through hearing, the development of the external, middle, and inner ear, and of the auditory brain centers, as well as behavioral and field studies, lead us to expect a high degree of perfection. This is corroborated by the physiology of the auditory system.

**SUMMARY**

The middle ear of birds is composed of parts morphologically different from those of the mammals. The function is rather similar, however. In the internal ear the structures are homologous, while the mechanisms involved seem to be different, depending upon the lack of a scala vestibuli in birds and the very short basilar membrane.

From the anatomy of the inner ear, it is deduced that damping plays an important role in its mechanism. This is confirmed by electrophysiological evidence.

The nervous pathway carrying auditory information to the brain of birds contains about the same number of first-order neurons as in mammals; this number is linearly related to the length of the basilar membrane. The secondary and tertiary centers in the medulla show a very conservative development in most birds, being almost uninfluenced by the birds' size. Some owls show a very special adaptation connected with auditory localization abilities.

**LITERATURE CITED**


The extensive investigations of Benoit and his colleagues on the photoperiodic testicular response in ducks have indicated that the essential elements of the photoperiodic control mechanism are the hypothalamic neurosecretory cells, the median eminence, the hypophysial portal system, and the adenohypophysis (Benoit and Assenmacher, 1955, 1959). Oksche et al. (1959) have shown that photoperiodic stimulation of highly photosensitive birds causes increased activity of the cells of the supraoptic nucleus, decrease of aldehyde-fuchsin positive neurosecretory material therein, and reduction of aldehyde-fuchsin positive material in the median eminence. These changes are accompanied by testicular growth. While we were studying the neurosecretory phenomena, we had difficulty in estimating precisely the amount of the neurosecretory material by means of the microscope, and we indicated the importance of exploring the possibility of a quantitative expression of the activity of the hypothalamo-hypophysial system (Kobayashi and Kambara, 1959). Hence, we designed semimicro methods for acid phosphatase measurement, which may reflect the level of general cellular metabolism, and also for catheptic proteinase measurement. These two methods were used on the supraoptic nucleus region, median-eminence region, the pars nervosa, and the adenohypophysis of the White-crowned Sparrow \( (Zonotrichia\ leucophrys\ gambelii) \). Only acid phosphatase determinations were made on the tissues from the White-throated Sparrow \( (Z.\ albicollis) \). These studies have been successful in demonstrating quantitatively the activity of the hypothalamo-hypophysial system (Kobayashi and Farner, 1960; Wolfson and Kobayashi, 1962; Kobayashi et al., 1962). The data will be presented briefly in this paper.

As mentioned above, the importance of the bird median eminence in the regulation of the release of gonadotropins from the adenohypophysis has been suggested by many investigators (see Farner and Oksche, 1962). Accordingly, we are attempting to study the fine structure of the bird median eminence in order to understand better the anatomical and functional relationship between the median eminence and the adenohypophysis. Although there are several light-microscope investigations on the median eminence, including that of birds, electron-microscope study has been restricted to examination of the median eminence of the guinea pig (Barry and Cotte, 1961)

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1Investigations by the author and his co-workers cited herein were mostly supported by grant No. A-3678 from the National Institutes of Health, United States Public Health Service. The author wishes to thank Miss H. Uemura for her help in preparing the manuscript.

and of the parakeet (Kobayashi et al., 1961). In our studies, attention was paid to the following problems: (1) the general structure of the outer surface of the median eminence, (2) whether or not the neurosecretory axons arising in the hypothalamic neurosecretory nuclei terminate in the median eminence, and (3) how the neurosecretory granules in the median eminence pass into the capillaries of the primary plexus of the hypophysial portal blood system.

Finally, we are attempting to determine what substance in the median eminence controls gonadotropin release from the adenohypophysis. For the first step, we have focused our attention on the neurosecretory material in the median eminence. This neurosecretory material was examined to see whether it contained neurohypophysial hormone(s), and, if so, whether the amount of hormone in the median eminence changes when the adenohypophysis releases the gonadotropins. So far as we know, no one has tried this kind of work.

In this paper I shall present the results that were obtained recently by my colleagues to elucidate the problems mentioned above which bear upon the functional relationship between hypothalamus and adenohypophysis.

MATERIALS AND GENERAL METHODS

For the phosphatase work the White-crowned Sparrow and the White-throated Sparrow were used. Details of the method have been described in previous papers (Kobayashi and Farner, 1960; Wolfson and Kobayashi, 1962). In brief, the method involves immediate removal of tissues (supraoptic nucleus region, median-eminence region, adenohypophysis, and pars nervosa) (Fig. 1), homogenation, incubation in a buffer-substrate mixture, centrifugation, and measurement of the optical density at 415 mμ of an ali-
Hideshi Kobayashi: Median Eminence of Birds

quot of the supernatant in saturated sodium carbonate. The substrate was p-nitrophenyl phosphate in acetate buffer. The incubation time was 1 hour at 37.5°C. The activity was expressed as μg of p-nitrophenol liberated in 1 hour per mg tissue.

For estimation of proteinase activity, the method of Anson (1937) with some modifications was used. The details have been reported in a previous paper (Kobayashi et al., 1962). Briefly, tissues from the same regions used for phosphatase assays (Fig. 1) and a small piece of the ventral part of the lateral forebrain bundle were removed immediately after decapitation. After homogenation, an aliquot was added to a buffer-substrate mixture and was incubated at 37.2°C for 4 hours. After stopping the reaction with trichloroacetic acid, the mixture was centrifuged. Then the measurement of the optical density at 700 mμ of an aliquot of the supernatant added to a mixture of NaOH and Folin-Ciocalteu phenol reagent was carried out. The substrate was 2.0 percent bovine hemoglobin (at pH 3.54 with acetic acid). The proteinase activity was expressed as μg of tyrosine liberated in 4 hours per mg tissue or per whole gland.

For the study of fine structure, the median eminence and pars nervosa of the parakeet and pigeon were exposed after rapid decapitation of the birds. The tissues were fixed at 0-5°C for 2-3 hours in osmium tetroxide buffered at pH 7.5 in veronal-acetate (Palade, 1952), or in potassium permanganate (Luft, 1956), or in OsO4 buffered at pH 7.4 in s-collidine (Bennett and Luft, 1959). The osmic acid-dichromate fixative of Dalton (1955), without added sucrose, gave the best results. The tissues were embedded in methacrylate after dehydration. Sections were made with glass knives on the Porter-Blum ultramicrotome and examined in RCA EMU 3 or JEM-5Y electron microscope. Details have been described in previous papers (Kobayashi et al., 1961; Oota and Kobayashi, 1962). For light-microscope examinations the median eminence was fixed in Bouin's fluid, embedded in paraffin, and sectioned at 10μ. The slides were stained with aldehyde–fuchsin staining method (Gomori, 1950).

Neurohypophysial hormone activity in the median eminence and pars nervosa was assayed by the frog-bladder method (Sawyer, 1960) and the rat-uterus method (Holton, 1948). In the rat-uterus method, Ringer's solutions with and without Mg were used. Four-point assays were performed and analyzed statistically by the method outlined by Holton for the rat-uterus assay. As the reference standard for the assays, the synthetic oxytocin “Syntocinon” (Sandoz) from the same batch was used in the experimental series in both of the rat-uterus and frog-bladder methods. Details of assay and of extraction have been described in previous papers (Ishii et al., 1962; Hirano et al., 1962).

RESULTS

Acid Phosphatase and Proteinase Activity in the Bird Hypothalamo-hypophysial System.—The White-throated Sparrows, which had been kept under
natural daily photoperiods, were divided into two groups and exposed to long
days and short days, respectively, beginning on 22 January. Following cycles
of 16-hour light and 8-hour darkness (16L–8D), the activity of acid phos-
phatase increased in adenohypophysis, supraoptic region, median-eminence
region, but not in pars nervosa (Fig. 2). Almost the same results were ob-
tained with the different photoperiodic schedule of 16L–32D. The birds
exposed to 16L–8D and 16L–32D showed a typical gonadal response. In the
birds treated with short daily photoperiods (6L–18D), some significant
changes in the hypothalamic region were observed, although there was no
gonadal response. Details of the data have been described in a previous

Fig. 2. Acid phosphatase activity in the hypothalamo-hypophys-
ial system of photosensitive White-throated Sparrows subjected to
long daily photoperiods (from Wolfson and Kobayashi, 1962). Or-
dinate: $\gamma$-nitrophenol liberated per mg tissue in 1 hour at 37.5°
C. AH, adenohypophysis; SO, supraoptic region; ME, median-emi-
nence region; PN, pars nervosa.
Similar results were obtained in the long-day (20L–4D) photosensitive White-crowned Sparrows, which had been kept under 8-hour daily photoperiods before the experiment started. In refractory White-crowned Sparrows, which do not respond to long photoperiods, acid phosphatase activity in the tissues examined did not increase following the prolonged daily photoperiods (20L–4D). Details of the data of the White-crowned Sparrow were presented in a previous paper (Kobayashi and Farner, 1960). The interesting point is that in the White-crowned Sparrow the activity of acid phosphatase of the adenohypophysis of photosensitive birds kept under 8L–16D for 3 months was significantly higher than that of the refractory birds maintained on 13L–11D.

Histochemical examination has revealed that acid phosphatase was distributed densely in the fibers in the palisade layer of the median eminence, in which the neurosecretory material is presumably concentrated.

The proteinase work was done on the White-crowned Sparrow. The activity of proteinase in the median-eminence region and adenohypophysis of the photosensitive White-crowned Sparrow increased significantly following long days (20L–4D) (Fig. 3 and 4), although an increase was not observed in the supraoptic nucleus region or in the ventral region of lateral forebrain bundle. The peak of the proteinase activity occurred on the 14th day of the experiment, both in the median eminence and the adenohypophysis, and thereafter the activity decreased in both tissues.

In the photorefractory birds exposed to long days (20L–4D), the enzyme activity showed a decrease in the adenohypophysis on the 6th and 28th days and in the median-eminence region on the 6th day of the experiment. The decrease occurred in parallel in both adenohypophysis and median eminence (Fig. 3 and 4).

Fine Structure of the Median Eminence of Parakeet and Pigeon.—The light-microscope observations will be mentioned only briefly. The anatomy of the median eminence of the pigeon and parakeet is similar to that of other birds considered by other investigators (Wingstrand, 1951; Farner and Oksche, 1962). The general anatomic relations of the hypothalamic neurosecretory system in the pigeon are shown in Fig. 5. The neurosecretory axons proceed perpendicularly to the capillaries of the hypophysial portal vessel in the median eminence. The neurosecretory material is densely concentrated around the glial cells.

The electron-microscope observations were concentrated on the region near the blood vessels of the primary plexus of the hypophysial portal system at the base of the median eminence (Fig. 5). The observations were almost the same in the pigeon as in the parakeet. In this region there are many nerve endings which contain mitochondria, synaptic vesicle-like structures, and neurosecretory granules, as well as many processes of glial cells and of ependymal cells. Some nerve endings appear to contain vesicles almost entirely of the “synaptic” type. These endings are presumably those of nonneuro-
secretory axons. Two types of synaptic vesicle-like structures were distinguished by their mean diameters (390 Å and 490 Å in the parakeet; 375 Å and 550 Å in the pigeon). The diameter of the neurosecretory granules ranges from 600 Å to 1,000 Å in the parakeet and from 550 Å to 1,560 Å in
In the pigeon median eminence and pars nervosa, the axonal endings which contain few neurosecretory granules have larger vesicles of 550 Å; the end-
ings which include many neurosecretory granules contain smaller vesicles of 375 Å. The relationship among smaller and larger vesicles in the parakeet median eminence and pars nervosa has been discussed in a previous paper (Kobayashi et al., 1961).

Between the parenchymal tissues of the median eminence and the endothelium of the capillaries of the primary plexus, there are parenchymal and endothelial basement membranes. Between the two membranes is a thick pericapillary connective tissue space, containing collagen fibrils and frequently fibroblasts. This thick wall frequently sends folds into the parenchyma of the median eminence. Extracellular granules were not observed in the pericapillary connective tissue space.

In the neurosecretory axons in the upper region of the palisade layer, "synaptic vesicles" were not found. This means that the upper region does not contain neurosecretory axonal endings. In the capillaries of the primary plexus a fenestrated endothelium was frequently observed. The fine structure of the outer surface of the median eminence is quite similar to that of the pars nervosa in both parakeet and pigeon. An intimate relation between the glial cells and the neurosecretory axons was frequently encountered.

**Neurohypophysial Hormones in Bird Median Eminence and Pars Nervosa.** Twenty-two young adult pigeons were divided into 3 groups, containing 10, 6, and 6 pigeons. A batch of the extract was prepared from the pooled tissues of each group (Fig. 5). The results obtained with rat-uterus and frog-bladder assay methods are given in Table 1. The median-eminence extract of the pigeon contained 3/5 of the potency of the pars-nervosa extract in rat-uterus activity and 3/5 potency in frog-bladder activity.

![Fig. 5. Parasagittal section of median eminence-pituitary region of pigeon, stained with paraldehyde–fuchsin (from Oota and Kobayashi, 1962). The tissue used for electron microscopy is located in the figure. ah, adenohypophysis; ame, anterior median eminence; oc, optic chiasma; pme, posterior median eminence; pn, pars nervosa; pv, portal vessels; sht, supraopticohypophysial tract; III, third ventricle.](image-url)
The extracts of the pars nervosa and median eminence showed higher activities with the frog-bladder method than with the rat-uterus method. The ratio of the frog-bladder activity to rat-uterus activity assayed without Mg was always higher in the median-eminence extract (200, 290, and 650) than in the pars nervosa (140, 170, and 170), although the values varied over a wide range in the former.

<table>
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<th>Tissues</th>
<th>Exptl. No.</th>
<th>No. of Birds in Expt.</th>
<th>Mean Dry Weight (mg per Individ.)</th>
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<th>Frog-bladder Activity (mg per Individual)</th>
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* From Ishii et al., 1962.

95 percent fiducial limits are indicated in parentheses if applicable, otherwise the activities are expressed by only geometric mean.

Effect of Long Daily Photoperiods on Neurohypophysial Hormone Activity of Median Eminence and Pars Nervosa.—In this experiment the passerine *Zosterops palpebrosa japonica* was used. The bird is known to breed in late spring under natural conditions. The photoperiodic conditions inducing the gonadal development have already been established in this bird by Miyazaki (1934, 1935) and Kobayashi (1954). The birds were obtained from a commercial source in November. They had been subjected to natural daily photoperiods before they were transferred to the laboratory. Before the experiment started, they had been maintained under 8-hour daily photoperiods for about 1 month in the laboratory. The experiment was carried out in December. The experimental birds were exposed to long days (16L-8D), and the control birds were retained under short days (8L-16D). The neurohypophysial hormone activities in the median eminence and pars nervosa following long days were assayed by the frog-bladder method.

The frog-bladder activity in the median eminence of *Zosterops* showed a significant increase on the 12th day of the experiment; thereafter the activity decreased. There was much more neurosecretory material in the median
eminence of the long-day birds killed on the 12th and 19th days of the experiment than in control birds. The long-day birds killed on the 28th day of the experiment contained about the same amount of neurosecretory material as did the control birds. These changes were accompanied by notable growth of the gonads. The activity in the pars nervosa increased significantly on the 19th day of the experiment.

**DISCUSSION**

The increase in acid phosphatase activity in the supraoptic nucleus region of the long-day White-throated Sparrows reflects increased general cellular metabolism, and suggests that the photoperiodic response involves increased activity in the supraoptic nucleus during photoperiodic stimulation (16L–8D; 16L–32D), although it is difficult to say that this increase in activity is entirely attributable to the neurosecretory cells therein. But it is definite that in the neurosecretory cells of the supraoptic nucleus the neurosecretory material increased in the long-day White-throated Sparrows. It is possible that the acid phosphatase activity in individual cells increased substantially more than is indicated in Fig. 2, since those cells with acid phosphatase activity constituted only a small part of the samples of the supraoptic region.

In the White-crowned Sparrow, the activity of acid phosphatase increased similarly in the supraoptic nucleus, but the neurosecretory material in the neurosecretory cells showed a decrease (Oksche et al., 1959). The discrepancy between the two species of sparrows in the amount of material in the neurosecretory cells may be due to the difference in the photoperiodic history preceding the onset of the experiment and also to the difference in the photoperiodic schedules. In the neurosecretory cells of the White-throated Sparrow the amount of neurosecretory material synthesized may be more than that of neurosecretory material transported to the nerve endings. In the White-crowned Sparrow the relation between synthesis and transport may be reversed. At any rate, the acid phosphatase activity increased in the supraoptic region of both species of birds.

The increased activity of acid phosphatase in the median-eminence region may be involved in the metabolism, which may be indirectly related to breakdown of the neurosecretory granules into small molecules and their transfer from endings to capillaries. Histochemical studies have revealed that the nerve fibers, presumably the neurosecretory axons, of the palisade layer of the median eminence showed a strong acid phosphatase reaction (Kobayashi and Farner, 1960). The occurrence of this enzyme in nerve fibers is well known (see, for example, Smith, 1948; Shimizu, 1950; Leduc and Wislocki, 1952).

The neurosecretory material in the median eminence of long-day photosensitive White-throated Sparrows tended to increase, but in long-day photosensitive White-crowned Sparrows the material decreased in the median eminence (Oksche et al., 1959; Wolfson and Kobayashi, 1962). As mentioned
below, the neurosecretory material increased in the median eminence of *Zosterops* following long-day treatment. The difference in the amount of neurosecretory material after long-day treatment in different species may be explained by different rates of storage and release in the median eminence in different species. In both species of sparrows the acid phosphatase activity in the median eminence increased following long days, regardless of whether the neurosecretory material increased or decreased.

Thus, in the long-day photosensitive birds the enzyme activity increased in the supraoptic region, median-eminence region, and adenohypophysis and was accompanied by testicular growth, but the photorefractory White-crowned Sparrow did not respond to long days by an increase in enzyme activity in any tissues tested. These findings suggest that acid phosphatase activity is a very useful parameter for a quantitative expression of the activity of the hypothalamo-hypophysial system. Furthermore, they suggest that the supraoptic region, the median-eminence region, and the adenohypophysis are involved in the photoperiodic stimulation of gonads. The enzyme activity of the pars nervosa did not show any change in the birds exposed to long days, although that of the median eminence increased.

The increased activity in the supraoptic and median-eminence regions in the White-throated Sparrow subjected to short days (6L–18D) may be related to phenomena other than gonadal growth. Another interesting point observed in the White-crowned Sparrow is that the enzyme activity of adenohypophysis was higher in the photosensitive birds kept under 8-hour daily photoperiods than the refractory birds maintained on 13-hour daily photoperiods. This difference was also evident in testicular weights. In the former it was 1.14 ± 0.15 mg and in the latter 0.60 ± 0.18 mg, in averages of 6 birds, respectively.

The increased proteinase activity in the median eminence of long-day birds may be related to breakdown of the neurosecretory granules into small molecules which can traverse the axonal membrane and the capillary wall. Thus, the components of neurosecretory material may reach adenohypophysis and perhaps stimulate directly or indirectly the release of gonadotropins. The peak of the activity of proteinase occurred on the 14th day of exposure to long days in both median eminence and adenohypophysis. Proteinase may also be concerned with the breakdown or synthesis of the secretory granules in the gonadotropic cells. We could not detect any activity change in the supraoptic nucleus. This may be due to a small number of the neurosecretory cells in the supraoptic nucleus. Although there has been much discussion of acid phosphatase and proteinase of the neurosecretory system with special reference to adenohypophysial activity, we do not know whether or not the neurosecretory substance released from the median eminence into adenohypophysis really plays a role in the gonadotropin-release mechanism.

Electron-microscope studies showed the presence of neurosecretory axonal endings containing synaptic vesicles around the blood capillaries of the pri-
mary plexus in the median eminence of pigeon and parakeet. A diagram of
the hypothalamo-hypophysial neurosecretory system based on our findings
has been given by Kobayashi et al. (1961). The pericapillary connective
tissue space between parenchymal tissues of median eminence and the endo-
thelium of the capillary is thick, as is true of other endocrine organs (Far-
quhar, 1961).

The larger synaptic vesicles in the endings containing neurosecretory gran-
ules may release neurohumor from the vesicles, and this neurohumor may in
turn trigger neurohormone release from the neurosecretory granules in the
same endings (Koelle, 1961). This neurohumor may also play a role in
release of neurohormone through the axonal membrane into the circulation.

We have not observed any continuity of the neurosecretory granule mem-
brane and the cell membrane which shows the process of discharging contents
of the granules into the pericapillary connective tissue space, as occurs in the
rat adenohypophysis (Farquhar, 1961; Ichikawa, 1959). The mechanism of
discharge of hormone from the cells may be different between the cells con-
taining synaptic vesicles and those without synaptic vesicles.

The electron-lucent neurosecretory granules may be “empty” granules
from which the neurosecretory material was released. We have found that in
the pars nervosa of dehydrated pigeon almost all the granules become
“empty” (Oota, 1962), and the neurohypophysial hormone activities tested
on frog bladder and rat uterus decrease to \( \frac{1}{10} \) of the control activity with a
marked decrease of neurosecretory material (Ishii et al., 1962).

The endings containing only synaptic vesicles are conceivably the endings
of nonneurosecretory neurons. It is possible that the interaction between
neurosecretory and nonneurosecretory axons plays an important role in regu-
lating the release of the neurohypophysial hormones from the median emi-
nence. The presence of two kinds of axons in the median eminence of the
guinea pig has been reported (Barry and Cotte, 1961). Although a close
relationship between glial cells and neurosecretory axons was observed, the
physiological meaning is not known at the present time. Protrusion of capil-
lary wall into the parenchymal tissue of median eminence is favorable for the
release of hormone by increasing the contact area between them.

The extract of the pigeon median eminence showed strong frog-bladder
activity and slight rat-uterus activity. The ratios of the frog-bladder activity
to the rat-uterus activity were 200, 290, and 650. The ratios of 200 and 290
coincide with the ratios obtained with arginine vasotocin alone, 210 and 270,
calculated from the data of Sawyer (1960) and Munsick et al. (1960), re-
spectively. The ratios obtained in this experiment show that the pigeon
median eminence contains predominantly arginine vasotocin or arginine vaso-
tocin-like substance. The nearly complete inactivation of activities in the
median eminence by sodium thioglycollate indicates that the pharmacological
properties in the extracts could not be due to 5-hydroxytryptamine, acetyl-
choline, adrenaline, histamine, or substance P. Furthermore, it indicates that
active principles in the extract have a disulfide bond in their structure (Ishii et al., 1962). Recently it was also found that the median eminence of the White-crowned Sparrow had neurohypophysial hormone activity (Sawyer and Farner, pers. comm.). In the pigeon pars nervosa the ratio was 140–170, which is close to the data obtained by Munsick et al. (1960) in the fowl pars nervosa. These values suggest the presence of both oxytocin and arginine vasotocin in the pigeon pars nervosa.

In the Zosterops experiment, the neurohypophysial hormone, presumably arginine vasotocin or arginine vasotocin-like substance, increased in the median eminence of long-day photosensitive birds. The neurosecretory material also increased in the median eminence of these birds, as in the White-throated Sparrow (Wolfson and Kobayashi, 1962). These changes in the median eminence were accompanied by gonadal growth. The results strongly suggest that there is a relationship between the amount of arginine vasotocin or arginine vasotocin-like substance in the median eminence and the secretion of gonadotropins of the adenohypophysis, although at the present moment the nature of the relationship is not thoroughly understood. It is also possible that the carrier substance of neurohypophysial hormone in the neurosecretory material may have a role in the release of gonadotropins from the adenohypophysis. The meaning of the increased activity of the pars nervosa on the 19th day of experiment is not known at the moment. The changes in the median eminence and pars nervosa did not parallel each other. This suggests that the control of the activities of median eminence and pars nervosa is mutually independent, as was suggested in the acid phosphatase experiments in White-crowned Sparrows and White-throated Sparrows. Furthermore, dehydration caused a decrease in neurohypophysial activity in the pars nervosa of the pigeon, but not in the median eminence (Ishii et al., 1962). Therefore, the median eminence is not a part of the osmoregulatory apparatus.

**SUMMARY**

Acid phosphatase activity in the hypothalamo-hypophysial system of the White-crowned Sparrow and White-throated Sparrow was measured. Proteinase activity in the same system was measured in the White-crowned Sparrow. In photosensitive birds subjected to long-day photoperiods there was a significant increase in acid phosphatase and proteinase activity in the median-eminence region correlated with an increase in the enzyme activity of the adenohypophysis and rapid gonadal growth. In the case of acid phosphatase, an increase of the activity of the supraoptic region was also observed. These changes were not as evident in either photosensitive birds kept under short-day photoperiods or in photorefractory birds exposed to long-day photoperiods. Acid phosphatase and proteinase are useful parameters to express quantitatively the activity of the hypothalamo-hypophysial system. Acid phosphatase was histochemically demonstrated in the fibers of the palisade layer of the median eminence.
The neurosecretory material increased in the median eminence of photosensitive White-throated Sparrows and Zosterops exposed to long-day photoperiods, but did not increase in the White-crowned Sparrow. This discrepancy was discussed briefly.

The light- and electron-microscope studies on the parakeet and pigeon median eminence have revealed the following: A number of neurosecretory axons arising in the hypothalamic neurosecretory nuclei proceed to the median eminence and terminate around the capillaries of the hypophysial portal system, as well as around the capillaries in the pars nervosa. The pericapillary connective tissue space is thick and sends many folds into median-eminence parenchyma. Four types of granules or vesicles were found in the axonal endings near the capillaries in both median eminence and pars nervosa: (1) smaller synaptic vesicle-like structures, (2) larger synaptic vesicle-like structures, (3) electron-dense neurosecretory granules, and (4) electron-lucent neurosecretory granules. The distribution of these granules and vesicles is different in different endings. The role of “synaptic vesicle” in the neurosecretory axonal endings was discussed in relation to release of material from the neurosecretory granules. In addition to the neurosecretory nerve endings, axonal endings of nonneurosecretory neurons were found in the outer region of the median eminence.

The pigeon median eminence showed neurohypophysial hormone activity. The activity is attributable mostly to arginine vasotocin or arginine vasotocin-like substance. Dehydration caused a decrease of neurohypophysial hormone activity in the pars nervosa correlated with a decrease of aldehyde-fuchsin stainable neurosecretory material, but not in the median eminence of pigeon.

Prolonged daily photoperiods caused increases of neurosecretory material and of neurohypophysial hormone activity in the median eminence of Zosterops palpebrosa japonica. Significant changes occurred also in the pars nervosa, but the changes were not parallel in the median eminence and pars nervosa. It is suggested that the activities of the median eminence and pars nervosa are independently controlled.

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Histologie de la Sécrétion Oesophagienne du Manchot Empereur

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Le Manchot Empereur (Aptenodytes forsteri) se reproduit en plein hiver à proximité de la côte antarctique entre les latitudes 66° et 78° S. La plupart des colonies de l'espèce sont établies sur la glace de mer de telle sorte que l'oiseau dispose des 9 mois qui séparent la formation de cette dernière de la débâcle estivale pour accomplir la totalité de son cycle annuel.

Au mois de mai les femelles, après avoir confié à leur partenaire mâle l'œuf unique qu'elles viennent de pondre, vont à la mer rechercher des aliments pour elles et pour leur poussin. Elles ont jeûné depuis près de deux mois et perdu près de 20 pour cent de leur poids d'arrivée. Les mâles, dont les réserves lipidiques sous-cutanées et péritonéales sont beaucoup plus importantes, assurent seuls l'incubation pendant 62–66 jours; leur relève est assurée par les femelles à l'approche de l'éclosion.

Cependant différents facteurs, comme l'état d'embonpoint au départ de la colonie, les difficultés de recherche de nourriture, la présence des prédateurs, sont susceptibles de prolonger la durée du séjour alimentaire de ces dernières.

Les poussins de ces femelles attardées auraient donc bien peu de chance de survivre si les mâles couveurs n'avaient la possibilité de leur fournir un aliment de secours. (Il n'est d'ailleurs pas exclu que le même phénomène se manifeste un mois plus tard chez les femelles. En effet ces dernières, même si elles ont épuisé leur contenu stomacal, devront attendre le retour de leur partenaire avant de pouvoir partir à la mer. Elles se retrouvent donc dans la même situation que les mâles un mois auparavant.)

Ces couveurs mâles sont en effet capables, en terme d'un jeûne physiologique dépassant quelquefois 3 mois, de sécréter au niveau de l'oesophage une substance particulièrement nutritive qui permet au jeune manchot de se maintenir et même de gagner du poids (Prévost, 1961).

ÉTUDE DE LA SÉCRÉTION OESOPHAGIENNE

L'obtention d'un échantillon de cette sécrétion n'est pas des plus aisée. Il faut en effet être certain du sexe de l'oiseau choisi, ce qui ne veut pas dire pour autant que la sécrétion sera présente au moment de l'autopsie.

Nous avons cependant eu la chance de trouver un spécimen intéressant le 10 août 1956. Cet oiseau arrivé à l'extrême limite du jeûne physiologique—il ne pesait que 20,600 kg et ne disposait que de traces de graisse—couvait un poussin de 500 g environ, à l'abdomen rebondi. Ce jeune oiseau était donc alimenté régulièrement depuis plusieurs jours puisqu'il avait dépassé de près de 200 g son poids de naissance.

Fortement dilaté, ses parois épaisses et très vascularisées, l'oesophage de l'adulte contenait des traces de mucus à la partie supérieure et de petits gra-
nules blancs dans les plis de la région inférieure. Au fond de l'estomac tapissé par une pellicule verdâtre, 182 g de sécrétion oesophagienne étaient accumulés en vue d'un régurgitation ultérieure (Fig. 1).

Le résultat de l'analyse de cette sécrétion, préalablement désséchée, figure au Tableau 1, colonne 2, avec celle de la sécrétion lactée du pigeon et celle du lait de lapine d'après les chiffres que nous avons empruntés à Dabrowska (1932). Si la richesse en protéines et en lipides est élevée chez les deux oiseaux, les glucides sont par contre totalement absents chez le pigeon. Ce
pHénomène paraît être propre au genre Aptenodytes. Il existe en effet chez le Manchot Royal, Aptenodytes patagonica, où la sécrétion sert d'aliment de survie aux poussins pendant la période hivernale (Stonehouse, 1960).

L'étude histologique de quelques fragments d'oesophage prélevés sur un certain nombre d'oiseaux des deux sexes nous a permis de dégager les traits essentiels du processus sécrétoire. Nous décrirons donc les variations d'épaisseur de la muqueuse oesophagienne, l'aspect histologique de la paroi oesophagienne et l'histochimie de la sécrétion:

1) **Variations de la masse du tissu épithélial sécrétant par cm\(^2\) de surface oesophagienne**

Les chiffres apparaissant au Tableau 2 reflètent l'importance des variations de la masse épithéliale chez quatre oiseaux tués à différents stades du cycle reproducteur annuel. Nous constatons que chez le n° 23, un mâle élevant son poussin dans les jours suivant l'éclosion, la masse épithéliale est infiniment plus développée que chez les autres; or cet oiseau n'est autre que celui dont l'estomac contenait 182 g de sécrétion oesophagienne. La preuve est donc faite d'une intense prolifération trophique de la muqueuse de l'oesophage en période de "lactation."

2) **Aspect histologique de l'oesophage et histochimie de la sécrétion**

Comparons l'oesophage "au repos" d'un oiseau en dehors de la période d'éclosion avec celui d'un mâle alimentant son poussin en fin de jeûne physiologique.

**Tableau 1.**—**Composition Chimique de la "Sécrétion Lactée" du Pigeon (1), du Manchot Empereur (2), et de la Lapine (3), (Substance Sèche)**

<table>
<thead>
<tr>
<th></th>
<th>(1)</th>
<th>(2)</th>
<th>(3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eau</td>
<td>0,00</td>
<td>0,0</td>
<td>0</td>
</tr>
<tr>
<td>Protéines</td>
<td><strong>57,41</strong></td>
<td><strong>59,3</strong></td>
<td>50,95</td>
</tr>
<tr>
<td>Lipides</td>
<td>34,19</td>
<td>28,3</td>
<td>34,26</td>
</tr>
<tr>
<td>Cendres</td>
<td>6,51</td>
<td>4,6</td>
<td>8,39</td>
</tr>
<tr>
<td>Glucides</td>
<td><strong>0,0</strong></td>
<td><strong>7,8</strong></td>
<td>6,39</td>
</tr>
</tbody>
</table>

**Tableau 2.**—**Variations de la Masse de Tissu Épithélial**

<table>
<thead>
<tr>
<th>Sexe</th>
<th>N° de l'Oiseau</th>
<th>Tissu Épithélial(^a)</th>
<th>Date Étude en 1956</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femelle</td>
<td>19</td>
<td>33 mm(^3)</td>
<td>9 juillet</td>
<td>Oiseau revenant de la mer l'estomac vide</td>
</tr>
<tr>
<td>Femelle</td>
<td>26</td>
<td>66 mm(^3)</td>
<td>10 septembre</td>
<td>Oiseau séjournant à la colonie</td>
</tr>
<tr>
<td>Mâle</td>
<td>6</td>
<td>137 mm(^3)</td>
<td>20 avril</td>
<td>Oiseau en couple séjournant à la colonie</td>
</tr>
<tr>
<td>Mâle</td>
<td>23</td>
<td>660 mm(^3)</td>
<td>10 août</td>
<td>Adulte élevant un poussin en l'absence de la femelle</td>
</tr>
</tbody>
</table>

\(^a\) Valeur calculée du vol. de tissu épithélial par cm\(^2\) de surface oesophagienne.
Chez le premier la paroi oesophagienne est relativement mince. L’épithélium malpighien bien que stratifié a une épaisseur réduite. Les glandes oesophagiennes en forme de massue étroite sont pratiquement dépourvues de lumière centrale et leurs cellules muqueuses, peu nombreuses, présentent une activité sécrétrice discrète (Fig. 2).

Cette organisation relativement simple est profondément remaniée chez les mâles sacrifiés à l’approche de l’éclosion du poussin. L’épithélium oesophagien dans son ensemble subit une hypertrophie considérable qui atteint à la fois le revêtement malpighien et les glandes muqueuses de l’oesophage. En effet, une intense multiplication mitotique des cellules basales augmente le nombre des assises malpighiennes superposées. Depuis la basale jusqu’à la couche la plus superficielle la cellule de cet épithélium garde un aspect jeune: noyau volumineux, cytoplasme abondant, pas de kératinisation.

Le tissu lui-même est richement vascularisé: une multitude de capillaires en “épingle à cheveux” irrigue dans toute son épaisseur le massif épithelial, favorisant aussi le métabolisme du territoire nouvellement formé; de nombreuses mitoses malpighiennes se localisent d’ailleurs au voisinage immédiat des capillaires ascendants.

L’extension tissulaire n’a pas lieu seulement en épaisseur, mais aussi en surface; faute de place disponible, la muqueuse oesophagienne en proliférant, soulève en de puissants plissements les crêtes longitudinales de la paroi oesophagienne du mâle, aboutissant à une augmentation énorme du volume épithélial (Fig. 3).

Fig. 2. Coupe de l’oesophage du mâle 6 (20 avril 1956). Trichrome de Masson (grossissement 33 ×).
Le massif malpighien puissant est le siège d’une élaboration intense de lipides (Fig. 4). Traité par un réactif spécifique (Oil blue N) la muqueuse apparaît colorée en bleu intense. Toutes les cellules malpighiennes, de la plus profonde à la plus superficielle, participent à cette élaboration; il ne s’agit point d’une dégénérescence graisseuse—ce sont toutes des cellules d’aspect jeune, chargées d’enclaves lipidiques abondantes. Les cellules les plus externes se détachent d’ailleurs et s’intègrent aux sécrétions déversées dans l’oesophage par les glandes muqueuses.

L’apport malpighien est donc complexe; les lipides intra-cellulaires forment l’aliment énergétique, la masse imposante des protéines cytoplasmiques et nucléaires représentant l’élément plastique de l’aliment destiné au poussin.

Comme nous l’avons annoncé, l’hypertrophie ne se limite point aux assises malpighiennes; les glandes muqueuses de l’oesophage sont également atteintes par des phénomènes de prolifération intense. Tubulaire et compacte à l’origine, chaque glande s’étale progressivement en une vaste formation bul-
beuse reliée à l’extérieur par un canal excréteur long et étroit. L’hypertrophie est telle que les culs-de-sac glandulaires forment par juxtaposition réciproque une vaste nappe s’étendant à la base du massif malpighien.

La paroi de chaque glande, unistratifiée, est constituée par un nombre considérable de cellules sécrétrices déversant leur produit d’élaboration dans une cavité centrale distendue (Fig. 5 et 6).

Le contenu de cette chambre collectrice semble hétérogène. Deux substances différentes sont juxtaposées: des plaques confluentes de substance colloïde sont enrobées d’une formation visqueuse. Non miscibles de par leurs propriétés physiques, les deux constituants diffèrent également par leur nature chimique.

La masse visqueuse d’enrobage est fortement colorée par la fuchsine paraldehyde (sans oxydation permanganique préalable). Cette mucine présente une métachromasie franche au bleu de toluidine même très acide. Elle est en outre la seule à retenir le bleu alcian au pH 0,8. Il s’agirait donc d’un mucopolysaccharide très acide, selon toute probabilité d’une mucine sulfatée.
La substance colloïde présente des caractères histochemiques d'une gluco-protéine neutre : colorable par la méthode de Mac Manus elle est réfractaire aux colorations des mucines. Nettement séparées dans la cavité collectrice les deux substances sont cependant élaborées par la même cellule glandulaire.

La cytologie de cette sécrétion est aussi originale qu'insolite. Dans une cellule glandulaire chargée de produits de sécrétion chaque grain élaboré est structuralement complexe : la partie centrale est formée d'une glycoprotéine neutre, P.A.S. positive, l'enveloppe par un mucopolysaccharide acide. Par une double coloration, Mac Manus-bleu Alcian acide par exemple, l'écorce se colore en bleu vert, tandis que le centre reste rouge. Cette dualité tinctoriale franche se maintient pendant toute l'élaboration intracellulaire. Le même grain de sécrétion s'accroîtra, se transformera en un enclave intracellulaire plus ou moins allongée et flexueuse, la glycoprotéine centrale demeurant isolée du cytoplasme par une mince écorce de mucine acide. Dans l'enclave expulsée hors de la cellule glandulaire les deux composantes fondamentales, se dissocient, les parcelles glycoprotidiques formant par coalescence de
Fig. 6. Les cellules sécrétrices d'une crypte oesophagienne—mâle 23—Gabe Hématoxyline (grossissement 530 X).

grosses masses P.A.S. positives, la mucine acide corticale alimentant l'excipient visqueux de la sécrétion glandulaire: nous retrouvons alors le contenu de la chambre collectrice dont nous avons parlé antérieurement.

COMMENTAIRES

En définitive la sécrétion oesophagienne du Manchot Empereur, proche par sa composition lipo-glycoprotidique du lait de Mammifère, apporte au poussin un aliment d'attente biologiquement équilibré. Le tissu mammaire hautement spécialisé d'une part et le tissu oesophagien épithélial d'autre part, bien que totalement différents par leur origine et leur texture, exercent la même fonction trophique en élaborant des substances chimiquement voisines.

Insolite dans ses aspects histochemiques l'activité sécrétoire de l'oesophage de cet oiseau apparaît moins singulière dans le cadre de la physiologie comparée de la nutrition.

Comme chez le manchot le lait du pigeon, destiné à l'alimentation de
l'oisillon est élaboré par un épithélium malpighien, celui du jabot. Il s'agit néanmoins dans ce cas d'un processus relativement simple: la desquamation massive des cellules kératinisées atteintes d'une dégénérescence graissouse profonde.

Nous retrouvons toutefois des phénomènes rappelant ceux que nous venons de décrire chez le Manchot Empereur chez certains vertébrés inférieurs. Aussi chez le *Nectophrynoides occidentalis* ou chez *Salamandra atra*, vivipares strictes, l'alimentation des jeunes intra-utérins est assurée par une sécrétion glycoprotidique de la paroi utérine, mais aussi par l'apport de mucopolysaccharides acides élaborées par l'oviducte maternel. Les deux substances, que nous retrouvons dans la sécrétion oesophagienne du Manchot Empereur, sont donc susceptibles d'assurer à elles seules le développement total des jeunes en croissance active. Chez ce dernier la complexité du métabolisme cellulaire atteint son point culminant.

Une cellule glandulaire oesophagienne destinée à élaborer des mucines sulfatées et des glycoprotéines alimentaires est potentiellement susceptible d'élaborer aussi des lipides identiques à ceux d'une cellule malpighienne en voie de transformation progressive. Cette même potentialité étendue caractérisera une cellule malpighienne de l'oesophage.

Nous savons que chez les Rongeurs une cellule malpighienne typique est susceptible de se transformer en cellule mucipare, c'est ce que l'on constate dans l'épithélium vaginal par exemple. Chez le Manchot Empereur c'est la cellule malpighienne de l'oesophage qui en se chargeant d'inclusions mucoides fournira le revêtement du canal excréteur de la glande.

C'est donc la polyvalence de la cellule épithéliale, capable d'élaborer des substances aussi différentes que des lipides, des protides, des glycoprotéines et des mucopolysaccharides, qui rend si singulier le cas du Manchot Empereur.

**RÉSUMÉ**

Les Manchots Empereurs mâles sont capables, au terme d'un jeûne physiologique de plus de 3 mois, de sécréter une substance glyco-lipo-protidique qui permet au poussin de se maintenir et même de gagner du poids en attendant les aliments apportés par la femelle. Cet "aliment de secours" est élaboré par la muqueuse oesophagienne qui atteint un développement considérable chez ces mâles nourriciers. Les substances protidiques comme les lipides proviennent de la desquamation des cellules épithéliales non kératinisées de la muqueuse oesophagienne. Les mucopolysaccharides et les glycoprotéines tirent leur origine des sécrétions complexes des glandes de l'oesophage, alors que les lipides sont formés au sein du massif épithelial de la muqueuse oesophagienne.

**BIBLIOGRAPHIE SOMMAIRE**

Physiologists have long known that smaller homiotherms have a higher metabolism per unit weight than larger ones. Hummingbirds are among the smallest warm-blooded animals in the world, and some species weigh considerably less than the smallest recorded mammal, the shrew Microsorex hoyi, which may weigh as little as 2.3 g, while the smallest-known hummingbird (Calypte helenae) has been recorded weighing as little as 1.7 g. Because of this extreme small size in the hummingbird family (Trochilidae), it was not surprising that Pearson (1950) reported very high metabolic rates for Anna’s Hummingbird (Calypte anna) and Allen’s Hummingbird (Selasphorus sasin). Resting and flight levels of 11–16 cc O₂/g hr, and 70–85 cc O₂/g hr, respectively, were recorded. The reported flight-metabolism values are the highest recorded from any vertebrate. On the basis of the apparent relationship between the metabolism of hummingbirds and shrews and larger homiotherms, Pearson (1953) concluded that 2.5 g was the lower limit of small size in homiotherms. Pearson further demonstrated the ability of hummingbirds to abandon their control of body temperature ($T_b$) at night, entering a state of torpor. Their $T_b$ drops to within 1° C of ambient temperature ($T_a$), and there is a marked decrease in oxygen consumption, heart and breathing rate, and other bodily processes. Hummingbirds were thought to be indifferent homiotherms (Pearson, 1960), abandoning their control of $T_b$ each night, except for advanced nestlings and incubating females.

Despite the intriguing nature of the physiology of hummingbirds, there have been surprisingly few studies concerned with this aspect of their biology. The information that is available from these studies is deficient in several respects. First, it is based on less than a dozen birds of but two species. Second, there is little indication of the relationship between $T_a$ and metabolism. Third, the methods used in obtaining the resting levels of metabolism are not comparable to those used in obtaining the basal metabolism of larger birds.

Since further study appeared warranted, it has been necessary to develop methods for capturing, transporting, and maintaining large numbers of hummingbirds (see Lasiewski, 1962a). With the kind cooperation of United Airlines, it was possible to transport 69 hummingbirds from California to Ann Arbor, Michigan, for detailed laboratory study (25 in 1960, 44 in 1961). The birds adapted nicely to laboratory conditions, and were maintained in good condition for periods exceeding 1 year. Natural mortality was negligible.

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ble, and it seems possible to maintain hummingbirds in captivity for as long as is deemed necessary.

With the maintenance of a large number of birds assured, it seemed profitable to quantify the physiological properties associated with their miniature size. I paid particular attention to the effects of $T_a$ upon such processes as oxygen consumption, heart and breathing rate, $T_b$ regulation, caloric intake, and rates of evaporative water loss. I was able to obtain these measurements on large numbers of individuals, using the following seven species: Black-chinned Hummingbird (*Archilochus alexandri*), Ruby-throated Hummingbird (*A. colubris*), Rufous Hummingbird (*Selasphorus rufus*), Allen’s Hummingbird, Costa’s Hummingbird (*Calypte costae*), Anna’s Hummingbird, and Calliope Hummingbird (*Stellula calliope*). Some of the data from these studies have been presented in the following papers: Lasiewski (1961); Shellabarger, Lasiewski, and Hyncik (1961); and Lasiewski (1962b).

This paper is concerned with one aspect of this research, the relation between oxygen consumption and small size in hummingbirds.

**MATERIALS AND METHODS**

The capture, maintenance, and transportation of hummingbirds is discussed in detail elsewhere (see Lasiewski, 1962a).

The oxygen consumption of resting and active hummingbirds was measured with a Beckman G-2 oxygen analyzer, connected to a Brown recording potentiometer. The oxygen consumption during flight was measured with an oxygen servo spirometer (Custom Engineering, Model 160). The hummingbirds were housed in 1-gal cans, fitted with exit and entry ports for air, and with a 3.5-inch glass port. During flight measurements, the chambers were equipped with containers for Ascarite and Drierite (CO$_2$ and H$_2$O absorbents, respectively), and with a small battery-operated fan. The chambers were placed in constant-temperature cabinets, and light, when needed, was provided by a 60-w incandescent bulb, controlled by a poultry timer.

Temperatures inside the chambers were recorded with copper-constantan thermocouples connected to a suitably calibrated Brown recording potentiometer.

All oxygen consumption values are expressed as volumes of dry gas corrected to 0°C and 760 mm Hg.

**RESULTS AND DISCUSSION**

The resting values of 11–16 cc O$_2$/g hr reported by Pearson (1950) are considerably higher than those predicted for birds of this size range by the weight–metabolism relationships of larger birds. The Brody and Proctor (1932) equation for birds:

$$\text{Metabolism (kcal/day)} = 89 \text{ Weight (kg)}^{0.64}$$

predicts a metabolism of 5.2 cc O$_2$/g hr for a 5-g bird, and 7.4 cc O$_2$/g hr for a 2-g bird. The validity of this equation has been questioned by King and
Farner (1961) because of a paucity of data in critical areas, and because of discrepancies in the conditions under which the original data were obtained. King and Farner reanalyzed the available data for birds, utilizing more rigid standards, and found that the following equation was more suitable for birds weighing more than 125 g:

$$\text{Metabolism (kcal/day)} = 74.3 \times \text{Weight (kg)}^{0.74}$$

The King-Farner equation is statistically indistinguishable from the comparable equation for mammals, while the Brody-Proctor equation is markedly different. There is no a priori reason why the weight-metabolism relationships of birds and mammals should differ from each other. The King-Farner equation predicts metabolism of 2.5 and 3.2 cc O$_2$/g hr for 5- and 2-g birds, respectively.

Pearson did not feel that it was possible to obtain metabolic values for hummingbirds resting in the dark, since his birds dropped into torpor when the light was removed. His resting values are for birds that were in the light, had food available to them, and were at $T_a$ of 22-24° C. These temperatures are below the zones of thermal neutrality for these species. The resting values reported by Pearson are not basal or standard metabolic values, and should not be compared to the basal levels of other birds and mammals. I was able to duplicate the resting levels reported by Pearson, by using comparable conditions.

I also found it possible to maintain hummingbirds resting in the dark, in a postabsorptive state, long enough to obtain temperature-metabolism curves comparable to those characterizing obligate homoiotherms (Fig. 1).

The levels of metabolism in the zones of thermal neutrality are considerably lower than previously reported metabolism values, with minimal levels in this zone ranging from 2.8 to 4.3 cc O$_2$/g hr. Thirty-seven values, representing 26 individuals, have been obtained with levels of 5.0 cc O$_2$/g hr, or lower. From the available data, I can detect no trend of metabolism with respect to body weight. The lability of $T_h$ in hummingbirds and the differences in the conditions of the birds in the 2 years make it difficult to assess species differences. In 1960, I was still developing the methods for maintaining hummingbirds in captivity, and the birds, although healthy, did not possess the fat stores that characterized the birds maintained in 1961. During the experimental period, the 1960 birds were more likely to enter torpor than the 1961 birds. The minimal values of metabolism in the zones of thermal neutrality are similar to those predicted for birds of this size range by the King-Farner equation, and are lower than those predicted by the Brody-Proctor equation.

The agreement of hummingbird metabolism with the King-Farner equation is somewhat surprising, since most of the smaller birds studied had values of oxygen consumption that were higher than predicted by this equation. However, most of the smaller birds that were investigated were passerines,
Fig. 1. Metabolism-temperature curves for six species of hummingbirds resting in the dark, in a postabsorptive state, and a point for *A. colubris*. Values were obtained 2–4 hr after the birds were placed in a darkened chamber at a constant temperature. Values obtained in 1960 are designated by open circles, while those obtained in 1961 are designated by closed circles. The lines are drawn along the lower limits of the zones of chemical regulation, and the values of the slopes are expressed as cc O₂(g hr °C⁻¹). (From Lasiewski, 1963.)
in many cases fringillids. Dawson (unpubl. observations) has noted a weight-regression coefficient of 0.7 among the passerines. It may be that passerine birds conform to a slope similar to that for other birds, but with a higher \( y \) intercept. More data are needed from small birds other than passerines to clarify this point.

Below the lower critical temperatures (27–30° C), metabolism increases sharply with decreasing \( T_a \). Hummingbirds regulating in the dark are characterized by a range of \( T_h \)'s of over 5° C, and, since a change in \( T_h \) will influence the metabolism, it did not seem justified to fit a least-squares line to these slopes. Instead, lines were drawn along the lower limits of the zones of chemical regulation. These lines extrapolate to temperatures of 33–37° C (except for \( S. calliope \)). From these data, one would predict that hummingbirds resting in the dark are able to regulate their \( T_h \)'s at levels lower than 40° C. This metabolic prediction is borne out by actual measurements of the core \( T_b \) in hummingbirds, which show that birds resting in the dark may regulate their \( T_b \) as low as 34.4° C for considerable periods of time without entering torpor. King and Farner (1961) have pointed out that the order of magnitude of the diurnal variation in \( T_h \) in birds is “at least in part an inverse function of body size.” Hummingbirds, the most diminutive of the birds, may have a diurnal temperature cycle of at least 8° C, excluding torpor.

The slope of the zone of chemical regulation, on a theoretical basis, is inversely proportional to the efficiency of the insulation. Steeper slopes have high conductance values and imply less effective insulative capacities. The values of the slopes of the zones of chemical regulation, in the six species of hummingbirds studied, range from 0.41 to 0.57 cc O\(_2\) (g hr °C\(^{-1}\))\(^{-1}\), and are among the highest measured for birds and mammals. The experimentally determined slope for \( S. calliope \) extrapolates to zero metabolism at a temperature of 45° C, strongly suggesting that the birds are lowering their \( T_h \) with decreasing \( T_a \). A line drawn from 35° C, an approximation of the lower \( T_h \) of hummingbirds resting in the dark, through the point at 16° C, has a slope of 0.61 cc O\(_2\) (g hr °C\(^{-1}\))\(^{-1}\). This is probably a more accurate value of the thermal conductance for \( S. calliope \), the smallest species studied. Generally, the conductance values are inversely related to the average body weight of each species. These values are consistent with that obtained by Morrison, Ryser, and Dawe (1959) for \( Sorex cinereus \), a very small shrew, of 0.60 cc O\(_2\) (g hr °C\(^{-1}\))\(^{-1}\).

Oxygen consumption over 24-hr periods was monitored continually, utilizing a 12-hr photoperiod. It was possible to calculate caloric expenditure per day (assuming that 1 liter of oxygen consumed = 4.8 Cal) over a wide range of \( T_h \)'s (Fig. 2). Generally, caloric expenditure per day increases with decreasing \( T_a \). Many of the birds studied did not enter torpor at night and are designated by a + superimposed over the species symbol. Hummingbirds that entered torpor at night generally had a lower expenditure of energy per
day than those that did not. However, the average differences rarely amounted to more than 20 percent of the total metabolism.

The metabolic rates of 4.88 Cal/day at 24°C, and 6.77 Cal/day at 12°C, reported by Pearson (1954) for specimens of *C. anna* confined to metabolic chambers, are consistent with the data from this study for hummingbirds that entered torpor at night. I have found that hummingbirds do not necessarily enter torpor at night, even at relatively low *Tₐ*'s. If in good condition, they may regulate their *Tₖ* all night at levels between 34.4°C and 40°C without entering torpidity. Hummingbirds are not strictly indifferent homoiotherms, as proposed by Pearson (1960), but generally fall into the category of stubborn homoiotherms, regulating their *Tₖ* over a wide range of *Tₐ*.

Under conditions of physiological stress, such as loss of plumage during molt, or low energy reserves, they may qualify as indifferent homoiotherms.

The low caloric-expenditure values of 2.9 and 3.1 Cal/day at 36°C amply demonstrate that the energetic cost of small size is lower than previously reported, particularly at temperatures within the zones of thermal neutrality. The hummingbird family is primarily a tropical group, although they may be found under a variety of climatic conditions. Outdoor temperatures at Barro Colorado, Panama, are usually 25–30°C (Scholander et al., 1950), and these temperatures correspond closely with the experimentally determined lower critical temperatures for the six species of hummingbirds studied.

Results from studies on the oxygen consumption of hovering hummingbirds have been reported in an earlier paper (Lasiewski, 1962b). Yapp
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(1962) has pointed out that Pearson's figures for flight metabolism "need critical examination," and that Odum's (1960) calculations (based on Pearson's figures) are misleading. Yapp suggested that a flight-metabolism figure lower than the 68–85 cc O₂/g hr reported by Pearson for C. anna and S. sasin is likely to be more nearly correct. By utilizing techniques similar to Pearson's, along with the assumptions implicit in these techniques, I obtained comparable flight-metabolism values for five species of hummingbirds, Calypte costae, C. anna, Selasphorus rufus, S. sasin, and Stellula calliope.

Fortunately, however, an immature male C. costae (3.0 g, Tₐ = 24°C) hovered constantly in the metabolic chamber for over 50 minutes, thereby allowing direct measurements of oxygen consumption during an extended period of flight without any of the aforementioned assumptions. The average flight metabolism for 35 minutes of constant flight was 42.4 cc O₂/g hr, and this value is undoubtedly more representative of the flight metabolism of hummingbirds than earlier values. Assuming that linear flight is no more strenuous than hovering flight, we can provide a revised estimate of the non-stop flight range of Archilochus colubris (Ruby-throated Hummingbird). We shall further assume that the Ruby-throated Hummingbird carries 2 g of utilizable fat (Odum and Connell, 1956), flies at a speed of 25 mph (Greenewalt, 1960; Van Riper in Strong, 1960:178; Pearson, 1961), and has an average flight metabolism of 42 cc O₂/g hr (present study). Utilizing these figures, we can calculate that A. colubris is capable of nonstop flight of over 600 miles, easily enough to span the shortest distance across the Gulf of Mexico. It seems likely that migrating hummingbirds may obtain some lift from linear flight, and the oxygen consumption during migration may be even lower than that of hovering. Migrating small birds regularly make use of favorable winds, and this would allow them an even greater margin of safety. The final word rests with the hummingbirds, and the consensus among ornithologists seems to be that A. colubris does make the migratory flight across the Gulf of Mexico.

ACKNOWLEDGMENTS

The present research was performed as part of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in The University of Michigan.

This investigation was supported by N.S.F. Cooperative Graduate Fellowships for the academic years 1960–61, 1961–62, and by funds from the Graduate Student Research Fund, Horace H. Rackham School of Graduate Studies, The University of Michigan. This work was also supported, in part, by grant G-9238 from the N.S.F. to W. R. Dawson.

Although this study would have been impossible without the kindness and assistance of many people, I am particularly grateful to W. R. Dawson for the use of his laboratory facilities, and for his unfailing support, stimulation, and guidance during the course of the investigation.
SUMMARY

The effects of temperature on the oxygen consumption of postabsorptive hummingbirds resting in the dark, and of hummingbirds over a 24-hr period, were determined in *Calypte costae*, *C. anna*, *Selasphorus rufus*, *S. sasin*, *Archilochus alexandri*, *A. colubris*, and *Stellula calliope*.

The temperature-metabolism curves for hummingbirds resting in the dark, in a postabsorptive state, are comparable to those of obligatory homoiotherms. The minimal levels of metabolism in the zones of thermal neutrality ranged from 2.8 to 4.3 cc O$_2$/g hr, and were similar to those predicted for birds of this size by the King–Farner equation. Thermal conductance is inversely related to body weight, with values ranging from 0.41 to 0.61 cc O$_2$(g hr $^\circ$C)$^{-1}$. Lines drawn along the bottoms of the zones of chemical regulation suggest that hummingbirds may regulate their body temperatures at levels lower than 40$^\circ$ C. Direct measurements of body temperatures for birds regulating in the dark confirm this prediction, and show that hummingbirds are capable of regulating at temperatures as low as 34.4$^\circ$ C for long periods of time without entering torpor.

Metabolism over 24-hr periods increases with decreasing ambient temperature, and birds that enter torpor have a somewhat lower expenditure per day than birds that do not.

The average flight metabolism for a *C. costae*, hovering constantly in a metabolism chamber for over 50 minutes, was 42.4 cc O$_2$/g hr. Calculations suggest that the Ruby-throated Hummingbird is capable of flying nonstop across the Gulf of Mexico during migration.

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The Concept of Faunal Elements or Faunal Types

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The purpose of this paper is to discuss a method for comparing the composition of local terrestrial faunas. It implies an analysis of the geographic origin of the species leading toward a system of zoogeographic classification. For this purpose zoogeographers have made use roughly of two methods of regional classification of the terrestrial faunas of the world. The first is a geographical one, the second a faunal one. The geographical method is static; it tries to define the borders of zoogeographical regions, districts, or provinces. It is part of the classic zoogeography of Philip Lutley Sclater and Alfred Russell Wallace. The faunal method is dynamic; it tries to detect and to describe the far-reaching intergradation of separate faunas throughout the continents. It was propagated by Stegmann (1938), also by Mayr (1951) and by Voous (1955). This method starts from the conception that there are distinct faunas but no distinct zoogeographic regions. This concept is no less arbitrary and no less disputable than that of the zoogeographic regions.

Recently I have tried to use this dynamic approach by applying the concept of "faunal type" to the zoogeographical classification of the breeding birds of Europe (Voous, 1960). As a poor definition of what I meant by faunal type I quote as follows: "To say that a species is of a particular faunal type means that it is a characteristic element of the regional fauna indicated. The characters of a regional fauna result from the habitats afforded in the range covered" (Voous, 1960:6). I will now try to show some implications that the application of the concept of faunal types has in view of a zoogeographical classification of land faunas in general. Illustrative examples are taken from the bird fauna of Europe, most of them from owls and other birds of prey.

HOLARCTIC FAUNA

The fauna of the cold, temperate and warmer regions of Europe, Asia, and North America is called the Holarctic fauna, following common practice that is derived from the classic classification of static zoogeographical regions. Reference to a particular species of bird as a Holarctic faunal type implies that the species has taken part in, or has been subjected to, the geographical and climatological history of the Northern Hemisphere continents at least during the Pleistocene and part of the Tertiary periods, and that its ecological characteristics and geographic distribution have been influenced by that history. The principal events of the ecological history of the Northern Hemisphere have been discussed by Moreau (1954, 1955) and can be summarized as follows: (a) a series of alternating expansions and contractions of glacial and arctic conditions and consequent shifts of all ecological zones;
(b) the diminution and consequent restriction of warm or subtropical forest areas and attendant forest fauna to small and isolated geographical regions, notably in countries surrounding the Mediterranean Sea, the South Caspian region, parts of Manchuria, China, and Japan, and small regions in western and southeastern North America; and (c) periodic changes of sea level causing, among others, the alternation of land connections and sea straits in the region of the Bering Sea, connecting and disrupting faunal contact over land between Asia and America.

Any species of bird that has faced this history and has taken part in the vicissitudes of the Northern Hemisphere I call "a Holarctic faunal element," which means an element of the Holarctic fauna.

Holarctic faunal types can be recognized by a presently wide and more or less exclusive geographic distribution in the Northern Hemisphere. Examples are *Aquila chrysaetos* (Holarctic range), but also *A. clanga* (Palaearctic range), *Milvus migrans* (Old World range), and even *M. milvus* (European range). The Holarctic faunal elements of the European avifauna comprise practically all of the breeding species, with the exception of what I have called Ethiopian (4 species), Indian–African (14 species), cosmopolitan (14 species), Antarctic (1 species), and the group of 5 species of unknown or highly uncertain zoogeographical relations (Voous, 1960:7). The Holarctic faunal types, therefore, comprise not only those species originally classed as "Holarctic" sensu stricto, but also all other groups historically restricted to any part of the Holarctic region, viz. the following faunal types (or sub-types) provisionally proposed:

<table>
<thead>
<tr>
<th>Arctic</th>
<th>North Atlantic</th>
<th>Palaeoxeric</th>
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<tr>
<td>Siberian–Canadian</td>
<td>European</td>
<td>Palaeo–xeromontane</td>
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<tr>
<td>Siberian</td>
<td>European–Turkestanian</td>
<td>Palaeomontane</td>
</tr>
<tr>
<td>Chinese–Manchurian</td>
<td>Mediterranean</td>
<td>Tibetan</td>
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<td>Palaearctic</td>
<td>Mediterranean</td>
<td>Mongolian–Tibetian</td>
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<tr>
<td>Nearctic</td>
<td>Sarmatic</td>
<td>Old World</td>
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<td></td>
<td>Turkestanian</td>
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In the bird fauna of Europe, Holarctic faunal types therefore comprise no less than 381 (91 percent) of the 419 known breeding species. If the Old World faunal types are excepted, the percentage is 86 percent for Holarctic faunal types in Europe. All these species have passed their recent history in some nontropical part of the Northern Hemisphere continents and have there developed their present ecological preferences and have there been subjected to influences inducing geographic variation and geographic species formation. In contrast, Ethiopian (*Falco biarmicus*) and Indian–African (*Aquila rapax, Hieraaëtus fasciatus*) faunal elements now in Europe have had their ecological imprinting and species-formation history outside the Holarctic region.

The history of the Holarctic fauna includes the geographic species formation by isolation in the Old World part (Palaearctic) and New World part (Nearctic) of the main ranges of a large number of species. Thus, apart from 5 North Atlantic species, there are 81 (19 percent) species of European
birds that are still equally distributed in the Nearctic and the Palaeartic parts of the range. These represent the Holarctic faunal type sensu stricto (42), the Siberian–Canadian faunal type (6), and the majority of the Arctic faunal types (33), e.g. Aquila chrysaetos, Buteo lagopus, Aegolius funereus, and Nyctea scandiaca. However, there are at least 274 others (65 percent), including 14 subtypes and a few arctic specimens (9) that, in their present distribution and speciation processes, show the consequences of Nearctic and Palaeartic geographic isolation and therefore must be called Palaeartic faunal types, e.g. Aquila clanga, Buteo rufinus, Haliaeetus albicilla, Falco subbuteo, Strix aluco, and Bubo bubo. In the European avifauna even 3 Nearctic faunal types and 1 Nearctic–Arctic type are known, which means that these species are North American by geographic origin and distribution, and only recently have extended their ranges into Europe, e.g. Gavia immer and Larus glaucooides.

A further subdivision of the Holarctic faunal types is made necessary by the presence of species that, as a result of the devastating effects of the Pleistocene glaciations on land and vegetation, have present distribution types restricted to the European or even the Mediterranean part of temperate Eurasia. These species have been classified as European and Mediterranean faunal types (28 and 29 species, respectively), or, in cases where they have suffered to a lesser degree from extermination during the Pleistocene glacial periods, as European–Turkestanian and Turkestanian–Mediterranean faunal types (24 and 16 species, respectively). Examples of these faunal types, which as a matter of fact are subclassifications of the broad Holarctic faunal types, are:

- **European**: Milvus milvus, Phylloscopus sibilatrix
- **Mediterranean**: Sylvia cantillans
- **European–Turkestanian**: Circus pygargus
- **Turkestanian–Mediterranean**: Hieraaetus pennatus

The dynamic aspect of a classification of a local fauna into faunal types is apparent when we realize that among the European owls, for example, are represented Turkestanian–Mediterranean (Athene noctua), Siberian (Strix nebulosa), and Siberian–Canadian (Surnia ulula, Aegolius funereus) subtypes of Holarctic faunal types; these are apart from Holarctic faunal types in the broad sense (Asio otus) and cosmopolitan types (Tyto alba). This is another way of saying that each of these species has a different geographical past, but that all of them have met with at least part of the geographical and climatological events to which the whole of the Holarctic fauna has been subjected.

The classification of faunal types in Europe has many more geographical implications, which need not all be discussed here. The main point is that, when classifying faunal types, we are looking for parts of a whole fauna that have details of a common geographical history, without showing rigid or constant geographical borders. This attempt at classification is therefore
applicable not only to species, but to (well-marked) subspecies, and of course to all other continents as well.

FAUNA OF THE SOUTHERN CONTINENTS

The intergradation of faunal types of different geographic and historic origins into one regional fauna is made noteworthy by the presence in the Ethiopian region (Africa south of the Sahara) of 22 Holarctic and southern Palaearctic faunal types (Voous, 1959). In their present distribution, some of these bear distinct witness to colonization from Eurasia into Africa, e.g. *Gyps fulvus* (Palaearctic faunal type), *Gypaëtus barbatus* (Palaeomontane faunal type), and *Buteo buteo* (Holarctic faunal type). In these cases it is irrelevant whether or not one considers the African representatives of these examples to have already passed the limit of species recognition.

In the Americas, the separation of North and South America during the greater part of the Tertiary period seems to be still apparent in the present distributional patterns of American land birds. There are South American faunal types in North and Middle America (e.g. *Spizaëtus ornatus*, *Harpia harpyja*, *Herpetotheres cachinnans*, *Caracara cheriway*) and North American (Nearctic) faunal types in South America (e.g. *Buteo* (buteo) *ventralis*, *Asio flammeus*; also *Eremophila alpestris*). Of course, there are also widely distributed Nearctic faunal types in North America (*Haliaeetus leucocephalus*) and those that probably, as a result of Pleistocene glaciations, are confined to either the eastern (*Buteo platypterus*, *Ictinia misissippiensis*) or western part (*Buteo swainsoni*) of North America.

In terms of faunal types, a species restricted in its present range to South America, like *Buteogallus aequinoctialis* or *Heterospizias meridionalis*, is no more a South American faunal type than one that has penetrated deeply northward, like *Spizaëtus ornatus* or *Elanoides forficatus*, because both of these seem to have experienced the same geographical history of isolation in South America. This example illustrates the historic approach by which the concept of the faunal type can be given a dynamic zoogeographic background.

In Africa, the present distribution of the land fauna reflects the vicissitudes of the climate and the consequent alternating expansions and contractions of the rain forests and the savannahs and steppes. Thus, there are wide-ranging Ethiopian faunal types (*Polemaëtus bellicosus*, *Bubo lacteus*), but also equatorial rain-forest faunal types (*Urtiorchis macrourus*, *Stephano-aëtus coronatus*), and several types possessing a savannah distribution.

There are furthermore widespread Oriental faunal types (*Spizaëtus cirrhatus*, from India to Malaysia and the Philippines), restricted Malaysian (*Bubo sumatranus*, throughout Malaysia) and even insular Sundanese faunal types (*Otus brookei*, Sumatra and Borneo), and other faunal types of even more restricted ranges (*Pithecophaga jefferyi*, eastern Philippine Islands; *Bubo philippensis*, Philippine Islands; *Harpyopsis novaeguineae*, New Guinea).
Australia has its broad-sense Australian faunal types (Aquila audax; also Podiceps poliocephalus). It has, too, another good example of the dynamic approach of the concept of faunal types. The Australian representative of Podiceps ruficollis, an Old World faunal type in Australia, has recently proved to have acquired species characteristics by inverting its manner of distribution and colonizing Indo-Malayan regions (New Guinea, Moluccas, Lesser Sunda Islands, Java), from whence it originally must have come. At present it lives, as a new Australian faunal type in Indonesia (Podiceps novaehollandiae), without hybridization alongside its stock of origin, the South and East Indonesian form of Podiceps ruficollis (vulcanorum).

SUMMARY

The concept of faunal elements or faunal types recently used by the author (Voous, 1960) in relation to a zoogeographical analysis of the bird fauna of Europe has been discussed. Instead of the descriptive, virtually static method of classifying zoogeographical regions of the world, a more dynamic, faunal approach has been adhered to. As an example, the bird fauna of Europe, consisting of 419 species, has been divided into 24 faunal types, all of which have had their own distinct ecological and distributional history. At least 363 (86 percent) of the present European species have taken part in the geographical and ecological vicissitudes of the Northern Hemisphere during the Pleistocene and are therefore classified in some way as Holarctic faunal elements sensu lato. Implications of the system of faunal elements on an analysis of the fauna of the southern continents have been tentatively added.

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Die ornithogeographischen Unterschiede des Östlichen und Westlichen Teiles der Taigazone

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Somit haben wir es also in jedem einigermassen grossen Gebiet mit Gruppen von Arten zu tun, die nicht nur zu den verschiedenen Faunulas gehören, wie P. P. Suschkin (1925) definierte, sondern auch mit Faunen, die für verschiedene Untergebiete oder zumindest für verschiedene landschaftliche und geographische Zonen charakteristisch sind. In folge des gemischten Charakters der örtlichen Fauna lässt sich zwischen den zoogeographischen Unterteilungen sehr schwer eine territorielle Grenze ziehen, während die Faunen als solche, unabhängig von ihrer Gebietszugehörigkeit, recht leicht einzuteilen sind. Schon im Jahre 1914 hat der Entomologe A. Bertenjew in diesem Zusammenhang geschrieben, man dürfe ein Land nicht mit kategorischer Bestimmtheit zu diesem oder jenem Gebiet zählen (er meinte dabei Paläarktis und Neoarktis), jedoch die Abgrenzungen der Fauna (nicht die geographischen) könnte man bis auf die Art genau angeben. Die genaueste Gliederung der Fauna (gerade der Fauna und nicht des Territories) der Paläarktis in mehrere Untergruppen, die sogenannten Faunentypen, ist von B. K. Stegmann (1938) vorgenommen worden. Seine Faunentypen, die allerdings im wesentlichen an bestimmte geographisch lokalisierte Existenzbedingungen (man kann sagen zonale Bedingungen) gebunden waren, können in einem beträchtlichen Raum miteinander existieren, wobei ein allmählicher Übergang von der Vorherrschaft der Arten eines Faunentyps zu Vorherrschaft eines anderen Typs erfolgt.

Erwähnenswert ist in diesem Zusammenhang ein hochinteressanter Versuch G. W. Nikolskis (1951), die Fischwelt des Amurstromes nach den sogenannten faunistischen Komplexen zu analysieren. Die Letztgenannten können den Faunentypen von Stegmann gleichgestellt werden, jedoch mit dem Unterschied, dass bei Nikolski jeder faunistische Komplex eine deutlich ausge-

Den Ornithologen steht in dieser Richtung noch eine grosse Arbeit bevor, um die ökologisch-geographische Charakteristik der Faunentypen festzustellen und insbesondere die Verhältnisse der gemeinsamen Existenz verschiedener Faunentypen zu klären. Zum Beispiel, ob es bei ihnen eine biotopische Abgrenzung gibt, oder ob sie bei unterschiedlicher zoogeographischer Herkunft in einer Biozönose gemeinsam existieren können. Solange das aber nicht getan wurde, besteht die reale Gefahr, dass die Forschung bei einer zoogeographischen Analyse der Faunentypen in beträchtlichem Masse einen abstrakten, vom Territorium losgelösten Charakter annimmt. Indessen muss jede Fauna ihr Gebiet haben, d.h. die Umwelt, welche sie hervorbrachte.


Doch selbst die Höchstzahl der Arten, d.h. 39 in Ostsibirien, ist nur ein kleiner Teil der dort nistenden Fauna. Der Taiga (sibirische) Faunentyp stellt nirgends, nicht einmal im Herzen der Taiga, an Zahl der Arten die überwiegende Mehrheit der nistenden Lokalfauna dar. Darum muss das quantitative Verhältnis der örtlichen Faunen, insbesondere dort, wo mehrere Faunentypen sind, genauer ermittelt werden. Von wesentlichem Interesse ist eine Erforschung der quantitativen Veränderung der Faunentypen bei der Vorwärtsbewegung in der Meridian- und in der Breitenrichtung und die Verbindungen der festgestellten Veränderungen mit Veränderungen der Landschaft (der Lebensbedingungen). Wir stellen den Faunisten und Zoogeographen solch eine Aufgabe, beschränken uns aber in unseren Ausführungen zunächst nur auf eine Teilfrage. Wir ziehen einen begrenzten meridionalen Vergleich innerhalb der landschaftlichen und geographischen Taigazone und halten dabei die Fauna der für die Taiga typischsten Orte nebeneinander,
also Ostsibirien und die verarmte Fauna unmittelbar westlich des Urals, wo diese Fauna immerhin hinreichend gut vertreten ist.


Das Vorland des Urals an der Kama befindet sich näher an der Südgrenze der Taiga (die in Europa schon beträchtlich eingeengt wurde), und es ist eine gewisse Durchdringung mit Landschaft des Steppentyps festzustellen.


Bei der Feststellung der Menge nistender Arten haben wir natürlich in Betracht gezogen, dass sich unsere systematischen Vorstellungen seit der Zeit der Arbeiten Iwanows, wie auch zum Teil nach den Forschungen Woronzows etwas verändert haben und die Beziehungen zwischen Vogel und Gebiet strenger beachtet werden, wobei nicht genau feststehendes Nisten nicht ein-
gerechnet wurde. Manche vom Autor als nistende bezeichneten Arten erwiesen sich bei einer späteren Nachprüfung als vorbeiziehend, bisweilen als sommerliche Irrgäste.


Nachstehend eine Aufzählung der obenerwähnten 45 Vogelarten, wobei die im Kamagebiet nistenden Vögel angekreuzt werden:


Rechnen wir dazu noch vier Arten, deren Gebiete zu beträchtlichem Grade mit der Taigazone zusammenfallen: *Tringa ochropus*, *T. glareola*, *Larus minutus* und *Circus cyaneus*.

Rechnet man alle obengenannten Vögel zusammen, dann kann man sagen, dass es in Jakutien, und zwar in seinem von uns untersuchten Zentralteil, 63 Arten Vögel gibt, deren Verbreitung mit der Taiga zusammenhängt, und im Kama-Gebiet 39 Vogelarten. Für Jakutien macht das 45% aller dort nistenden Vögel aus und für das Kamagebiet 23%.

Mit welchen Faunentypen weisen aber die übrigen Vogelarten Jakutiens und des Ural-Vorlandes Verbindungen auf? Was das Ebengenannte betrifft, macht sich dort ein grosser Einfluss des europäischen Faunentyps bemerkbar,
zu dem 29 Arten gehören. Diese Vögel sind gebietsmässig mit den breitblättrigen Wäldern des europäischen Typs verbunden. Es lassen sich noch Arten hinzufügen, die ökologisch nicht an die europäischen Laubwälder gebunden sind, geographisch aber dennoch mit der Verbreitung der Laubwälder zusammenhängen. Es sind das: *Crex crex*, *Ixobrychus minutus*, *Circus pygargus*, *Caprimulgus europaeus*. In Jakutien kommen sie nicht vor.


Man kann noch eine Gruppe von Arten erwähnen, deren Verbreitungszentrum die europäischen Laubwälder sind, die aber auch in der Taiga weitgehend vorkommen. Zu dieser Gruppe gehören acht im Vorland des Urals anzutreffende Arten, drei davon (die angekreuzten) nisten auch in Jakutien: *Gallinago media*, *Anthus trivialis*, *A. pratensis*, *Certhia familiaris*, *Parns ater*, *Regulus regulus*, *Phylloscopus trochilus*, *Ph. collybitus*.


Hierzu kann man wohl auch den Wasserläufer *Tringa incana brevipes* und den Polar-Ammer *Emberiza pallasi* rechnen, deren Verbreitung mit dem

Durch intrazionale Steppenlebensräume dringen aus dem Süden in die Waldzone das Blässhuhn und der Fischreiher vor, die man sowohl im Westen als auch im Osten der Waldzone, folglich in Jakutien und auch im Vorland des Urals antrifft. Nur in Jakutien gibt es Wasserrallen. Im Vorland des Urals aber nisten die in Jakutien nicht vorkommenden Coturnix coturnix, Columba livia, Porzana porzana, Vanellus vanellus und Chlidonias nigra.

Schliesslich taucht in Jakutien gelegentlich ein einziger Vertreter des mongolischen Faunentyps auf und zwar Anthus richardi.

Ausser der obenangeführten Einteilung der Vögel nach verschiedenen Faunentypen und der Berücksichtigung der zu den Faunentypen tendierenden Arten bleibt noch eine bedeutende Gruppe Vögel übrig (im Vorlauf des Urals 83 Arten und in Jakutien 56 Arten), die in das von Stegmann entwickelte Schema der Faunentypen nicht hineinpassen. Diese Arten transpaläarktischer und kosmopolitischer (oder beinahe kosmopolitischer) Verbreitung haben sich sowohl in der Waldzone als auch in anderen weitgehend verbreitet.

Zusammenfassend kann man sagen, dass in Ostasien (Zentral-Jakutien) etwa die Hälfte der dort nistenden Vogelarten zum sibirischen, d.h. zum Taigatypus der Fauna gehört. In der europäischen Taiga (Vorland des Urals an der Kama) gehören zu diesem Faunentypus weniger als ein Viertel aller dort nistenden Arten. In der Anzahl der Arten steht der sibirische Faunentypus im Kama-Vorland des Urals dem europäischen Faunentypus nach (europäischer Typus 46 Arten, d.h. 27%), der etwas erweitert betrachtet wird. Echte Vertreter des europäischen Faunentypus gibt es in Jakutien nicht, jedoch bei einer etwas erweiterten Auffassung dieses Typs kann man in Jakutien drei Arten, d.h. etwas mehr als 2% vorfinden. Der chinesische Faunentypus ist in Jakutien durch 11 Arten, also 8% der nistenden Fauna vertreten und im Vorland des Urals durch drei Arten, d.h. etwas mehr als 2%. Vier Prozent der jakutischen Fauna (6 Arten) sind arktisch, während es im Vorland des Urals zwei Arten, d.h. etwas mehr als 1% arktischer Vögel gibt.


Auf Grund des gesagten darf man anzweifeln, dass sich die Vogelwelt im Vorland des Urals als Taiga-Fauna charakterisieren lässt. In noch stärkerem Masse bezieht sich das auf die westlichere Gebiete des europäischen Teiles der Taiga, worüber schon seinerzeit J. M. Woronzow geschrieben hat (1941). Zu berücksichtigen ist noch ein Umstand, auf den wir hier nicht näher eingegangen sind. Gerade in der europäischen Taiga erweisen sich Arten, die dem
europäische Faunentypus angehören, als die vielzähligsten und in den Gemeinschaften dominierenden.


**SUMMARY**

*The Ornithogeographic Differences between Eastern and Western Parts of the Taigal Zone*

It is known that true taigal species (Siberian-faunal type after Stegmann) are better represented in eastern Siberia and particularly in the parts of the taigal zone east of the Yenesee. In the western European parts of this zone, there are fewer taigal species, and a significant admixture of western species is observed (European-type fauna after Stegmann). However, quantitative correlations (in a number of species) have not been known until the present time.

Our investigation has shown that in Yakutea (surrounding Yakutsk) 63 species of birds, comprising 45 percent of the general total (139) nesting there, belong to the Siberian type of fauna (taigal species). A large number of species (56) belong to transpalearctic and other broadly distributed species; weakly represented is the Chinese type (11 species), Mongolian type (1 species), and Arctic (2 species).

In the territories west of the Urals (the Kama River region of the Ural foothills) 39 species of birds, i.e., 23 percent of the total nesting species (173), belong to the Siberian type. The European birds are represented by 46 species (= 27 percent of the total nesting birds), and 83 species belong to transpalearctic.

Thus if one does not count the most numerous group of broadly distributed birds, first place in terms of number of species is occupied in Yakutea by the taigal fauna—about one-half of all birds nesting there belong to this group. The fauna occupying the taiga west of the Urals has, on the other hand, the predominantly European type, rather than the taigal, Siberian type.
QUELLENNACHWEIS


----- 1949. Die Vögel des Kama-Vorlandes des Urals (des Permer Gebiets). Gorki. 113 S.
Zoogeographical Aspects of the Birds of the Subarctic

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I have for many years been engaged in a study of the arctic bird fauna, originally in northern Asia and in the area of the Bering Sea, then in northern Europe, and lastly, in Canada. In recent publications (Johansen, 1956, 1958), I have treated only the bird fauna of the arctic zones proper: the High Arctic and the Low Arctic. For two reasons I omitted a study of the subarctic fauna: (1) I was anxious to exclude all forest birds living in the Subarctic, so that I could more easily reach a conclusion on the origin of the arctic birds; (2) I was not, at that time, very familiar with the North American Subarctic. With regard to the High and Low Arctic, I found it unnecessary to work in North America, as the bird fauna there is not significantly different from that of Europe and Asia, whereas the difference is more important in the Subarctic.

Therefore, I did not begin my study of the Subarctic until I had seen the bird collections from this region and had had a chance to observe subarctic conditions in North America. I am greatly indebted to the ornithologists of the American Museum of Natural History in New York, and to those in Ottawa, for their kind help, and last but not least, for the economic assistance granted by the Frank M. Chapman Memorial Fund in New York. Furthermore, the Ministry of Northern Affairs in Ottawa was kind enough to organize the best possible working conditions for my study of the subarctic forest-tundra at Churchill, Hudson Bay.

In order to avoid misunderstandings I shall first explain my definition of the Subarctic and the way in which I divide the Arctic into two zones: the High Arctic and the Low Arctic. The first consists of regions with a July mean temperature below +5° C, and includes the ice and rock deserts as well as the high-arctic sedge-lichen tundra. The Low Arctic has a July mean temperature between +5 and +10° C, and is also subdivided into two sections: the colder typical lichen and moss tundra, and the southern milder scrub or shrub tundra without real tree vegetation.

A little more complicated is the next zone, which is usually called Subarctic, but is included in the Hudsonian Zone by some Americans. As this is the transition region between the low-arctic tundra and the boreal-forest zone, the vegetation and fauna contain representatives from both these zones. There is, therefore, some disagreement on the terminology. Some biologists (the Russians, see Grigoriev, 1956) include it with the Arctic, others (e.g. Porsild, 1958) with the forest zone. The northern part, with prevailing tundra and scanty clumps of trees, has more relation to the Arctic, and has sometimes been called "Hemiarctic" (Rousseau, 1952). The southern part,
with prevailing open forest interspersed by tundra, seems to belong more to the forest zone. Consequently, the biologists who divided the region in this way defined only this wooded part as "Subarctic."

As the transition is very gradual over vast distances, with intrusions of both zones northward and southward, there is no possibility of drawing a clear line between the two sections. I therefore prefer to regard the region as a unit of the Arctic and denote it by the term Subarctic. We can thus divide the Arctic into three zones: the High Arctic, the Low Arctic, and the Subarctic, each with two subzones. With regard to subdivisions of the Subarctic, I would call the southern part tundra–forest and the northern part forest–tundra.
The Subarctic runs in a circumpolar direction similar to the High and Low Arctic, but its character is dependent on the different geographical conditions which are somewhat more varied in the meridional direction. In Scandinavia the Subarctic is mostly mountainous, and the characteristic tree is the birch, which here has its most northern range. In European Russia the tundra is mostly flat, and the spruce is the species with the most northern range of all trees. In western and middle Siberia the larch is the characteristic tree, whereas in the mountainous Asiatic Far East the birch and alder, and also *Pinus pumila* (in Russian, "creeping cedar") are more important. Finally, in the northern part of North America the characteristic trees in the Subarctic are chiefly the white and black spruce, tamarack (larch), and to some extent, the poplar and alder. On the whole, however, the subarctic zone is much the same in all parts of the Northern Hemisphere, and I, being no botanist, could not see any appreciable difference between the Siberian and Canadian Subarctic—despite the trees being of different species. The character of the bird fauna is also very similar in all subarctic countries. As with the plants, there are, of course, differences in the species and subspecies, but I could not see any significant differences in the behavior of the replacing bird species.
One finds the same phenomenon in all subarctic countries. After journeying through the monotonous, treeless tundra of the North, the field ornithologist appreciates finding many more species and much more life in the forest-tundra. On the other hand, the same thing happens when one comes from the south, leaving the monotony of the northern boreal forest. One is fascinated by the richness and variety of the birds, both in the number of species and in the quantity of the individuals.

The explanation is simple. The Subarctic has almost all of the tundra biotopes from the Low Arctic, and also many biotopes of the boreal-forest zone. Additionally, the combination of open tundra with the shelter of woodland develops a series of new biotopes. Therefore, this region has not only a large number of arctic tundra birds, as well as many from the forest zone, but also some bird species that breed only in the Subarctic.

According to my computation, all together 115 bird species breed in the High Arctic and the Low Arctic, and of these, 92 (or 80 percent) also breed in the Subarctic. Of course, not all of them are "true arctic birds": 35 species have a very wide distribution outside the Arctic (e.g. *Anas acuta*, *Falco peregrinus*, *Corvus corax*), and 9 are oceanic species that are impossible to enclose within a subarctic zone, as most of them penetrate far south along the coasts. After subtracting these species, there are still 48 true arctic birds in the Subarctic.
The proportion of forest birds in the Subarctic is similar. The actual number in the northern boreal forest is difficult to state because there are many different species in the Old and in the New World, but it is possible to reckon their approximate number at about 100 species. Of these, about 60 are found to breed in the Subarctic.

In this way, 108 species are accounted for. Furthermore, there are a number of endemic subarctic birds. After excluding those with a very limited distribution, 9 species remain. All together, there are about 117 species, which is more than there are in the High and Low Arctic put together, and also more than in the northern boreal forest.

Consequently, the subarctic bird fauna consists of three faunal elements: arctic birds, forest birds, and endemic birds. I have paid particular attention to the last category because very little is known about these birds, and because they must have a significant importance for the zone. The number is not large, 13 in all: 6 in the Old World, 5 in the New World, and 2 in the area of the Bering Sea. It must be admitted that the distribution of some of them is very limited and, in some cases, not very well known. This applies to the Bristle-thighed Curlew (Numenius tahitiensis) in western Alaska, and to the Great Knot (Calidris tenuirostris) in eastern Siberia. Two gulls are not very good examples of endemic subarctic birds. The Red-legged Kittiwake (Rissa brevirostris) breeds only on islands in the Bering Sea and is mostly an oceanic bird. Ross' Gull (Rhodostethia rosea) actually breeds only in subarctic conditions in northeastern Siberia; otherwise it is found all the year round in the Low and High Arctic, so it is perhaps more in order to regard this as a real arctic bird.

The distribution of the remaining nine species of endemic subarctic birds is obvious enough. From the Old World there are four: the Lesser White-fronted Goose (Anser erythropus), from Scandinavia to eastern Siberia; the Red-breasted Goose (Branta ruficollis), endemic throughout the western Siberian Subarctic; the Spotted Redshank (Tringa erythropus), throughout the whole Eurasian Subarctic; and finally, the Pechora Pipit (Anthus gustavi), from the eastern European forest–tundra to the Bering Sea. There is one additional species, the Rock Sandpiper (Erolia ptilocnemis), from both sides of the Bering Sea and islands south to the Kuriles where subarctic conditions prevail.

From the American Subarctic there are four endemic species: the Black Turnstone (Arenaria melanocephala), from the shores of western and southern Alaska; the Tree Sparrow (Spizella arborea), represented by two subspecies from Alaska to Quebec and Labrador; Harris' Sparrow (Zonotrichia querula), from the Mackenzie Delta to northern Ontario; and finally, Smith's Longspur (Calcarius pictus), from Alaska to northern Ontario, and commonly in the forest–tundra of Churchill, Hudson Bay.
As a rule, these birds breed only in the Subarctic, but some individuals find suitable breeding conditions in the Low Arctic (e.g. Calcarius pictus), or in the boreal-forest zone (e.g. Spizella arborea).

The endemic bird group points to a more independent character of the Subarctic. However, more important is the fact that a number of arctic birds and boreal-forest birds have their chief breeding range inside the Subarctic. There are eleven arctic birds that occupy only a relatively small part of the Low Arctic, but almost the whole Subarctic; e.g. Micropalama himantopus, Limosa haemastica, Phalaropus lobatus, and Calcarius lapponicus. On the other hand, nine boreal birds have their chief area in the Subarctic; e.g. Gavia arctica, Aythya marila, Numenius phaeopus, and Tringa flavipes.

I am of the opinion that it would be more advisable to consider these as typical subarctic birds rather than arctic or boreal birds. In this way, we attain about 30 predominantly subarctic birds. This is a considerable number—no less than the number of predominantly Low and High Arctic birds taken together.

As to the question of the origin of subarctic birds, why should it be assumed that these birds penetrated from the Arctic or from the recent boreal forest into the Subarctic? Why, indeed, should the opposite not be the case? I think it far more likely that some of the recent arctic and forest birds have had their origin in the Subarctic and have spread from there to the neighboring zones. There are many reasons for this assumption. As mentioned, the subarctic zone has a multitude of suitable biotopes, plus good feeding conditions. Furthermore—and this is very important—the Subarctic is more ancient than the Low and High Arctic.

In my publication on arctic birds in 1958, I gave some conclusions on the origin of the High Arctic and Low Arctic birds. I then stated that the arctic bird fauna must be comparatively young, as it could only have arisen during arctic conditions, which could not possibly have existed before the end of the Tertiary. In the Middle Tertiary the polar areas had a temperate climate and were probably occupied by birds of a worldwide distribution. Later, during the gradual cooling, a number of them became adapted to the more severe conditions, and these birds are the ancestors of many of our recent arctic genera and species. During the alternating glacial and interglacial periods in the Pleistocene, several changes took place. Some arctic birds disappeared, others became adapted to various habitats, dividing into different species and subspecies, and finally, a number of new species invaded the Arctic during the interglacial periods.

All developments of the Arctic and its flora and fauna must have passed through a subarctic stage, as the forest could not have become established immediately after arctic conditions and vice versa. The Subarctic has always been the introductory stage to all changes in the arctic zones, and there have been many changes—even up to recent times. The subarctic conditions have also been the primus movendi for the most adaptive changes in bird species.
I am, therefore, convinced that the vital and agile, everchanging subarctic zone has been the cradle for many arctic and boreal species, and, of course, particularly for the predominantly subarctic birds.

From all this, it is evident that the Subarctic is more than merely a transition region between tundra and forest. It is the beating pulse of the Arctic and, as such, must have a status equal to that of the High Arctic and the Low Arctic.

SUMMARY

In the present paper, a short preliminary account is given of my studies on birds of the Subarctic. The Arctic is divided into three zones: the High Arctic, the Low Arctic, and the Subarctic. The latter is defined as the circumpolar area between the treeless tundra and the boreal-forest zone. As this is a transition region, the vegetation and fauna are representative of both zones. The northern section, with prevailing tundra and only scanty clumps of trees, I call forest–tundra; the southern section, with prevailing forest interspersed by tundra, I call tundra–forest.

In spite of meridional differences in the vegetation and many different species of birds, the Subarctic zone is much alike in all parts of the Northern Hemisphere. One of the most interesting phenomena is the richness and variety of the birds compared with the Low Arctic and the boreal-forest zone. A number of species, both in the Old and New Worlds, breed only in this area. Most important, however, is the fact that many arctic and boreal-forest birds have their chief breeding range inside the Subarctic. I am convinced that this zone, as the introductory stage of all changes in the Arctic, has the responsibility for many adaptive peculiarities of the arctic birds. I believe, therefore, that the Subarctic must have a status equal to that of the High Arctic and the Low Arctic.

LITERATURE CITED

In the first part of the twentieth century the climate of Europe became warmer. This alternation was not uniform. The principal center was situated in the North Atlantic, but another was in the Balkans. This was important for the birdlife of Central Europe, especially in Hungary. Different species began to spread their ranges north along the Wardar and Morava rivers. Naturally it is difficult to record the range expansion of common species or even of those that have bred before in Hungary. Therefore in this paper I will discuss only three species: the Collared Turtle-Dove (Streptopelia decaocto), the Syrian Woodpecker (Dendrocopos syriacus), and the Olivaceous Warbler (Hippolais pallida), which are not known to have occurred in Hungary before 1925.

The three species had the same characteristic in their range extension: They were coming from the South through the valleys of the Wardar and Morava rivers, but the increase in their geographic range required different periods of time. When they reached the Danube, even the characteristic direction of their spread became quite different.

The Collared Turtle-Dove increased its range explosively, i.e. the first settlements were far to the north of its original breeding range, and the places between these two points were occupied years later. The spreading was fan-
like (Fig. 1), and the Turtle-Dove followed certain routes only after it went to the north and to the west of the basin of the Carpathians, using especially the river valleys. The Collared Turtle-Dove was also the quickest of the three species, and it has now arrived in England, in Norway, and in Finland. The first observation of its range extension was made in 1932, and occupation of the Carpathian basin was completed in 1939.

The Syrian Woodpecker was slower. Its spread was neither explosive nor fan-like, but rather step by step (Fig. 2). However, its possibilities for population increase were greater. The Syrian Woodpecker lives not only in towns and human settlements, but also in orchards, vineyards, groves (gallery forests of rivers), and so forth. The first observation of this species in the Carpathian basin was made in 1928, earlier than that for the Collared Turtle-Dove, but the woodpecker reached Budapest only in 1939, and today is known only from Lower Austria and from South Moravia, but not farther to the west or to the north. The occupation of the basin of the Carpathians was completed in 1951.

The slowest species of the three was the Olivaceous Warbler, which was first recorded in the Carpathian basin in 1937. Only later was it known that this species bred even in 1928 near Zenta on the Tisza River. Now it is a common bird in northern Yugoslavia, in the Batshka (= Voivodina) in towns and in gallery forests of the Tisza River, and in Hungary along the Tisza and Maros rivers (Fig. 3), but it has not reached the 47° N parallel. It was

Fig. 2. The range expansion of the Syrian Woodpecker in the basin of the Carpathians.
not yet found near the Danube, but only in Yugoslavia near the Drava on the western side of the Danube in 1954.

All three species have found in their new area nearly related species, which occupy seemingly similar ecological niches with respect to food, nest site, nesting material, singing perch, and so forth: the Collared Turtle-Dove and the Turtle-Dove (*Streptopelia turtur*), the Syrian Woodpecker and the Great Spotted Woodpecker (*Dendrocopos major*), the Olivaceous Warbler and the Icterine Warbler (*Hippolais icterina*). There is this difference: The indigenous species do not prefer the cultivated habitats in contrast to the newly arrived birds. It seems that the indigenous species freely "offered" the cultivated habitats to the invaders. We have very few records of actual combats that were observed between these birds. The indigenous but related species retired to the woods, which were more adequate for them. This was the case of *Str. turtur* vs. *Str. decaocto* and of *D. major* vs. *D. syriacus*. The Icterine Warbler does not have such a density that there must be a change of its habitat.

Later, however, quite different birds presented some settlement difficulties for the invaders. In Hungary, we can regularly observe that the European Blackbird (*Turdus merula*) pushes about the Collared Turtle-Doves. These chases are often very intense and can easily cause a fatal accident. Especially in Budapest, we have often ascertained that the European Blackbird has occupied the nest of the Collared Turtle-Dove and built its nest over that of

Fig. 3. The range extension of the Olivaceous Warbler in the basin of the Carpathians.
the dove and, in contrast, the Collared Turtle-Dove has built its nest on that of the European Blackbird. In this connection I believe that we cannot speak of the Jackdaw (*Coloeus monedula*), which is a regular plunderer of the nest material, eggs, and young of the Collared Turtle-Dove (Peter Beretzk, verbal comm.).

The Syrian Woodpecker today competes with the Starling (*Sturnus vulgaris*). Szlivka (1957) and Keve (1960) have published many such instances. I give only two newer observations. Both of these concern the struggle of the two species at the nesting hole, where the Starling usually succeeds in occupying the hollow: In the first half of April 1961 in the northern suburb (Óbuda) of Budapest, William Veto (verbal comm.) observed a Syrian Woodpecker closely pursuing a Starling. They fought even in the woodpecker’s hollow. The Starling had laid an egg which the Syrian Woodpecker evicted from the hollow. But finally the Starling occupied the nest. J. E. Kakass writes on 7 April 1961 of a somewhat similar case at Balaton Lake.

**SUMMARY**

*S. decaocto* reached Hungary in 1932 and expanded its range explosively in fan-like fashion to the north and west. *D. syriacus* appeared in 1928 and did not complete its occupation of the basin of the Carpathians until 1951. *H. pallida* has invaded the basin in still slower fashion. All three have filled man-made habitats not well occupied by indigenous species. Competition with *T. merula* and *S. vulgaris* for nest sites is evident.

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Immigration and Distribution of the Alcidae in the Baltic Area

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In our time three species of Alcidae breed in the Baltic, i.e. the Razorbill (*Alca torda*), the Common Murre (*Uria aalge*), and the Black Guillemot (*Cepphus grylle*). The immigration, habitat, and present distribution of these species in the Baltic have been thoroughly discussed by many Scandinavian zoologists on account of the varying stages of isolation from the sea, which have been followed by changes in the salinity of the Baltic during the different climatic periods of Postglacial Time.

**Distribution**

At present the Razorbill breeds on skerries along the coast of middle and northern Sweden and along the Finnish coast. It also occurs in the Gotland area, and farther south it breeds on the Danish islet of Græsholmen, near Bornholm, where the colony was not established until the 1920’s. Formerly there was a colony on the northwesternmost part of Bornholm, but it has been unreported since 1886. This place was also inhabited by a fairly considerable number of the Common Murre, which disappeared at the same time and probably moved to the Karlshägar, off Gotland, where the population of this species was very small in the 1880’s. Nowadays the Common Murre is perhaps the most numerous of the Baltic Alcidae; in reality, however, it is a fairly rare bird in the Baltic as a whole, because roughly 95 percent of the total number of perhaps a little more than 100,000 birds breed in the West Gotland area. Late in the 1920’s this species settled on Græsholmen, mentioned above, and today about 1,000 Common Murres breed there. Further scarce and often irregular breeding has been reported elsewhere in the Baltic; the northernmost place is the skerry of Bonden, a little more than halfway between the Aland Islands and the innermost part of the Gulf of Bothnia. The Black Guillemot breeds along the coasts of Sweden and Finland, as well as along those of Estonia, but not so far south as the Bornholm area. Then it breeds again in the outer Danish waters, where it is the only summer resident among the Alcidae.

An old breeding record of the Razorbill in southern Kattegat has been quoted rather often in literature, quite recently by Vouus (1960:170, no. 203). There is no evidence for this record, however, for the Razorbill would never have been able to breed on the low islet concerned, nor would it have used the surrounding shallow waters as a feeding place. The record is clearly due to misidentification of Black Guillemots, and the latter species still occurs in this place.

The Great Auk (*Pinguinus impennis*) undoubtedly never entered the Bal-
tic. The southernmost discoveries of bones of this species originate from the northern part of the Øresund, the sound between Sealand and the Swedish coast. I must mention an eggshell, however, which was found in 1895 in early arctic fresh-water clay in southwestern Scania, near the limit between the Baltic and the Sound; it was interpreted as belonging to the Great Auk and has been widely quoted in the literature. The geological age of this specimen is 12,000 to 14,000 years—about 8,000 to 10,000 years older than the bones of the Great Auk from the Danish kitchen middens. Renewed investigation (Løppenthin, 1952) revealed that this find probably constitutes the oldest known breeding record of the Whooper Swan (*Cygnus cygnus*) in the world; this species also might be expected with greater probability in this ancient arctic fresh-water lake. Quoting my paper, Greenway (1958: 285) says that the egg “is now thought more likely to be that of a swan”; the shape, size, and shell structure of the specimen are, however, indisputably those of a Whooper Swan’s egg.

**GEOLOGICAL HISTORY**

In the beginning of the Late Glacial Time, when the melting ice cap of the Würm Glaciation withdrew from the southern part of the present Sweden, a cold fresh-water lake, the Baltic Ice Lake, was situated south of the ice border. By about 10,000 B.C., a sound was formed across Middle Sweden, and the Yoldia Sea, named after the arctic mussel *Yoldia (= Portlandia) arctica*, with salt water came into existence. Lake Ladoga was part of this system, South Sweden was connected by land with Denmark, and both were parts of the European continent (Zeuner, 1952). By about 8,000 B.C. the Middle Swedish Sound began to close because of upheaval, and the Baltic became the huge Ancylus Lake of Boreal Time, named after the small freshwater snail *Ancylus*. It covered a much wider area than the Baltic of today, because the water level was higher. Öland, Gotland, and Saaremaa (Ösel) occupied only small parts of their present spaces; big areas of the Stockholm region and the Åland Islands were submerged, and Lake Ladoga was still openly connected with the main part of the big lake, the water of which was fresh or slightly brackish. This stage lasted for 2,500 to 3,000 years, when the first Litorina transgression came. At about 5,000 B.C. the salt water from the ocean overflowed the Danish area, and an open connection was formed through Øresund, the Great Belt and the Little Belt. In this period, Atlantic Time, the climate was somewhat warmer and more humid, and the salinity of the Baltic or the Litorina Sea was higher than today. The water level was lower than in Boreal Time, and Lake Ladoga was cut off by the Karelian Isthmus. In the next two millennia, Subboreal Time, the climate became a little cooler and more arid.

**EVIDENCE FOR REFUTATION OF THE RELIC THEORY**

Several authors have regarded the present populations of the Alcidae in the Baltic as late-glacial relics, originating from birds that, some 10,000
years ago, had come to the Yoldi Sea by the Middle Swedish Sound. Ekman (1922:261) was of that opinion, especially as concerns the Razorbill, and he compares its Baltic occurrence of today with that of the Ringed Seal (*Phoca hispida*), which must be accepted among the indisputable late-glacial relics in this area. He says that there is no counter evidence to the relic theory concerning this bird, but on the other hand he is a little cautious as regards its flying capability; he considers, however, that its relic status is most probable. The birds are supposed to have survived the fresh-water period of at least 2,500 years in the Ancylus Lake, in complete isolation from their marine congeners, and they were then supposed to have been able to hold their own until the present time. Quite recently, Voous (1960:132, 134) and Paludan (1960:210, 223, 236) have supported the view that the Razorbill, the Common Murre, and the Black Guillemot are relics in the Baltic. As to the Common Murre, which has much less sedentary habits than the other two species, Spärck (1942:72) has expressed the point of view that the immigration into the Baltic took place in Atlantic Time from the South through Danish waters.

In the Yoldi Sea there was certainly a good deal of drift ice, among the floes of which the Black Guillemot may have been able to thrive. As to the Razorbill, the matter looks a little more doubtful, and regarding the Common Murre it seems fairly impossible; this bird is strongly attached to open and fairly deep water, and it would certainly never have been able to pass the ice-stuffed Middle Swedish Sound.

There is not the slightest evidence in the form of fossil bones of any Alcidae known from deposits of the Yoldi Sea, nor from the Ancylus Lake or the Litorina Sea. Bones of the Razorbill and the Common Murre are reported from Danish coastal kitchen middens of either Atlantic or early Subboreal Time; but the Black Guillemot has not been reported in this material, and because of the climate I believe that this is not a matter of chance. The bird has certainly still not immigrated. The nearest kitchen midden, where contemporary remnants of the Black Guillemot have been found, is on the coast of western Sweden, not far from the Norwegian frontier (Henrici, 1935:39). In the later Subboreal Time (ca. 2,500–500 B.C.), however, all these species of Alcidae have lived in the Baltic; many fossil bones have been found in neolithic layers of a cave on Stora Karlsö, which was inhabited for about 1,000 years (Rydh, 1931:104–105).

The biology of the Alcidae prevents permanent occupation of waters that become totally ice-covered, although this is not the case every winter. During the cold season the Ringed Seal is able to survive in the water, breathing through blow-holes in the ice, which are kept open from below. This cannot possibly be done by any birds, including the Alcidae and even the penguins, because the feathers will get soaked and the birds will be drowned when admittance to the open air is cut off. We know that the Alcidae never deliberately make migratory movements over land; and from their low power of
resistance in captivity, which has been observed for example in the zoo at Copenhagen, it is obvious that there is a limit to their tolerance to fresh water. Therefore, it is incredible that the Razorbill, the Common Murre, and the Black Guillemot have survived isolation in the Ancylus Lake for thousands of years; this area was certainly not less ice-bound during the winter than is the Baltic of today, but rather more, because the climate was more continental than now.

Declines in the Baltic populations of the Razorbill after the three very hard, consecutive winters of 1940-42 proved to be nearly fatal (Wahlin, 1943; Paludan, 1960:210). In the Danish colony just north of Bornholm, the number of the breeding specimens was reduced to 20 percent; on the Karlsöar off Gotland only 10 percent survived, and at Bonden in the Gulf of Bothnia only 1 percent of the birds returned after the last of the severe ice-winters. From Finland the reports were similar (Merikallio, 1958:88). Obviously the Baltic Razorbills do not get much farther away during winter than to the inner Danish waters, and when these and the Kattegat became totally covered with ice, they died by thousands.

The Common Murre also suffered from the effects of the ice-winters in the beginning of the 1940’s, but on a much smaller scale than the Razorbill. Their more migratory habits gave these birds a chance to get away to open waters, before the ice-cover set in.

The Black Guillemot is also said to have decreased in the Baltic due to the cold winters during World War II; but no very convincing counts are available. In spite of its fairly sedentary habits, this species is probably more able to pull through, when its habitat is frozen over, than birds that are less at home in the drift-ice belt.

"THE LAKE LADOGA STORY"

Finally, an unacceptable record from Lake Ladoga should be mentioned. It is due to Hildén (1921:61–62), who claims the occurrence of Razorbills and Black Guillemots in a report on a boat excursion that he and a companion undertook in the neighborhood of the skerries of Wossina and Jalaja on 3 June 1920. He reports having seen Black Guillemots and credits his companion with the record of this species nesting here; only the companion seems to have been responsible for reporting “the fairly numerous breeding of the Razorbill.” Hildén draws parallels to the Lake Ladoga population of the Ringed Seal and seems to have presupposed that these birds had been confined to Lake Ladoga since ancient times. The occurrence of these birds in winter is, however, just as incredible as regular migratory flights across the Karelian Isthmus and swimming movements up and down the Neva River. There is no proof whatsoever, only sight records, which are partly secondhand. In spite of the fact that Hildén (1921:60) actually mentions the Velvet Scoter (Melanitta fusca) and the Tufted Duck (Aythya fuligula) in his report, I am of the opinion that a couple of flying Velvet Scoters may
have been misidentified as Black Guillemots on account of their dark plumage and white wing-spots, and a swimming flock of male Tufted Ducks may have been taken for Razorbills.

I have discussed this mysterious breeding record of Alcidae in Lake Ladoga with Finnish colleagues, and they were most reluctant to acknowledge it as reliable; but it has often been quoted in the literature. Today the northwestern part of Lake Ladoga is out of the scope of Finnish ornithology, because this area was overtaken by the Soviet Union after World War II. Göran Bergman translated Hildén’s original Finnish text into Swedish, and in November 1960 I tried unsuccessfully to contact him by letter. His record has, however, passed into the ornithology of the Soviet Union (Dementiev and Gladkov, 1951:176, 202; 1960:131, 134; see also Kartashev, 1960: 17–18, 65–67). Voous (1960:170–171) has outlined the breeding of the Razorbill in southern Lake Ladoga, but he did not map the Black Guillemots of Hildén. I consider it improbable that Alcidae have ever bred in Lake Ladoga.

SUMMARY AND CONCLUSIONS

The present Baltic populations of the Razorbill, the Common Murre, and the Black Guillemot unquestionably originate from birds that have immigrated from, or through, Danish waters, i.e. from the South. In Atlantic Time they probably were unable to spread by this means on account of the fairly warm and humid climate, but it is evident that they had established themselves in the Baltic by Subboreal Time. The age of these populations may be considered to be about 4,000 years, hardly much more, and not about 10,000 years, as propounded by the relic theory.

LITERATURE CITED

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Avifaunal Notes on the Outer Mongolian Gobi Desert

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This paper is a preliminary report on the results of three zoological expeditions in 1958–60 that the author, together with his Mongolian colleagues (Prof. D. Zevegmid, A. Dashdorjee, and collaborators of the Mongolian University A. Shagdarsuren, A. Bolod, and M. Bavassan, as well as some others), undertook in the Gobi Desert within the limits of the Mongolian People’s Republic. These explorations were conducted in an almost inaccessible and poorly investigated region situated in the extreme south of the Mongolian People’s Republic on its frontier with the Chinese provinces of Sinkiang and Ningsia. The present paper is a slightly condensed version of a report in Russian that appeared in Ornitologiya (4:376–382) in 1962.

The area studied is the northern outpost of the Central Asia Deserts situated to the south of the Mongolian and Gobi mountain ranges of the Altai. The name of this region is widely used and well known in the literature as the Transaltaian Gobi, although many geobotanists (for example, V. I. Grubov) distinguish three regions inside of it: the Dzungarian Gobi on the west, the Transaltaian Gobi sensu stricto, and the Alashan Gobi on the east. However, within the scope of our present zoological knowledge (which, as a rule, does not spread beyond the limits of the vertebrate fauna), one may combine these three regions into a single term, the Transaltaian Gobi, which will be used in this paper in its broad sense.

PHYSICOGEOGRAPHICAL ASPECTS

One of the causes producing intrazonality in the distribution of steppe and desert lands and, as a consequence, mosaic spreading of the fauna, is the high elevation of Mongolia and the Gobi above sea level. The deserts, in the proper sense of the word, occupy a relatively small area of the Mongolian Republic, making up about 14 percent of the whole country. The natural conditions of the Mongolian deserts are very rigorous. The climate is severely continental with wide variations of both seasonal and daily temperatures. The Transaltaian Gobi mainly represents a rocky waste desert, a lot of its area being devoid of any vegetation. Sandy plots are not numerous. The mantle of soil and vegetative cover are poorly developed. The vegetation is typically characteristic of the Central Asia Deserts, varying slightly in the western and eastern parts of the Transaltaian Gobi, as mentioned above. Water sources are rare. Well springs are of great importance, although most of them go dry by autumn. Not numerous are the oases with fairly abundant vegetation, such as rush and groves of heterophyllous poplar (tore in Mongolian). The most important oasis, called Zakhoi, is situated in the

north of the Transaltaian Gobi; resident people there cultivate certain agricultural crops.

The relief of the Transaltaian Gobi represents sharply broken grounds. The flat plots of ground, as well as the slopes, are broken by numerous dry stream beds alternated with hillocky areas and many isolated mountain ridges. The flat lands to the north of the Takhiin-chara-nuru Mountains have a mean elevation of about 2,000 m; the altitude of those to the south of the Ederenghiin-nuru Range is 750–1,000 m above sea level. The peaks of the mountains are: Atass-ula, 2,702 m; Takhiin-chara-nuru, 2,275 m; Baytyk-bogdo, 3,187 m; Adjee-bogdo, 3,067 m; Edjee-khairkan-ula, 2,260 m; Oni-unduriin-nuru, 2,075 m; Ederenghiin-nuru, 1,939 m; Otkhon-ula, 1,675 m; Elestu-ula, 1,293 m; Tsagan-bogdo, 2,380 m; and so forth.

From the standpoint of biogeography it is worth mentioning that in the mountain systems, on their high parts, there are steppe-like plots where the hydrological regime quite naturally is more favorable as compared with the flat lands.

In the middle and southern regions of the Mongolian People's Republic, the demarcation between steppe and desert is inevitably conditional. A large intermediate zone is formed by arid steppes or semideserts. This zone passes approximately between the south hillside of Khangai and the north slopes of the Mongolian and Gobi Altai. However, within both the desert and steppe belts, purely intrazonal inclusions of other types of landscape are spread widely. For instance to the north of the Altai there are plots of ground characteristic of semideserts. Here Sharghin-Gobi, or Ushgiin-nuru, lies in the semidesert and steppe zone, but the vegetation and fauna of this area is of a desert character: saxaul and such animals as Podoce hendersoni, Oenanthe deserti, and so forth. One may take likewise the above-mentioned plots in the mountains of the desert zone, for instance Tsagan-bogdo, Atass-ula, and so forth. On the desert plots to the north of the Transaltaian Gobi limits are such characteristic eremophylic species of vertebrates as Meriones meridianus, Rhombomys opimus, and Gazella subgutturosa, and, in birds, Podoce hendersoni, Sylvia nana, Oenanthe deserti, and Otis undulata.

On the other hand, such inhabitants of the steppes as Ochotona daurica or Aquila rapax, Buteo hemilasius, Syrhapses paradoxus, and even the Mongolian lark Melanocorypha mongolica penetrate into the areas of the desert, especially into its outlying northern districts.

The onager (Equus h. hemionus), which can be found at present only in the deserts of the Mongolian People's Republic, was quite recently an inhabitant of the semideserts, reaching as far as the valley Begeer in the middle part of the Gobi Altai. As could be foreseen, the interpenetration of different faunistic elements is well displayed in the mountain fauna of the Transaltaian Gobi.

I have already mentioned that the mosaic distribution of the animal-dwelling sites in the Transaltaian Gobi is of great importance from
biogeographical and ecological points of view. I should add a few more words on the distinction existing between the plots of the desert: the flat, mainly *hammada-like* areas which are at times quite lifeless or represent only small portions of the territory with poorly fixed and "loose-running" sands, on the one hand, and on the other hand, the areas with various ecological inclusions, such as hills, outliers, mountains, dry stream beds, and ephemeral water basins, to say nothing of the oases.

There is almost no or a very small human population resident in the desert. This population is mainly concentrated within the territories of the few existing oases (Zakhoi and some others). However, in the desert, except during the period October–December (this season is drought-affected, the grass gets dry, and water reservoirs become empty), there are some roaming cattle breeders—*arates*—with their herds of camels, horses, horned cattle, sheep, and goats. The human activity affects the bird fauna of the Gobi very little, but this situation is different with respect to the ungulates.

**AVIFAUNAL ANALYSIS**

The ornithological–geographical literature on the Transaltaian Gobi is very scanty, the data being occasional and quite fragmentary. Although our research expeditions took place in the autumn, the main body of the desert fauna has been found to be resident, and I believe that the list of breeding species given below presents an adequate picture of the composition of the breeding fauna. It does not completely encompass the list of wintering and migratory species, for which our records should, of course, be supplemented with new data. The list below contains only those species that have been discovered in the Transaltaian Gobi by our expeditions. No account is taken here of the data known from the scanty literary sources; this is postponed until all of our materials are completely worked up and the terrestrial vertebrate fauna of the Gobi is fully investigated. For the same reason we leave alone at present the question of subspecific identifications. The breeding species below are marked by the letter *n*. The total number of the bird species recorded by us amounts to 88, which seems quite significant considering the severe natural conditions of the Transaltaian Gobi. This list is as follows:

- *Corvus corax* (*n*)
- *C. frugilegus*
- *Pyrrhocorax pyrrhocorax* (*n*)
- *Nucifraga caryocatactes*
- *Podoces hendersoni* (*n*)
- *Sturnus vulgaris* (*n*)
- *Rhodopechys mongolica* (*n*)
- *Carduelis flavirostris* (*n*)
- *Petronia petronia* (*n*)
- *Passer anmodendri* (*n*)
- *P. montanus* (*n*)
- *Emberiza buchanani* (*n*)
- *E. pusilla*
- *E. aureola*
- *E. leucocephalos*
- *E. fucata*
- *E. pallasi*
- *E. rustica*
- *E. schoeniclus* (*n*)
- *Calcarius lapponicus*
- *Eremophila alpestris* (*n*)
- *Galerida cristata* (*n*)
- *Alauda arvensis*
- *Calandrella pispolaletta*
- *Molachilla alba*
- *M. flava*
- *M. cinerea*
- *Anthus spinoletta* (*n*?)
When one analyzes the composition of the breeding avifauna in the Transaltaian Gobi, its typical “main body” in particular, it is easy to determine the following three basic groupings:

1) Species characteristic of the level plots of the desert:

<table>
<thead>
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<th>Species</th>
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<tbody>
<tr>
<td>Passer montanus</td>
</tr>
<tr>
<td>Podoces hendersoni</td>
</tr>
<tr>
<td>Passer ammodendri</td>
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<tr>
<td>Rhodopechys mongolica</td>
</tr>
<tr>
<td>Calandrella pispoleta</td>
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</tbody>
</table>

2) Species characteristic of the oasis “inclusions” (it should be kept in mind that this is a supplement to the list given for the plain desert, since the species characteristic of this desert inhabit the oases as well):

<table>
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<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Passer montanus</td>
</tr>
<tr>
<td>Emberiza schoeniculus</td>
</tr>
<tr>
<td>Galerida cristata</td>
</tr>
</tbody>
</table>

3) Species characteristic of the mountain “inclusions”:

<table>
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<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pyrrhocorax pyrrhocorax</td>
</tr>
<tr>
<td>Carduelis flavirostris</td>
</tr>
<tr>
<td>Primella fulvescens</td>
</tr>
<tr>
<td>Falco cherrug</td>
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<td>F. tinnunculus</td>
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As can be seen from the above lists, there is a great likeness in the typical complex of the characteristic “main body” of the breeding avifauna of the...
Transaltaian Gobi and that of the deserts of Middle Asia (Turkestan). However, it is not difficult to note some quite essential distinctions, mostly negative ones, which are likely to be engendered by the generally severe conditions of life in Middle Asia as compared to those in Fore-Asia (Western Asia).

In the fauna of the Gobi there are no sand-grouse (*Pterocles alchata* or *P. orientalis*) which are so characteristic of the Middle Asian, Fore-Asian, and African deserts. It is of no less importance to note the absence of representatives of species of *Hippolais*. *Buteo rufinus*, which is so characteristic of the deserts and semideserts of Africa and Middle West Asia, cannot be found in the Gobi, and its nearest relative, *B. hemilasius* in Mongolia, inhabits steppes, semideserts, and mountains rather than deserts. The Middle Asian jay (*Podoces panderi*) inhabiting the deserts is replaced in the Gobi by the other species, *P. hendersoni*. The desert finch (*Rhodospiza obsoleta*), which is characteristic of the Middle Asian desert regions, cannot be found in Mongolia. In the Gobi it is replaced by *R. mongolica* (the latter also inhabits Middle Asia but under conditions other than those of Mongolia).

It is also worth mentioning that in the Gobi such species as *Charadrius leschenaultii*, *Cursorius cursor*, *Caprimulgus aegyptius*, *Scotocerca inquieta*, *Passer simplex*, and *Parus major* cannot be found.

Although the characteristic features in the composition of the fauna of mammals of Central Asian, Middle Asian, and Fore-Asian deserts are more pronounced when compared with those of the avifauna, the main zoogeographic characteristics of the Gobi, obtained on the basis of the ornithological materials, can be applied to it as well. It is also important to note that such species of mammals as *Diplomesodon pulchellum*, *Meriones libycus*, *M. tamaricinus*, *Allactaga severtzowi*, *A. bobrinskii*, *Pygyrethmus platyurus*, *P. zhitkovi*, *Paradypus ctenotactylus*, *Jaculus lichtensteini*, *J. turcmenicus*, *Felis margarita*, and *F. caracal*, which are so characteristic of the Middle Asian deserts, are not to be found in the Transaltaian Gobi. These are no more than mere examples. One should take into consideration that both the composition and special features of desert faunas depend to a great extent on the “southern” type. The “southern” type of Palaeartic deserts is represented by Libya, Arabia, Fore-Asia, and Middle Asia’s Kara Kum; the “northern” type, by Central Asia and Kazakhstan. In the end, one may draw general conclusions as to the great and very deep community of the Central Asian, Middle Asian, Fore-Asian, and North African desert faunas in relation to the composition of the basic indicator species and the zoogeographic origins of the various species that compose these faunas. At the same time, examination of the avifaunal composition proves once more the complexity and diversity of the problems that arise in connection with different stratifications produced at different epochs and exert their influence on the basic mid-Tertiary faunistic complex of the great zone (belt) of the Palaeartic deserts.

These general conclusions relating to the Gobi correspond with the results
of recent work on the paleogeography, geology, botany, and zoology of the Sahara.

In this connection, a few preliminary remarks on the character of bird migration in the Transaltaian Gobi should be made (as mentioned above, our observations relate to the autumn season, from August until October). The migration of birds in the Transaltaian Gobi is a remarkable one. The birds fly in an extended front, although a certain concentration is to be found within the oases and in some mountain plains (along dry stream beds called sairy). Most of the migrant species breed north of Mongolia or in eastern Siberia.

SUMMARY

In this preliminary report of the results of autumnal expeditions carried out in 1958–60, the breeding avifauna of the Transaltaian Gobi is shown to include 88 species, of which 10 are characteristic of level parts of the desert, 6 more inhabit the oases as well, and 10 are characteristic of mountain inclusions. In general, the main body of this avifauna is similar to that of the Middle Asian deserts, but a number of species are absent (Pterocles alchata, P. orientalis, Hippolais spp., Buteo rufinus, and so forth), others are replaced, and certain subspecific distinctions are evident.
The Ornithogeography of the Koryak Highlands (U.S.S.R.)

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In a previous communication in the Proceedings of the XI1th International Ornithological Congress (Helsinki, 1958 [1960] p. 615–620), I recorded the first results of my ornithological field work in the Koryak land on the shores of Korf Bay. In 1959 (30 May–29 September) and 1960 (28 May–21 September), these explorations continued and were extended owing to my participation in the Kamchatkan Expedition of the Academy of Sciences of the U.S.S.R. At my disposal were five assistants of different rank, who continued field explorations from my departure until 17 May 1961. In 1959 we worked the shores of Olutorsk Bay, near the mouth of the Apuka River, and the neighboring hills. In 1960 we entered the inner, most elevated parts of the Koryak Highlands and established our base camp in the upper basin of the Achai-Wayam River.

The Koryak Highlands extend from the Anadyr Basin to the Kamchatka Peninsula and represent a system of intercrossed mountain chains of various altitudes. According to our geologists’ view, this system is a formation of very young age. In its most elevated parts, the whole of this landscape has a fairly typical alpine character (Fig. 1), with knife-edge ridges, craggy summits, precipitous walls, steep slopes, and large areas of scree. The summits near the Icy Mount (“Ledyanaya”), a very high point in the Koryak Highlands, are covered by glaciers, and here a sterile environment prevails.

The alpine belt occupies the widespread bare areas on the mountain summits, but near the seashores its lower limit descends to 200–300 m above sea level. The general type of vegetation is a mountain tundra, alternating with scree slopes and flat-topped hills. The most common bird of the alpine belt is Anthus spinoletta härmsi Zar., which is fairly abundant everywhere. The highest altitudes with craggy ridges are the breeding habitats of Leucosticte arctoa curilica (Pall.) and locally of Plectrophenax nivalis pallidior Salom., but both and particularly the second are rather scarce. The most remarkable inhabitants of the alpine belt must be considered Calidris tenuirostris (Horsf.) and Charadrius mongolus stegmanni Port. (Fig. 2 and 3). They were observed to breed at a not-great altitude, 200–300 m above sea level, near Apuka. Curiously enough, Calidris tenuirostris was absent from the great altitudes in the heart of the Koryak Highlands near our base camp. We found only one family of Charadrius mongolus at high altitudes, while several broods were scattered on the lower plateaus in the Achai-Wayam Valley. Lagopus mutus (Mont.) were breeding near the upper limit of the subalpine belt. Oenanthe oenanthe oenanthoides (Vig.) was seen in rocky places and only within limits of the alpine belt. The comparative scarcity of...
alpine avifauna that we noted on the Koryak Highlands can find its explanation in a very late melting of snow, which covers vast areas until midsummer and later.

The middle and lower slopes of over 1,000 m above sea level and downward to the foothills are clothed by creeping cedar (*Pinus pumila* (Pall.)), and alder bushes (*Alnus fruticosa* Rupr.), which represent a prevailing type of vegetation in the whole of this country. The combination of cedar and alder thickets interspersed with patches of tundra and meadows (Fig. 4) we consider as a subalpine belt. The most characteristic birds of the cedar thickets are *Nucifraga caryocatactes kamtschatcensis* Barr.-Ham. and *Pipitola enucleator kamtschatcensis* (Dyb.). The mixed shrubberies are favored by *Calliope calliope anadyrensis* Port., *Prunella montanella badia* Port., *Lanius c. cristatus* L., *Rubicilla erythrina* (Pall.), and others. *Lagopus lagopus* (L.) and *Acanthis flammea exilipes* (Coues) are mainly confined to the willow growths. Whereas the silence in the alpine belt would be broken only by the sound of wind and by the cry of pikas (*Ochotona hyperborea* (Pall.)), in the subalpine belt was heard the melodious song of *Turdus ruficollis eunomus* Temm. and *Calliope calliope* (Pall.). To them yielded *Oreopneuste fuscata homeyeri* (Dyb.), but all of these were surpassed by the incessant warbling of *Acanthopneuste borealis* (Blas.).

The interzonal elements of the mountain landscape are inhabited by birds that breed independently of the altitude. Building their nests among the rocks are such birds of prey as *Buteo lagopus* (Pontopp.), *Hierofalco rusti-
culus (L.), Falco peregrinus Tunst., and Corvus corax L. Here, at the higher altitudes are found also *Apus pacificus leucopyga* (Pall.) breeding in colonies and a few *Delichon urbica lagopoda* (Pall.), which also seem to be breeding. Some species are confined to the banks of mountain streams—*Motacilla cinerea* Tunst. and *Actitis hypoleucos* (L.)—and along the deeper streams may be found *Histrionicus histrionicus pacificus* Brooks and *Heteroscelus incanus* (Gm.). It is of interest that at highest altitudes near the Icy Mount we found *Heteroscelus i. incanus* (Gm.), whereas *H. i. brevipes* (Vieill.) bred lower exclusively. On the shingly fields along the upper Achai-Wayam River could also be found nesting *Charadrius hiaticula tundrae* (Love) and *Mergus serrator* L. Sometimes *Capella solitaria* (Hodgs.) was seen, but its breeding grounds remained unknown.

The elevated plateaus on the sides of the river valleys are covered by meadow and stony tundra, interspersed by lakes and bushes. In particular
in the wet areas, overgrown with stunted willows, *Schoeniclus pallasi minor* (Midd.) was more numerous than elsewhere. In the U.S.S.R. I do not know another locality where these birds would form the base of any native avifauna. On similar plateaus along the foothills we observed *Lagopus mutus* (Mont.), and on the patches of stony tundra we found broods of *Charadrius mongolus* Pall. In open terrain with tundra vegetation *Pluvialis apricaria fulva* (Gm.) would be seen in some places, but more frequently *Pelidna alpina sakhalina* (Vieill.), *Anthus c. cervina* (Pall.), and *Calcarius lapponicus* (L.).

Especially rich and plentiful is the avifauna in the wide valleys of the rivers Achai-Wayam and Apuka, where the bushes owing to drainage attain an arborescent appearance. Here, clumps of *Populus suaveolens* Fisch and *Chosenia macrolepis* (Turcz.) Kom. are scattered. In the tall poplars a few of the large birds of prey build their nests: *Accipiter gentilis albidus* (Menzb.), *Aquila chrysaetos* (L.), *Haliaeetus albicilla* (L.), and *Thalassoaetos pelagicus* (Pall.). In these clumps breed such forest species as *Xylocopus minor* im-
maculatus (Stejn.), Picoides tridactylus albidior (Stejn.), Pentheastes montanus anadyrensis (Belop.), Sitta europaea albilors Tacz., Siphia parva albicilla (Pall.), Fringilla montifringilla subcuneolata Kl., and Acanthis f. flammae (L.). Here, Cuculus canorus telephonus Heine and C. saturatus horsfieldi Moore were taken.

Fig. 4. The valley of the upper Achai-Wayam. In the foreground is a wet plain inhabited by Schoeniclus pallasi, Chrysophrys pusilla, Cyanosylvia svecica, Oreopneute fuscata, Anthus cervina, and others. Farther to the left is a low plateau, the breeding haunts of Charadrius mongolus and Calcarius lapponicus. At the summits of the mountains are the homes of Leucosticte arctica, Corvus corax, Oenanthe oenanthe, and a colony of Apus pacificus. Photo by L. A. Portenko, 27 June 1960.

The shrubbery in these valleys is inhabited by many birds of the upper belts, together with abundant Lagopus lagopus (L.), Cyanosylvia s. svecica (L.), Motacilla alba ocularis Swinh., Budytes flavus tschutschensis (Gm.), Anthus g. gustavi Swinh. (near the mouth of the Apuka), Chrysophrys rustica latifascia (Port.), C. pusilla (Pall.), and considerably fewer Hypocentor a. aureola (Pall.).

In the floodplains, in the immediate vicinities of rivers and lakes, have been found breeding Gavia s. stellata (Pontopp.), G. arctica viridigularis Dwight, fewer Pedetaithya griseigena holböllii (Reinh.), and Dyties auritus (L.); among the Anseriformes are Melanonyx fabalis serrirostris (Swinh.), Dafila a. acuta (L.), Nettion c. crecca (L.), Mareca penelope (L.), and more rarely Aythya marila (L.), Clangula hyemalis (L.), Oidemia nigra americana Swains., and Melanitta fusca stejnegeri (Ridgw.); among the waders breed Numenius madagascariensis (L.), Rhyacophilus glareola (L.), Capella g. gallinago (L.), and Phalaropus lobatus (L.); among the Lari-
formes may be encountered Larus canus L., L. argentatus vegae Palm.,
Sterna hirundo longipennis Nordm., and Stercorarius parasiticus (L.).

A quite particular bird fauna is peculiar to the seashores. On the high and
steep cliffs are disposed various rookeries, inhabited by Phalacrocorax pelagi-
cus aequus Swinh., Larus schistisagus Stejn., Rissa tridactyla plicoaris Ridgw.,
Uria lomvia arra (Pall.), and U. aalge inornata Salom., while Cepphus grylle
columba (Pall.), Lunda cirrhata (Pall.), and Fratercula corniculata (Naum.)
breed here in considerably lesser numbers.

On the low plateaus along the beach Alauda arvensis pekinensis Swinh.
is common and we found a family of Limonites temminckii (Leisl.). Here, I
discovered a brood of Eurynorhynchus pygmaeus (L.) and at the mouth of
the Apuka a colony of such a rarity as Sterna camtschatica Pall.

SOME ZOOGEOGRAPHICAL CONCLUSIONS

The limits of distribution of many birds pass across the Koryak land. The
following species and subspecies enter this country from the Kamchatka side:
Spatula clypeata (L.), Mergellus albellus (L.), Thalassoëtus pelagicus
(Pall.), Glottis nebularia (Gunn.), Actitis hypoleucos (L.), Numenius
madagascariensis (L.), Larus ridibundus L., Picoides tridactylus albidior
(Stejn.), Apus pacificus leucopyga (Pall.), Alauda arvensis pekinensis
Swinh., Delichon urbica lagopoda (Pall.), Corvus corone orientalis Eversm.,
Sittæ europæa albifrons Tacz., Siphipparva parva albicilla (Pall.), Motacilla cinerea robusta (L. Brehm), Fringilla
montifringilla subcuneolata Kl., Acanthis flammea (L.), Pyrrhula pyrrhula
cassini Baird, and some others. All of these do not spread farther north
and do not breed in the middle and lower Anadyr Basin. About 40 Kamchatkan
species and subspecies do not reach the Koryak Highlands. The following
arctic and subarctic birds have their southern limits in the territory of the
Koryak land: Clangula hyemalis (L.), Somateria mollissima v-nigra Gray,
Pluvialis apricaria fulva (Gm.), Charadrius hiaticula tundrae (Love), Nu-
menius phaeopus variegatus (Scop.), Heteroscelus i. incanus (Gm.), Eury-
norhynchus pygmaeus (L.), Limonites temminckii (Leisl.), Pelidna alpina
sakhalina (Vieill.), Penthestes montanus anadyrensis (Belop.), Oenanthe
oenanthe oenanthis (Vig.), Oreopneuste fuscata homeyeri (Dyb.), Budy-
tes flavus tschutschensis (Gm.), Acanthis flammea exilipes (Couses), and
Chrysophrys pusilla (Pall.). More than 20 species that nest in the Anadyr
Basin or on the shores of the Anadyr Gulf do not enter the Koryak land.
Although this number is almost half that of the Kamchatkan species not
reaching Koryak land, both numbers are approximately equivalent from the
zoogeographical point of view, because the number of species in northern
countries is, in general, less than in southern ones.

Comparison of the above-mentioned lists leads one to believe that the
avifauna in the Koryak land has a mixed composition of northern and south-
ern forms, and there are many reasons to consider it as an intermediate one.
On the other hand, it is impossible to set a real zoogeographical boundary line between the Kamchatkan avifauna and that of northeastern Siberia. First, there are no natural barriers for such a line; second, various species enter the Koryak Highlands, from both the northern and southern sides, from different distances.

Based on the extreme geographic points of nesting discoveries, it is very often impossible to delineate a continuous frontier of distribution. Sometimes the limits form long prominences or even isolated islets. They change in time, and advance and retreat. Birds can breed in a given area quite sporadically. At least in such a ravine-intersected country as the Koryak Highlands, where almost each valley and each ridge has to a certain degree its own features, it is extremely difficult to map distributional limits.

The general character of the Koryak avifauna is now more or less clear. The Kamchatkan avifauna is separated from that of northeastern Siberia not by the most narrow isthmus of the Kamchatka Peninsula, the so-called “Parapolski Dol” (Parapolski plateau), but by the vast Koryak Highlands. It is necessary to renounce the value of the Parapolski Dol as a zoogeographic boundary.

Discussions about the fauna of any locality in northeastern Asia always consider the influence of the vicinity to North America. In the avifauna of the Koryak land this influence exists but to a slight degree. We have failed to obtain the clutches or broods of any North American birds, but have observed and collected a few adults of some species. *Grus canadensis* (L.) is a rather common summer resident along the lower Apuka. Here, on 7 March 1960 a young male of *Mergus merganser americanus* Cass. was shot. In the highlands near the Icy Mount we obtained specimens of *Heteroscelus i. incanus* (Gm.); and in the vicinities of Apuka and Tilichiki we repeatedly met with *Limnodromus scolopaceus* (Say), and some specimens were collected. Finally, on 10 June 1960 near Apuka a male of *Passerculus sandwicensis anthinus* Bp. was taken as a passage straggler.

Such are the first conclusions about the avifauna, studied during 3 years in a country that up to the present time has remained ornithologically among the most unknown in the total territory of the U.S.S.R.

**SUMMARY**

Connecting the Anadyr Basin to the Kamchatka Peninsula, the Koryak Highlands have an avifauna that is chiefly eastern Siberian in its affinities, with the addition of species or subspecies derived from Kamchatka. It is impossible to draw a sharp faunal boundary between the Koryak land and Kamchatka, as the low isthmus (the so-called “Parapolski Dol”) that connects the two regions does not constitute an adequate faunal barrier. Such barrier as exists consists of the mountain ranges. A few species derived from North America breed in these mountains, but only in very small numbers.
The chief aim of zoogeography is the causal analysis of animal distribution, and the focus of such studies is the distributional range, i.e. the geographical area in which the population of the species lives. The primary task thus is the obtaining of accurate faunistic knowledge, for on such knowledge are based all ecological considerations of the biotic communities, of which the species populations are members. The present distribution, in relation to the distribution of communities, is the clue to understanding the zoogeographical picture of the past, including the evolution of the species and the dynamics of their range. While the wintering and passage areas of migrants, as Salomonsen (1955) emphasized, are important from both evolutionary and distributional points of view, in birds the breeding range is generally a better indicator of the effect of ecological and historical factors on the past and present status of the species.

It is possible and often useful to map the composite distributional range of higher taxonomic units such as genera, families, and so forth. It follows from the current definitions of these units that the consequences derived from their zoogeographical treatment, ipso facto, apply in very broad terms, i.e. they reveal only broad ecological affinities at the biome level, as well as geographical ties to subcontinents or continents (cf. Mayr, 1946).

These taxonomic units are only abstractions for the geographer who studies the present and past composition of the biosphere of our planet. The individual animals, which make up the population of a species within its range, live in close and mutual relationship with animal and plant partners using the same habitat, and together with them they compose biotic communities.

Yet it is well known that birds do not rely exclusively on single biotic communities in their selection of breeding habitats, but rather on a broader range of life forms of plants occurring in several related communities (Pitelka, 1941). Vicissitudes of past history and dispersal, and changing adaptation processes, add to the discrepancies between community ranges and ranges of their member animals (Udvardy, 1958).

Therefore, causal analysis of species' ranges can seldom be achieved on the basis of environmental requirements and taxonomic relationships alone. Two avenues, or the combination of them, are open for such research. An analytical method would consider the population density and dynamics of a species throughout its range, and in the different communities it frequents. No such study of birds has yet been undertaken, for sufficient field data on population densities are as yet barely available. A synthetic method has been successfully used by plant geographers (e.g. Hultén, 1937, and Raup, 1947; Hultén...
superimposed range-outline maps of a great number of species and thus arrived at "equiformal areas" occupied in common by a large number of species that he considered to be historically related); Stegmann (1938) used the same method for Palaearctic avifaunas.

This synthetic method reveals centers of distribution for groups of species that now show similar geographical and ecological occupancy. Providing we work with sufficient numbers of species in establishing such a faunal (distributional) group, ecological and historical relations become easily clarified. Stegmann (1938) points out that the ratio of such faunal groups in any local avifauna characteristically reveals the past and present zoogeographical status of the area (cf. Keve and Udvardy, 1951) much better than any division into zoogeographical regions with sharp boundaries.

In our present work (Udvardy, 1960) of mapping the distributional ranges of the North American avifauna (north of Mexico), we outlined the ranges of passerine species on a tentative basis for general orientation. The A.O.U. Check-List (1957), the Mexican check-list (Friedmann et al. 1950, 1957), Voous's (1960) atlas, and numerous local avifaunistic works have been consulted. The range maps were then grouped according to superficial geographical resemblances. The final grouping for the purpose of this paper was arrived at through geographical and ecological considerations, then by superimposing the related range maps and drawing a composite map of the "fauna," or its subdivisions (see Appendix and Fig. 1–28).

The range limits, which serve as the basis of these composite maps are not accurate in details, and certain modifications will follow as we gather all the published data that are available for each species. It is unlikely that the group pattern will change substantially where more than five or six species are treated in the present paper. These faunal groups are considered to be provisional for two reasons: (1) the nonpasserine fauna (less arboreal than the passerines, in general) and especially the limnic (water and shore) birds in it will probably reveal some additional distributional faunal types; (2) in the Southwest the boundary taken is political and not natural. For these reasons we do not attempt at this time to reach any conclusions about the reality, ecology, and history of the 17 faunas and their composition. The centers (black on the maps) of the faunal groups are not centers of origin as in Hultén's (1937) work, but suggest the present location of the major eco-geographical units to which the avifaunal group in question belongs. Similarly, the range outlines, which surround these centers in progressively wider circles, do not necessarily indicate progressive expansion of ecologically or dispersionally more dynamic members of the faunal group. Such causal conclusions will be drawn elsewhere and at a later date.

By publishing these faunal groups, we hope to stimulate the completion of accurate faunistic work of those parts of North America where the details are still obscure, and we hope to get stimulating criticism and suggestions about our zoogeographical work which is now in progress.
The field (ecological reconnaissance) and laboratory (plotting and mapping) work was supported by a grant from the Penrose Fund of the American Philosophical Society and by renewed grants of the National Research Council of Canada. I am obliged for the technical assistance given in the course of this work by R. Drent, P. Grant, O. Horváth, L. Rétfalvi, and F. Tompa. The maps used in this paper were based on Goode Base Maps copyrighted by the University of Chicago and used by permission of the University of Chicago Department of Geography.

I. The Arctic Fauna may be divided into three groups of birds.

1) Six widespread species inhabit the arctic tundra (Fig. 1):

*Anthus spinoletta*  
*Spizella arborea*  
*Acanthis hornemanni*  
*Calcarius lapponicus*  
*A. flammea*  
*Plectrophenax nivalis*

All but *Spizella* are circumpolar; I have grouped *Anthus spinoletta* with the subarctic species because this circumpolar bird is not an exclusive inhabitant of the Arctic but in North America is mainly arctic-alpine in its distribution.

2) Species of the Old World Arctic barely penetrating arctic North America are as follows (Fig. 2): *Oenanthe oenanthe* penetrates the North American Arctic quite widely from both west and east; *Motacilla alba* and *Anthus pratensis* colonized East Greenland from arctic Europe. The arctic–subarctic colonizers of Alaska from Siberia are:

*Parus cinctus*  
*Luscinia svecica*  
*Phylloscopus borealis*  
*Motacilla flava*  
*Plectrophenax hyperboreus* (not mapped) is an insular endemic in the Bering Sea; *Emberiza rustica* (not mapped) pioneers the Aleutian Islands.

3) The following subarctic species (Fig. 3) occupy the tundra–forest (sensu Johansen, 1963):

*Hylocichla minima*  
*Anthus spinoletta*  
*Lanius excubitor*  
*Zonotrichia querula*  
*Z. leucophrys*  
*Calcarius pictus*  
*Zonotrichia leucophrys* and *Anthus spinoletta* extend south along the alpine tundra and woodland of the Rocky Mountains; the former has a woodland subspecies in the Pacific Northwest and in the northern Appalachians; the latter inhabits coastal barrens in Newfoundland (Peters and Burleigh, 1951) as well. *Hylocichla minima* likewise has a nonsubarctic subspecies in the Northeast.

II. The boreal forest fauna consists of 41 species, the center of distribution of which is the Coniferous Forest Biome of Pitelka (1941). Three geographically quite distinct faunal groups can be distinguished.

1) The northern taiga belt of North America is occupied by seven species which do not range south into the western coniferous forest or to the Appalachian coniferous forest areas (Fig. 4):
Fig. 1. Superimposed distribution of five widespread species of the Arctic Fauna.

Fig. 2. Superimposed distribution of three east-arctic, and five west-arctic species of the Arctic Fauna.

Fig. 3. Superimposed distribution of five subarctic species of the Arctic Fauna.

Fig. 4. Superimposed distribution of seven taiga species of the Boreal Forest Fauna.

Black area shows the greatest concentration of species. The different patterns refer to lower concentrations as shown by the key in each figure.
This group includes three circumpolar Holarctic species, all of them associated even in the Old World with the northern belt of the taiga.

2) The majority of the 24 species forming the boreomontane faunal group (Fig. 5) occupies, besides the taiga, the coniferous forest-clad western coastal and mountain areas; some of the species also occupy the coniferous altitudinal belts of the Appalachian Mountains:

- Empidonax traillii
- Nuttalornis borealis
- Iridoprocne bicolor
- Perisoreus canadensis
- Parus atricapillus
- Sitta canadensis
- Certhia familiaris
- Troglodytes troglodytes
- Hyllocichla guttata
- H. ustulata
- Regulus satrapa
- R. calendula
- Vireo solitarius
- Vermivora celata
- Dendroica coronata
- D. auduboni
- Wilsonia pusilla
- Hesperiphona vespertina
- Carpodacus purpureus
- Pinicola enucleator
- Spinus spinus
- Loxia curvirostra
- Passerella iliaca
- Melospiza lincolni

Four species and 9 genera are Holarctic. Most members of this distributional group are forest birds. As can be expected from such widespread species, all but three show subspeciation, some of them very markedly; this subspeciation usually does not split the northern taiga area of the ranges, but is extensive in the West and in the Northeast. Three examples—1 vicarious species pair (Dendroica coronata and auduboni, cf. also Rand, 1948), 4 species with disjunct ranges, and 5 species that range south to the Isthmus of Tehuantepec (3 to Guatemala's, and 2 to Nicaragua's mountains)—indicate that this faunal group, as a whole, underwent considerable shifting and splitting of its range during at least the Pleistocene glaciations. The three sections of the range of Regulus satrapa (West Coast and Rocky Mountains forest; eastern taiga and Appalachian Mountains; the Sierra Madre del Sur of Mexico and Guatemala) are still separated by two gaps of several hundred miles' distance, and will be useful in tracing this group to three glacial refugia.

3) The 10 eastern taiga species (Fig. 6) are all blocked off from the western coniferous forests by the Rocky Mountains (except for some spilling over through the Peace River gap) but do not follow the Appalachian chain southward; two or three of the species live in ecotone-edge situations not in the coniferous forest proper, and Melospiza georgiana is classed here by virtue of the geography of its distribution alone; nevertheless the group seems to form a unit. Pitelka in his (1941) discussion of Empidonax flaviventris pointed out that its range might be ecologically limited by the factors limiting dense coniferous growth; this suggestion could be followed in analyses of all 10 eastern taiga species.
Fig. 5. Superimposed distribution of 24 boreomontane species of the Boreal Forest Fauna.

Fig. 6. Superimposed distribution of ten eastern taiga species of the Boreal Forest Fauna.

Fig. 7. Superimposed distribution of five eastern ecotone species of the Eastern Ecotone Fauna. The western disjunct area belongs to *Vermivora ruficapilla*.

Fig. 8. Superimposed distribution of seven Eastern-Middle Western species of the Eastern Ecotone Fauna.

Symbols as in Fig. 1-4.
III. The eastern ecotone fauna includes 19 passerine species, and the center of this faunal group seems to lie around the Great Lakes and eastward in the northeastern outposts of the Appalachian Mountains, where all 19 species occur, and also along the southern Appalachian slopes south to northern Alabama.

1) Five species (Fig. 7) are more or less restricted to this core of the ecogeographic range of the fauna:

- \( V. \text{peregrina} \)
- \( D. \text{fusca} \)
- \( D. \text{caerulescens} \)
- \( W. \text{canadensis} \)

2) Seven species (Fig. 8), of which 5 are parulid warblers, expand along the coniferous forest–prairie ecotone as well, some of them occurring in the deciduous element of mixed and seral growths within the taiga belt, others \((S. \text{phoebe}, S. \text{aurocapillus}, S. \text{rutila})\) even within the prairie and deciduous biome areas where they occupy associations that are subclimax, etc. (Pitelka, 1941; Kendeigh, 1961).

- \( S. \text{magnolia} \)
- \( D. \text{virens} \)
- \( S. \text{aurocapiilllis} \)

3) A group of seven species (Fig. 9) occupies the ecotone region south of the Great Lakes, but diverges widely along the central and western part of their range; the species are ecologically divergent (2 coniferous ecotone, 1 deciduous forest-edge, 3 grassland, 1 marsh bird).

- \( C. \text{platensis} \)
- \( P. \text{ludovicianus} \)
- \( P. \text{kentuckiensis} \)
- \( P. \text{henslowii} \)
- \( P. \text{gramineus} \)

The whole fauna seems to have occupied its large range for a relatively short time since only 6 of the 19 species have subspecialized further.

IV. The eastern deciduous forest fauna includes ( provisionally) 28 species, all of which are at present members of the deciduous-forest biome. Three subdivisions were set up according to the distributional picture:

1) Eight Mississippi Valley–Appalachian forest birds (Fig. 10) occupy the range of the biome (Pitelka, 1941), with some extensions northward into the ecotones. One prairie finch, and two or three forest-edge species show the same distribution as the forest birds.

- \( H. \text{vermivorus} \)
- \( I. \text{galbula} \)
- \( P. \text{olivacea} \)
- \( S. \text{ameritana} \)
- \( S. \text{pusilla} \)
Eastern Ecotone Fauna. The Central and South American disjunct range belongs to *Cistothorus platensis*.

Fig. 9. Superimposed distribution of seven ecotone–grassland species of the Eastern Ecotone Fauna. The Central and South American disjunct range belongs to *Cistothorus platensis*.

Fig. 10. Superimposed distribution of eight Mississippi Valley–Appalachian forest species of the Deciduous Forest Fauna.

Fig. 11. Superimposed distribution of 15 deciduous climax forest species of the Deciduous Forest Fauna.

Fig. 12. Superimposed distribution of five forest-edge species of the Deciduous Forest Fauna.

Symbols as in Fig. 1–4.
2) The inhabitants of the undisturbed deciduous forest (Fig. 11) show considerable uniformity in their ranges, living in the southeastern quarter of North America; the relatively even boundaries, however, are due only to the fact that the zigzags of the details have not yet been mapped. These 15 species compose the bulk of the deciduous-forest passerine avifauna, although Kendeigh (1961) surmises that 7 of them originally belonged to the southeastern branch of the sclerophyllous Madro-tertiary communities.

- *Myiarchus crinitus*
- *Empidonax virescens*
- *Contopus virens*
- *Parus bicolor*
- *Hylocichla mustelina*
- *Vireo flavifrons*
- *Protonotaria citrea*
- *Parula americana*
- *Dendroica dominica*
- *D. pinus*
- *D. discolor*
- *Oporornis formosus*
- *Wilsonia citrina*
- *Icterus spurius*

3) Five species are much more widespread, and therefore we show them on a separate map (Fig. 12); these are forest-edge species following deciduous growth through river galleries, through the prairies, and up the foothills of the western mountains, and even through the Rockies, but not quite reaching the Pacific Coast. Further study of some of the still-unanalyzed, widespread (transcontinental) forest-edge birds would undoubtedly broaden this group.

- *Cyanocitta cristata*
- *Toxostoma rufum*
- *Dumetella carolinensis*
- *Vireo olivaceus*
- *Quiscalus quiscula*

Only 8 of the 28 species, less than one-third of the total fauna, are split into subspecies.

V. SOUTHEASTERN PINE-OAK FAUNA (Fig. 13). Kendeigh (1961) provisionally defined a “south-eastern mixed biociation,” and the 8 species I united into this faunal group are mostly members of this biociation, 3 of them almost reaching the Mexican border in the west and another 3 penetrating the Gulf coastal areas of Mexico. As Kendeigh (1961) points out, faunal elements of the Madro-tertiary sclerophyllous flora could be surmised by the distribution and synecological relations of these species.

- *Parus carolinensis*
- *Sitta pusilla*
- *Thryothorus ludovicianus*
- *Vireo griseus*
- *Linnothlypis swainsonii*
- *Vermivora bachmani*
- *Passerina ciris*
- *Aimophila aestivalis*

VI. The ATLANTIC COASTAL FAUNA is a meager one. *Corvus ossifragus* is mostly coastal but follows the Mississippi Valley woodland habitats as well; the Seaside Sparrow species (*Ammospiza maritima*, *A. nigrescens*, and *A. mirabilis*) are entirely restricted to coastal salt marshes.

VII. The TROPICAL WEST INDIAN FAUNA is represented by two passerine species in Florida: *Tyrannus dominicensis* and *Vireo altifloquus*.

VIII. The PRAIRIE FAUNA is a very meager group, as far as passerine species are concerned, for only seven such birds can be listed and mapped (Fig.
Fig. 13. Superimposed distribution of the eight species of the Southeastern Pine-Oak Fauna.

Fig. 14. Superimposed distribution of seven species of the Prairie Fauna. The James Bay and Atlantic coastal range belongs to Ammospiza caudacuta.

Fig. 15. Superimposed distribution of the five coast forest species of the Western Coniferous Forest Fauna.

Fig. 16. Superimposed distribution of four northwestern forest-edge species of the Western Coniferous Forest Fauna.

Symbols as in Fig. 1-4.
IX. The western coniferous forest fauna contains 17 passerine species which occur more or less widely in the forests of the West. These are predominantly coniferous forests. However, the coniferous-forest passerine fauna of the West includes the 24 boreomontane species, which have been dealt with already. The 17 species discussed here are endemic in the area of North America west of, and including, the Rocky Mountains from the Yukon Territory to southern Mexico; some of them even extend into the continuing mountain chains of Central America. Quite obviously this huge expanse shows major climato-ecological differences in its components. Thus, in the wet and temperate Pacific Northwest the coniferous forest covers the coastal area as well; in the Central Plateau area, which includes the Great Basin, the coniferous forest is restricted to higher elevations and windward slopes; in the Mexican part of the plateau and farther south, the coniferous-forest belt is restricted to still higher elevations, and is very poorly represented by species of this widespread group. Following these major ecological subdivisions of the coniferous-forest belt in the West, three faunal groups can be surmised on the basis of the species scrutinized here. Although species with ranges entirely within the political boundaries of Mexico have not been considered, it is unlikely that their inclusion would considerably alter the picture. The range of these species would join onto the southern part of the range of faunal type XV. The three groups are as follows:

1) Coast forest birds (Fig. 15). Five passerine species occupy mainly the coastal wet belt, and inland counterparts on the wet slopes. The range of the three warblers is partly allopatric, thus the group (without its nonpasserine members) is very small.

- *Parus rufescens*  
- *Ixoreus naevius*  
- *D. occidentalis*  
- *D. nigrescens*  
- *D. townsendi*

2) Northwest forest-edge birds (Fig. 16). Four species that are not confined to the climax forests are distributed rather similarly to the first group, but are more widespread.

- *Empidonax hammondii*  
- *Oporornis tolmiei*  
- *Piranga ludoviciana*  
- *Junco oreganus*

Very similar in its distribution to the previous two groups, but living only in the subalpine forest belt of the mountains, is *Parus gambeli* from northern
Fig. 17. Superimposed distribution of seven Cordilleran species of the Western Coniferous Forest Fauna.

Fig. 18. Superimposed distribution of six species of the Western Woodland-edge Fauna.

Fig. 19. Superimposed distribution of nine sagebrush-arid-woodland species of the Great Basin Fauna.

Fig. 20. Superimposed distribution of five northwestern arid-woodland species of the Great Basin Fauna.

Symbols as in Fig. 1–4.
British Columbia to northern Chihuahua; thus, it seems to be a unique case among the passerine endemics of the West, and so far I have not included it in any of the groups.

3) Seven passerines show Cordilleran distribution (Fig. 17), i.e. they stretch from Alaska deep into the mountains of Mexico, or even farther south:

- *Empidonax difficilis*
- *Contopus sordidulus*
- *Tachycineta thalassina*
- *Cyanocitta stelleri*
- *Cinclus mexicanus*
- *Myadestes townsendi*
- *Vireo huttoni*

The double core of the composite map is caused by *Vireo huttoni*, which resides in the coastal forest west of Arizona, has a disjunct range in Lower California occupied by an endemic subspecies, and also breeds on the Mexican plateau down to Guatemala. The discontinuity of its two main ranges is paralleled in several other species in the form of subspecific boundaries and minor gaps, and represents an interesting basis for causal and historic consideration. Thus it might suggest two, or three, separate refugia in the coniferous portion of the Arcto-tertiary forest during recent glaciations, as does also the picture presented by Dillon (1956) of the western *Colaptes* woodpeckers.

X. The alpine tundra and shrub fauna. This group is very ill-founded at the present moment, the only passerine endemics of the alpine tundra being the genus *Leucosticte* (the three species of which, *L. tephrocotis*, *atra*, and *australis*, are allopatric vicars) and *Zonotrichia atra*. The two arctic–alpine species, *Anthus spinolletta* and *Zonotrichia leucophrys*, have been treated in the arctic–subarctic group; *Spizella breweri taverneri* is an alpine subspecies of an arid woodland species, although I. McT. Cowan (in litt.) suspects, on the basis of its ecology and behavior, that it perhaps deserves the rank of a species.

XI. The western woodland-edge fauna represents a tentative grouping which is heterogeneous as far as habitats are concerned and is formed by six species (Fig. 18). These have common ranges that extend from the Pacific coastal areas through the open uplands—and marshes (2 species)—eastward through the prairies to reach the Mississippi Valley or even the Great Lakes.

- *Tyrannus verticalis*
- *Sturnella neglecta*
- *Xanthocephalus xanthocephalus*
- *Euphagus cyanocephalus*
- *Passerina amoena*
- *Chondestes grammacus*

Several even more widespread species have not been analyzed, but all are eurytopic open-country and edge birds, and further analysis of such types is not possible at present.

XII. The great basin fauna, on the other hand, has rather sharp range limits. The species fall, geographically and ecologically, into two groups:

1) The sagebrush–arid-woodland faunal group (Fig. 19) centers on the
range of cold winter desert between southern British Columbia and north-central Arizona, and only 2 of its 9 species are restricted to the sagebrush (Artemisia tridentata) biociation; the rest occur in the ponderosa pines (Pinus ponderosa) and in the piñon–juniper woodland:

- Empidonax wrightii
- Nucifraga columbiana
- Gymnorhinus cyanoccephala
- Vermitornis virginiae
- Oreoscoptes montanus

2) Five species form the northwestern arid-woodland faunal group (Fig. 20). Besides the Great Basin, they also range into the arid or open woodlands farther north and reach the subarctic woodland. (Spizella breweri accomplishes this by having different subspecies in sagebrush–bunchgrass (Artemisia–Festuca) prairie, and in alpine grassland.)

- Sayornis saya
- Empidonax oberholseri
- Sialia currucoides

Subspeciation is very limited in the Great Basin fauna, indicating that many of its members had quite recently themselves been subspecies.

XIII. The chaparral (Mediterranean type of scrub) and desert scrub of the Southwest harbors many distinct endemic groups. Those north of the Mexican boundary are here grouped as Southwestern Endemic Faunas:

1) The upper California fauna (Fig. 21A) has already been described by Miller (1951). He listed 5 nonpasserine and 8 passerine species among the members of this fauna, considering their distribution in and near California only. Vireo huttoni, which Miller (1951) included, has a widespread distribution, and I classed it elsewhere in this study. Thus remain:

- Pica nuttalli
- Parus inornatus
- Psaltriparus minimus
- Spinus lawrencei

Parus inornatus and Psaltriparus minimus, birds of the sclerophyllous-coniferous woodland have a more widespread distribution but do not warrant, at this time, any special consideration.

2) The lower California fauna (Fig. 21B) contains 4 species on the mainland of Baja California and 4 insular species. Undoubtedly, a detailed analysis, like that of Davis (1959), will show more endemic subspecies, and inclusion of the nonpasserine birds will also raise the number of endemics. The peninsular endemic species are:

- Toxostoma cinereum
- Turdus confinis

3) The Sonoran fauna (Fig. 22). This group, and many of the following ones, does not include all the passerines, for I have only considered those breeding species whose range extends into the United States of America. Our knowledge of distribution ranges and habitat relations of many Mexican
Fig. 21. Superimposed distribution of (A) 7 species of the Upper Californian Fauna, (B) 4 of the Lower Californian Fauna, and (C) 2 of the Chihuahuan.

Fig. 22. Superimposed distribution of seven species of the Sonoran Fauna of the Southwestern Endemic Faunas.

Fig. 23. Superimposed distribution of four species of the Edwards Plateau Fauna of the Southwestern Endemic Faunas.

Fig. 24. Superimposed distribution of 16 Mexican highland species of the Arid Southwestern Fauna.

Symbols as in Fig. 1–4.
birds is still incomplete, although rapid progress is being made in this respect at present. Therefore, these groupings should be considered more tentative and provisional than the previous ones.

<table>
<thead>
<tr>
<th>species</th>
<th>species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Toxostoma lecontei</em></td>
<td><em>Pipilo aberti</em></td>
</tr>
<tr>
<td><em>T. bendirei</em></td>
<td><em>Aimophila carpalis</em></td>
</tr>
<tr>
<td><em>Vermivora luciae</em></td>
<td><em>Vireo vicinior</em></td>
</tr>
</tbody>
</table>

*Icterus parisorum*

The Sonoran desert forms the center of distribution of these species of the dry lowlands, desert scrubs, canyon woodlands, and piñon–juniper–oak woodlands. *Vireo vicinior* breeds in the northern half of the Sonoran and Chihuahuan desert areas.

4) A **CHIHUAHUAN** *fauna* below the U.S. border includes only two species (Fig. 21 C) that also breed north of Mexico: *Vermivora crissalis* and *Spizella wortheni*.

5) The **EDWARDS PLATEAU** area of western Texas and neighboring dry, brushy woodlands harbors four endemics (Fig. 23):

<table>
<thead>
<tr>
<th>species</th>
<th>species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Muscivora forficata</em></td>
<td><em>Dendroica chrysoparia</em></td>
</tr>
<tr>
<td><em>Vireo atricapilla</em></td>
<td><em>Aimophila cassini</em></td>
</tr>
</tbody>
</table>

6) *Parus atricristatus* (an ecological vicar of *P. bicolor*, cf. Blake, 1953) and *Toxostoma longirostre* are endemics of the arid **GULF SLOPE** of Mexico. (*Icterus gularis* and *I. graduacauda* range farther south and west.)

XIV. The **ARID SOUTHWESTERN FAUNA** is a provisional, large faunal group which will be complete when the Mexican endemic passerines that do not breed in the U.S.A. are included. The presently analyzed 27 species show a marked division into two groups:

1) The majority of the species, 16 in number, spread from the Tehuantepec gap of southern Mexico to the northern Mexican highlands, arid plains, desert scrub, and the oak–pine woodlands; these include the areas in which we found the center of distribution of the restricted local endemic groups (Californian, Sonoran, and so forth). These groups are undoubtedly related. The Mexican highland species (Fig. 24) are:

<table>
<thead>
<tr>
<th>species</th>
<th>species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aphelocoma ultramarina</em></td>
<td><em>T. dorsale</em></td>
</tr>
<tr>
<td><em>Cortus cryptoleucus</em></td>
<td><em>Polioptila melanura</em></td>
</tr>
<tr>
<td><em>Parus sclateri</em></td>
<td><em>Phainopepla nitens</em></td>
</tr>
<tr>
<td><em>P. wollweberi</em></td>
<td><em>Pyrrhuloxia sinuata</em></td>
</tr>
<tr>
<td><em>Auriparus flaviceps</em></td>
<td><em>Aimophila ruficeps</em></td>
</tr>
<tr>
<td><em>Troglohydridus brunneicollis</em></td>
<td><em>A. botteri</em></td>
</tr>
<tr>
<td><em>Campylorhynchus bruneicapillum</em></td>
<td><em>Junco phaeonotus</em></td>
</tr>
<tr>
<td><em>Toxostoma curvirostre</em></td>
<td><em>Spizella airogularis</em></td>
</tr>
</tbody>
</table>

2) Most of the 11 southwestern woodland species (Fig. 25) occupy moderately dry habitats, such as the deciduous growth of canyons or river bottoms, and have a wider distribution to the north than the above group. These 11 birds are equally widespread (although we have no information on their breeding densities) in the Great Basin area, where many of them are migratory, and in the California chaparral.
Fig. 25. Superimposed distribution of 11 southwestern woodland species of the Arid Southwestern Fauna.

Fig. 26. Superimposed distribution of 16 species of the Trans-Tehuantepec Montane Fauna.

Fig. 27. Superimposed distribution of four species of the South American Disjunct Fauna.

Fig. 28. Superimposed distribution of eight species of the Tropical South American Fauna.

Symbols as in Fig. 1-4.
All of these faunal elements are restricted southward by the Tehuantepec gap. Practically all members of both groups are markedly subspeciated, indicating vicissitudes in the history of the fauna. The second group shows, in addition to subspeciation, strong affinities in the form of species closely related to eastern American avifaunas (III, IV, V); *Aphelocoma coerulescens* itself has a relict, disjunct subspecies in the East in Florida. Comparison of the eastern and western forms of these species pairs will help in disentangling the details of history and ecology of the avifaunas.

XV. The tropical Middle American or **trans-tehuantepec montane fauna** (Fig. 26) extends along the mountains of Guatemala and El Salvador, to Nicaragua and Panama. Many of the bird species are widespread and euryecious (i.e. they can occupy a wide variety of habitats). Those of arid foothills and lowlands constitute the group that peters out toward the north just where the Mexican plateau species of the previous fauna did, i.e. at the northern border of the warm-winter (lowland) desert areas of the western U.S.A.

XVI. **south American disjunct fauna** (Fig. 27). A small number of species show the same Central American distribution as the preceding fauna and, in addition, have widespread populations in South America. This group undoubtedly will increase when the nonpasserines are included. It can also be surmised that several members of the genuine southwest North American faunal groups have vicarious species partners in South America, disjunct from their northern counterpart because of the Panamanian gap with its lowland type of tropical ecosystems.

XVII. **tropical south American fauna** (Fig. 28). Many members of the tropical South American habitats are euryecious enough to penetrate Central America through the Panamanian and Tehuantepecian areas and some of
them even reach the U.S. border, enabling us to constitute this faunal group.

- *Tyrannus melancholicus*
- *Pitangus sulphuratus*
- *Myiarchus tuberculifer*
- *Sayornis nigricans*
- *Parula palustris*
- *Cassidix mexicanus*
- *Piranga flava*
- *Spinus psaltria*

There are four South American species that are too widespread in North America to be included in any of these groups.

Two more such passerines have the disjunct type of range, exhibiting the Panamanian hiatus. Ten widespread North American passerines spread southward along the mountains of Mexico and Central America, and 12 more stop in the South at the Tehuantepec gap.

These unanalyzed groups, as well as 8 additional, widespread temperate North American species and 3 insular species, are those that I have not taken into consideration in this preliminary grouping. When the details of their distribution are brought together, and when their relative frequency in different communities is known, they may be incorporated into a new and broadened analysis.

**SUMMARY**

In causal zoogeography, basic knowledge consists of the distributional data and the ecological relationships of the species. The published comprehensive accounts of the North American avifauna, supplemented by the range-mapping work of the author's study group, permitted an attempt at a preliminary grouping of the passerine birds. Descriptions and maps of the proposed faunal groups (or “faunas”) form the bulk of this paper. These groups are composed of species whose ranges are similar and more or less overlapping. Most of them also stand well as ecological entities. Thus, this synthetic approach reveals centers of distribution for species that show similar geographical and ecological occupancy at present. The core areas of each “fauna” are not thought to be centers of origin, for each such ecogeographic unit doubtless underwent large-scale geographical shifting, splitting, or migration with changing past climates, and its composition also had a dynamic history and evolution. It is the author’s opinion that the ecological and faunal history of a geographic area is best described by its ecogeographic faunal patterns.

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APPENDIX

Ecogeographic Faunal Groups of the North American Passerine Birds

I. ARCTIC FAUNA
   1) Widespread arctic species
   2) East- and west-arctic species
   3) Subarctic species

II. BOREAL FOREST FAUNA
    1) Northern taiga species
    2) Boreomontane species
    3) Eastern taiga species

III. EASTERN ECOTONE FAUNA
     1) Eastern ecotone species
     2) Eastern–Middle Western ecotone species
     3) Ecotone–grassland species

IV. EASTERN DECIDUOUS FOREST FAUNA
    1) Mississippi Valley–Appalachian forest species
    2) Deciduous climax forest species
    3) Forest-edge species

V. SOUTHEASTERN PINE–OAK FAUNA

VI. ATLANTIC COASTAL FAUNA

VII. TROPICAL WEST INDIAN FAUNA

VIII. PRAIRIE FAUNA

IX. WESTERN CONIFEROUS FOREST FAUNA
    1) Coast forest species
    2) Northwest forest-edge species
    3) Cordilleran species

X. ALPINE TUNDRA AND SHRUB FAUNA

XI. WESTERN WOODLAND-EDGE FAUNA

XII. GREAT BASIN FAUNA
     1) Sagebrush–arid-woodland species
     2) Northwestern arid-woodland species

XIII. Southwestern Endemic Faunas
    a) UPPER CALIFORNIAN FAUNA
    b) LOWER CALIFORNIAN FAUNA
    c) SONORAN FAUNA
    d) CHIHUAHUAN FAUNA
    e) EDWARDS PLATEAU FAUNA
    f) GULF SLOPE FAUNA

XIV. ARID SOUTHWESTERN FAUNA
     1) Mexican highland species
     2) Southwestern woodland species

XV. TRANS-TEHUANTEPEC MONTANE FAUNA

XVI. SOUTH AMERICAN DISJUNCT FAUNA

XVII. TROPICAL SOUTH AMERICAN FAUNA
Avifaunistic Analysis of the Great Basin Region of North America

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Avifaunistic exploration in Utah has resulted in three races being described from the eastern part of the Great Basin, namely, a Dusky Grouse (Behle and Selander, 1951a), a Horned Lark (Behle, 1938), and a Fox Sparrow (Behle and Selander, 1951b). This circumstance suggested that the area represents a center of differentiation for birds. If so, there was the question of its relationships with other such centers in the region. Then there was the broader problem of the influence, if any, of the Great Basin per se on avian distribution. It was toward these questions that the present study was directed.

MEANING OF CENTER OF DIFFERENTIATION

In discussions of speciation in birds the phrase "center of differentiation" is often used. This expresses the concept that the area so designated contains several geographic races representing different species and genera, that the ranges of the several kinds coincide rather closely, and that the characters of each kind are best developed in the particular region. These features imply that the different races have originated in the area either because of the modifying influence of some environmental factor or factors that have had an effect on the several forms, or a barrier of some sort has delimited the several kinds so that they show a common distributional pattern (fide Miller, 1941). Other terms used in this connection are distributional areas and faunal areas. While Grinnell (1914) conceived of a faunal area being a subdivision of a life zone with the principal determining factor being humidity, other students of distribution have not so restricted the usage of the expression. Rather they use it to cover all the distinctive forms regardless of zonal or altitudinal distribution. This is the usage in this paper, and the several terms are used interchangeably.

Evidence in support of the concept of centers of distribution or distributional areas for birds has been amassed by Grinnell (1915, 1928) and others of the University of California’s Museum of Vertebrate Zoology group. The centers are most evident in highly diversified coastal areas, while in interior continental regions they are less well defined. This is the case of the Great Basin of western North America, the area presently under consideration. There is the added complication that certain areas have been proclaimed as centers of subspecific differentiation without the facts conforming to the criteria of the concept. Thus, Miller (1941) showed that two alleged centers, the White Mountains of eastern California and the Warner Mountain–Warner Valley region of southern Oregon and northeastern California, are not in

themselves differentiation centers, although it seems to me that the larger surrounding areas may be so regarded.

DESCRIPTION OF THE GREAT BASIN

It might be supposed that the Great Basin would exert some general, widespread influence on its avifauna. This large, dry, interior basin constitutes one of the subdivisions of the Basin and Range Physiographic Province of western North America (Fenneman, 1931). It lies principally in Nevada and Utah, being hemmed in by the mountain escarpments of the Sierra Nevada on the west and the Wasatch line on the east. Unlike the more or less abrupt east and west margins, the Great Basin gradually merges to the north with the Columbia Plateau Province, the northern limits being reached in southeastern Oregon, northern Nevada, and southeastern Idaho. At its southern limits it extends into California. To the south is the Sonoran Desert. The extent of the Great Basin is shown in Fig. 1. From the standpoint of drainage this area is indeed a great basin, there being no outlet to the ocean at the present time. However, as late as the Pleistocene there was

Fig. 1. Extent of the Great Basin in western United States (after Fenneman, 1931).
in the eastern part, for a time, an outflow from Lake Bonneville to the Snake–Columbia river system. Despite the present lack of drainage to the ocean, the term Great Basin is misleading, for instead of there being a single, large, mountain-fringed basin, the region is actually made up of about 90 interior drainage basins, and there are many mountain ranges that loom up like islands from the surrounding more or less flat terrain. Nearly all of these extend in a north and south direction. They are for the most part unconnected, and one can progress east and west across the basin without surmounting a major range simply by skirting the ends of the various ranges. (For a discussion of the geological background, see Blackwelder, 1948; for climatic changes, Antevs, 1948.)

Climatically the region is dry, being situated in the rain shadow of the Sierra Nevada–Cascade Cordillera. The amount of precipitation varies with elevation, being scant in the lowland desert valleys and increasing as one progresses up the mountains. While there are some summer showers, most of the moisture comes from winter storms. Snow melt temporarily sustains springs, creeks, and a few small-sized rivers. The humidity is low. There are great changes in temperature seasonally and diurnally.

**DISTRIBUTIONAL AREAS REPRESENTED IN THE GREAT BASIN**

In plotting the ranges of the races of 50 geographically variable species that occur in the Great Basin and surrounding areas, it develops that the Great Basin is not in itself a large center of differentiation. Rather several smaller distribution areas exist that embrace parts of the Great Basin as well as surrounding regions. These are shown in Fig. 2. The races of the various species found in each area are summarized in Table 1. The designations are for the most part in accord with the Fifth Edition of the American Ornithologists' Union *Check-list of North American Birds* (1957), but in a few instances I have exercised my own judgment as to identifiable races and their distribution e.g. *Empidonax traillii*, *Psaltriparus minimus*, and *Catherpes mexicanus*. Because of ecological factors, not all species are represented in all areas. This in itself is significant in the evolutionary picture, but even more so are differences in races between the areas where the requisite niche conditions are provided and a particular species is thus represented in two or more areas.

1) *Warner Region.*—In discussing the restricted region of the Warner mountains and valley, Miller (1941:258) notes the diversity of the area in terms of avian habitats and points out that the valley is the westernmost of a series of desert valleys that are typical of the northern Great Basin, but which also constitutes the western edge of the Oregon desert. The Warner Mountains are isolated, but constitute an outlier of the Sierra–Cascade mountain system. Eighteen kinds of birds have been described from there, 17 by Oberholser (1932) and 1 by Swarth (1918). Miller has analyzed these, finding some unrecognizable and others wide ranging. The few that
are restricted do not center geographically in the Warner region. He concluded, therefore, that the restricted Warner Mountain–Warner Valley area is not a true center of differentiation. However, it seems to me that the broader region of southern Oregon, northeastern California, and northwestern Nevada shows sufficient differences in its avifauna, as compared with the

adjacent Sierra Nevada and Western Great Basin distribution areas, to justify considering it a separate distribution area. The Warner region shares 20 races with the Sierra Nevada and 32 with the Western Great Basin. It differs in 13 races from the Sierra Nevada but in only 9 from the Western Great Basin. On the whole, the affinities of the Warner region are closer to the Western Great Basin than to the Sierra Nevada.

2) *Sierra Nevada.*—The Sierra Nevada with its abrupt eastern escarpment constitutes a physical and ecological barrier to lowland forms. A hiatus exists between the Sierra Nevada and the closest ranges of the Great Basin

(Text continued on page 1174)
Table 1.—Races of Geographically Variable Birds in the Distribution Zones of the Great Basin and Surrounding Regions

<table>
<thead>
<tr>
<th>Species or Genus</th>
<th>Warner Region</th>
<th>Sierra Nevada</th>
<th>Western Great Basin</th>
<th>Eastern Great Basin</th>
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<tr>
<td>Dendragapus obscurus</td>
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<td>sierrae</td>
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<tr>
<td>Bonasa umbellus</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<td>Otus asio</td>
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<td>nataliae</td>
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<td>orius</td>
<td>orius</td>
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<td>Picoïdes sp.</td>
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<td>P. arcticus</td>
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<td>P. t. dorsalis</td>
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<td>Empidonax traillii</td>
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<td>adustus</td>
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<td>tenuissima</td>
<td>nelsoni</td>
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Table 1.—Races of Geographically Variable Birds in the Distribution Zones of the Great Basin and Surrounding Regions (Concluded)

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so that a barrier also separates the Boreal races of the two regions. In keeping with the physiographic and climatic differences of the two regions, the Western Great Basin and Sierra Nevada share only 14 of the 50 species listed and differ in 16. To further accentuate the break, there are several cases where one race is common to the several other areas while a different race occurs in the Sierra Nevada. Examples are *Sphyrapicus varius*, *S. thyroideus*, *Dendroica auduboni*, *Wilsonia pusilla*, and *Vermivora celata*. In addition, a different species of three-toed woodpecker, *Picoides arcticus*, occurs in the Sierra Nevada whereas *Picoides tridactylus* occurs in the Rocky Mountains and outlier ranges. Similarities and differences between the Sierra and Warner regions have been noted. Those in connection with the Inyo region are discussed under the latter area.

3) Western Great Basin.—Why there should be differences in the races of several species between the eastern and western parts of the Great Basin is an enigma. Although there are many similar races, namely in 26 species, there are 14 instances of racial differences involving both Sonoran and Boreal forms. The portion of the Great Basin covered by the Western Great Basin distribution region is less in extent than that of the Eastern. The former embraces the Lahonton basin where the Pleistocene Lake Lahonton occurred and was contemporary with Lake Bonneville in the eastern portion of the Great Basin. Perhaps as climatic changes occurred and the lakes dried up and the areas were populated by present species, the racial stocks of the Western Great Basin were derived from the Sierra-Cascade region, whereas the spread into the Eastern Great Basin distribution area was from the Rocky Mountain area.

4) Eastern Great Basin.—This part of the Great Basin includes the Bonneville basin where the Pleistocene Lake Bonneville occurred. It is, however, much more extensive, embracing a small part of Oregon and much of Idaho and eastern Nevada. There is no sharp line of demarkation in Nevada between the Western and Eastern Great Basin distribution areas. This points up the limitations of a graphic scheme such as presented in Fig. 2 which is thus misleading. There is more of an abrupt change between the Eastern Great Basin and Rocky Mountain distribution areas because the Wasatch line represents a sudden physiographic change. The term Wasatch line refers to the west-facing escarpment of the Wasatch Mountains (known as the Wasatch Front) as well as the west-facing bases of the chain of mountains and high plateaus to the south of the Wasatch Mountains, which curl off to the southwest. These uplifts serve as somewhat of a barrier to the eastward spread of various races, such as *Dendragapus obscurus oreinus*, *Eremophila alpestris utahensis*, *Petrochelidon pyrrhonota hypopolia*, *Aphelocoma coerulescens nevadensis*, *Parus atricapillus nevadensis*, and *P. gambeli inyoensis*. The transition between these races and those contiguous to the east in the Rocky Mountain distribution area is not as abrupt as a massive mountain barrier would lead one to suppose. Probably this is because the barrier is not con-
tinuous; canyons cut through, allowing some inosculnation of breeding stocks, and intergradational areas thus occur immediately east of the Wasatch line.

Fig. 3 represents a composite map showing the ranges of the three races mentioned above, together with a fourth kind, *Parus atricapillus nevadensis*, described by Linsdale (1938a) from extreme northeastern Nevada. This is to be compared with Fig. 74 and 75 in Miller's paper (1941) on the Warner and Inyo areas. The ranges of these four races from the Eastern Great Basin region are less widespread than those figured by Miller and thus center more on the Bonneville basin area, but they are by no means entirely coincident. The characters of the races are best shown in the Eastern Great Basin area. Of the four kinds figured, one is Boreal (the Dusky Grouse) in its distribution, one is Transitional (the Fox Sparrow), and two are essentially Upper Sonoran but may range to high elevations (the chickadee and Horned Lark). There would seem to be more justification for considering the Eastern Great Basin as a center of differentiation than the Warner and White mountains.
A closer relationship exists between the Eastern Great Basin and Rocky Mountain distribution areas than between the Western Great Basin and the Sierra Nevada. The Eastern Great Basin and Rocky Mountain areas share 31 kinds and differ in 12 races. In addition, three species, which have their center of abundance in the Rocky Mountain area or its western and northern fringes, have penetrated westward into the Eastern Great Basin, establishing outposts in suitable habitat. The Black Rosy Finch (*Leucosticte atrata*) has been reported from the Deep Creek Mountains in western Utah (Behle, 1955:29) and Jarbidge Mountains in Nevada (Miller, 1955:306), the latter substantiated with specimens. The American Pipit (*Anthus spinolaletta*) has been reported from the Deep Creek Mountains (Behle, 1955:26). The three-toed woodpecker (*Picoides tridactylus dorsalis*) has been reported from the Snake Mountains in eastern Nevada (Linsdale, 1936:73).

5) **Rocky Mountains.**—The Rocky Mountain distribution area commences with the Wasatch Mountains, which constitute a western outlier, includes the high plateaus of southern Utah, the mountainous area of Wyoming and southeastern Idaho, and continues eastward to embrace the Rocky Mountains of Colorado. Its affinities with the other neighboring differentiation areas are noted elsewhere. There is yet another consideration. In the physiography of western North America there are two roughly parallel major mountain systems, the Sierra Nevada-Cascade Cordillera of the Pacific coastal region and the Rocky Mountain system of the interior. The Great Basin lies between them for much of their length in their southern extent. Whereas there is a high percentage of races shared between many of the adjacent regions under consideration, there is little similarity in the avifauna of the Sierra Nevada and Rocky Mountain areas. Of the 50 species listed, these areas share only 7 wide-ranging races. Thus, the Great Basin with its desert, isolated mountains, and considerable extent seems to have effectively separated the avifauna of these two mountain systems, so that the birds inhabiting each have shown divergent evolution.

6) **Northern Idaho.**—This section of western North America, in terms of its avifauna, has much in common with the Rocky Mountains, yet there are a surprising number of forms that differ in their races. The two areas share 18 forms and differ in 26. The area of transition is similar for several races and seemingly occurs in a general belt running east and west across the state in the central part of the state. In addition to the differences brought out by Table 1, the Winter Wren (*Troglodytes troglodytes*) breeds only in this of the several distribution areas under consideration, except that it also occurs south to central California.

7) **Inyo Region.**—The distributional distinctions of this general region of eastern California east of the Sierra Nevada south of Lake Tahoe to latitude 35° and including the Owens Valley at the foot of the Sierra Nevada and the Panamint, Inyo, and White mountains were included by Grinnell (1915:12) in his Inyo distribution area, one of several that he listed and outlined
for California. According to Miller, up to the time of his paper (1941:258), 10 races of birds had been described from the area, 5 montane and 5 of lower levels. Three of these are not included in Table 1, since they are restricted in their ranges and do not otherwise extend into the Great Basin. They are *Lophortyx californicus canfieldae*, *Pipilo fuscus eremophilus*, and *Oreortyx pictus eremophilus*. The first two are seemingly endemic in the Inyo area. The Inyo region shares 28 races with the Western Great Basin but differs in 10 others. It shares 11 with the Mohave and differs in 4. Its distinctness from the Sierra Nevada is indicated by their sharing only 16 kinds, while differing in 16.

8) **Mohave Desert.**—Grinnell (1915:12) designates the Mohave Desert as one of the differentiation areas of California. The area also extends north and northeast into southern Nevada and into extreme southwestern Utah along the Virgin River to Zion Canyon. There are not many species represented in both the Great Basin and Mohave Desert, hence the Mohave shares only 7 with the Eastern Great Basin while differing in 7. It shares 6 with the Western Great Basin, differing in 6. Relations with the Inyo area are considered under that form. The Mohave shares 4 kinds with the Colorado Desert and differs in 6 others. In addition, there are several kinds that are shared only by the Mohave and Colorado deserts that do not appear in the table, since they are for the most part not geographically variable. These are listed under the latter region.

The Charleston and Sheep mountains of extreme southwestern Nevada, which are isolated Boreal islands rising out of the Mohave Desert, have been considered by some as a differentiation center largely on the basis of the work of van Rossem (1931), who described four races from there (see also van Rossem, 1936). However, the case has been weakened by the failure of subsequent workers to corroborate the distinctness of the Steller’s Jay (*Cyanocitta stelleri percontatrix*) or the Oregon Junco (*Junco oreganus mutabilis*). The race of creeper (*Certhia familiaris leucosticta*) has been found to be more widespread, extending into southern Utah and probably north to central western Utah and central eastern Nevada. This leaves only the Pygmy Nuthatch (*Sitta pygmaea canescens*) as endemic.

9) **Colorado Desert.**—This differentiation center includes the Lower Colorado River Valley from Searchlight, Nevada, south to the Gulf of California. It has been intensively studied by Grinnell (1914). The avifauna consists of lowland, desert forms with no Boreal increments. For the most part the representatives do not extend up into the Great Basin. The following Sonoran forms occur in both the Colorado and Mohave areas and only in these two among the ten distribution areas under consideration: *Lophortyx g. gambelii*, *Zenaida asiatica mearnsi*, *Geococcyx californianus*, *Chordeiles acutipennis texensis*, *Calypte costae*, *Dendrocyos scalaris cactophilus*, *Sayornis nigricans*, *Pyrocephalus rubinus flammens*, *Auriparus flaviceps acaciarum*, *Toxostoma l. lecontei*, *T. dorsale coloradense*, *Phainopepla nitens lepida*, *Vireo bel-
lil arizonae, Vernivora luciae, Icterus cucullatus nelsoni, Guiraca caerulea interfusa, and Pipilo aberti dumeticolus. Not shown in Table 1 are three kinds found in the Colorado Desert area that are not known from the Mohave, namely Colaptes chrysoides mearnsi, Centurus uropygialis, and Polioptila melanura lucida.

10) Navajo Country.—This includes the red-rock canyons of the Colorado Plateau region of the “four corners” area of southeastern Utah, southwestern Colorado, northeastern Arizona, and northwestern New Mexico. It is closely affiliated with the Rocky Mountains, having 33 of its races in common with the adjacent distribution area to the north, yet there are a few differences that justify this region being considered a separate distribution area. These total seven.

Other Distributional Considerations.—This study was undertaken to test the hypothesis that the Great Basin, a subdivision of the Basin and Range Physiographic Province of the western United States, constitutes a center of differentiation for birds at the subspecific level. A comparative study was made of the distribution of the races of fifty species that occur in the Great Basin and surrounding areas. Instead of one large center there are several distribution areas in or touching on the Great Basin. In only a few instances are races endemic to any one area. The usual situation is for several areas to share a particular race. However, when comparisons are made between regions in terms of the races present, sufficient differences show up to justify the designation of each region as a separate distribution area. While a pattern of distribution has emerged from this comparative study, no one species shows exact conformance. The closest approach is shown by the races of the Horned Lark, which is for the most part a resident, ground-dwelling form.

It is not clear to what extent broad environmental factors in the different areas have led to their distinctions in terms of races or to what extent common barriers have restricted several races, causing an overlap in parts of their ranges. As they pertain to the Great Basin, doubtless both factors are operative. The barrier explanation seems to apply to the eastern and western margins of the Great Basin where the Wasatch line and Sierra Nevada escarpments are present. As indicative of a general environmental effect, Linsdale (1938b) points out that many Great Basin races of birds are paler and grayer than surrounding races, which fact would seem to be correlated with scarcity of plant cover. This pallor affords a measure of protective coloration which appears even in the downy young. Especially in the Horned Lark, which is essentially a ground-dwelling species, is the concealing coloration evident. The length of their wings and tails suggests stronger powers of flight as an adaptation to wind. Stronger vocal powers are supposedly correlated with scattered distribution and the need to communicate over relatively greater distances. The greater frequency of flight may be of significance in connection with the scarcity of perches. By inference, birds of the Great Basin deserts have long-range vision and are resistant to heat, al-
though frequently they perch in the shade off the ground on hot days. Linsdale further notes that their nests are in low strata in or near the ground, again presumably because of the limitation of plant cover, and they are most often found on the southeastern sides of bushes, conceivably as an adjustment to some environmental factor like sunshine or prevailing direction of wind. It would seem that such structural adaptations and features of behavior are in the nature of adaptations to the Great Basin environment.

Linsdale also notes some clines that are manifest in the geographically variable birds of Nevada. In 4 nonpasserine species with more than one breeding race, there is a decrease in size toward the south, with the largest individuals occurring in the northeastern corner of the state. White coloration is most conspicuous in this group of birds in the northeastern corner of the state. In 33 passerine species with one or more breeding races in Nevada, the bill usually becomes shorter and stubbier toward the east and smaller toward the south. The wings and tail are generally longer toward the east. The general coloration becomes paler and grayer toward the east and in some instances brighter and darker in the Colorado River area.

Not only do these observations suggest that broad environmental factors like temperature, humidity, and wind have influenced the characters of races in the Great Basin, but at the same time a clue is provided as to why the Great Basin is not one large differentiation center, namely that the Great Basin is too diversified in terms of the basic environmental factors to have influenced in some common way all the geographically variable birds that inhabit the region. But this still doesn’t explain why there should be a transition for many forms in areas where there are seemingly no barrier effects or pronounced environmental differences. Somehow the individual histories of the various kinds in terms of point of origin, movements, and dependence on plant associations tie in here. Thus, the significance of the pattern of distribution will only emerge as studies are made of many individual species in terms of their environmental relationships and behavior. As Linsdale has said, the factors that influence the distribution of vertebrates are the same as those that affect the daily routine of behavior of individuals, and the factors that delimit ranges are the same as those that determine local habitats. As data on individual species accumulate, the precise identity of the environmental factors and how they operate may then be revealed.

SUMMARY

In testing the hypothesis that the Great Basin of western North America is a center of differentiation for birds at the subspecific level, a comparative study was made of the breeding ranges of 50 polytypic species occurring throughout the region. The sample included both Boreal and Sonoran forms. The data show that, instead of one large center of differentiation, there are ten distribution areas either in or impinging on the Great Basin. These are: Warner Region, Sierra Nevada, Western Great Basin, Eastern Great Basin,
Rocky Mountain, Northern Idaho, Inyo Region, Mohave Desert, Colorado Desert, and Navajo Country. In only a few instances were races found to be endemic to any one area; rather it was similarity in regions of intergradation for several forms, or the common delimitation of ranges, that revealed a pattern of distribution.

In interpreting the distributional features, barriers such as the mountain ranges on the eastern and western margins of the Great Basin account in some instances for the similar distribution, but more often common transitional areas occur where there is no physiographic diversity. The explanation probably lies in a combination of two sets of factors. Environmental influences are probably operating at present to control differentiation and distribution and, although the Great Basin comprises one of the subdivisions of the Basin and Range Physiographic Province, it is too diversified in terms of basic environmental factors to have influenced in some common way all the geographically variable birds that inhabit the region. Thus, the several distribution areas reflect the distinctive environmental complexes of the general Great Basin region. However, part of the explanation is to be sought in historical factors of Pleistocene and Recent times involving climatic change, with consequent forced movements of plant–animal associations from various points of origin. The full significance of the pattern of distribution must await detailed studies on many individual species in terms of their environmental relationships and behavior.

LITERATURE CITED


Recent Changes in Distribution of Color Phases of
Chen c. caerulescens

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The recent warming of the eastern Canadian Arctic has produced changes in the distribution of many species of animals. This paper is concerned with changes in the distribution of color phases of Chen c. caerulescens, particularly the penetration of the blue phase into regions where apparently there were, until recently, only white-phase birds. Ecological factors influencing the observed changes have been described elsewhere (Cooch, 1961b).

It is probable that the two forms were once isolated from one another, either by low population numbers, inability to occupy suitable habitat, or by tradition. Segregation into two populations, which may have been established during the Pleistocene (Johansen, 1956), was probably maintained by the discrete nature of the nesting, migration, and wintering areas. It is probable also that during the immediate post-Pleistocene period unsuitable climatic conditions elsewhere restricted blue-phase birds to a limited area (Bowman Bay) in southern Baffin Island (Cooch, 1961b).

The recently observed spread of blue-phase birds is apparently correlated with the climatic warming presently occurring east of 100° W (Cooch, 1961b), or post-Pleistocene emergence (Sim, 1960), or both. Possibly, both phases extended their range into newly suitable areas and thus came into secondary contact. Reproductive isolating mechanisms had not evolved fully by the time the secondary contact was made; hence, successful interbreeding resulted. This interbreeding was not random (Cooch and Beardmore, 1959) but assortative, and like tended to pair with like; consequently, the full impact of the secondary contact was retarded until an appreciable number of mixed pairings occurred. This paper attempts to document the rate of increase of blue-phase birds.

Color appears to be the only measurable distinction between the two phases. For the purposes of this paper, blue-phase birds are considered to include white-bellied heterozygotes, i.e. all individuals not generally white in appearance. Not included are predominantly white-phase birds with dark alulae, although sensu stricto these also exhibit blue genes. In all further references to one phase or the other, “predominantly” is implied.

The historical record of blue-phase increase has been obscured by nomenclatural changes and by the intermittent “lumping” and “splitting” of the two phases. Many valuable historical records from Hudson Bay have been made useless because some early authors considered Blue Geese to be immature forms of Lesser Snow Geese (Chen h. hyperborea). Thus, records by Bell (1880, 1883) and many anonymous Hudson’s Bay factors cannot be

used here. Generally, however, arctic and subarctic records are surprisingly complete.

There is a significant lack of data from the settled part of North America because many records combine Blue Geese and "Lesser Snow Geese" and present total numbers instead of relative abundance. The large collections in museums are of academic interest, but have not been used here since color variants were undoubtedly collected selectively to some extent.

**SUMMER DISTRIBUTION ON THE BREEDING GROUNDS**

The present center of blue-phase abundance is at Bowman Bay (62°20' N, 73°35' W), Baffin Island. That colony now contains nearly 97 percent blue-phase and only 3 percent white-phase geese. Breeding colonies to the west and north support an increasingly higher proportion of white-phase birds, until eventually no blue-phase are found. It is not known definitely that the Bowman Bay colony is the ancestral breeding area of blue-phase geese, but for the purposes of this discussion it is considered to be so. From there, blue-phase birds have spread to other breeding colonies on Baffin Island, Southampton Island, Eskimo Point, Perry River, and Banks Island. Data are available which demonstrate that in recent years blue-phase birds have been colonizing new areas, and in other districts increasing in numbers at the expense of the white-phase. It is also apparent that in every area except one (Bowman Bay) the rate of blue-phase increase has accelerated greatly since 1929.

In most other studies of polymorphic species, ecological disturbance of breeding areas by man is considered to be a factor that permits one form to gain an advantage over another. This cannot be the case in the present situation because visits to the breeding grounds by man are still rare.

There is no evidence to indicate that population levels at any major colony have changed radically since 1929. Admittedly, numbers have fluctuated from year to year, but always within fairly narrow limits. Despite the apparent stability in the number of birds at each breeding colony, the proportion of blue-phase birds is steadily increasing at each one except Bowman Bay. This is especially true on Southampton Island, at Eskimo Point, on Baffin Island north of Cape Dominion, and at Perry River. The known history of each breeding area is summarized briefly below, population data being given in terms of adults only, except where otherwise stated. A map showing the location of each breeding colony appeared in *The Auk* (78:73) in 1961.

**Bowman Bay** (65°20' N, 73°35' W).—This colony was discovered by J. D. Soper in 1929 (Soper, 1930). Soper estimated that in excess of 95 percent of the population was the blue phase. Manning (1942), Loughrey (1952), and Cooch (1955) arrived at a similar estimate of the blue: white ratio. Cooch estimated that the colony occupied 250 sq miles and numbered 185,000 adult geese in 1955.

**Cape Dominion** (65°50' N to 66°22' N, 70° W).—This site was also discovered by Soper in 1929. Soper gave no information on the blue: white ratio. Manning (1942) observed a 50:50 blue-white ratio in 1940. Cooch (1955) estimated that in the 1955 the blue: white ratio was 80:20 and that 90,000 birds occupied 240 sq miles of habitat.
Koukdjuak River (66°20' N, 73°55' W).—Manning (1942) estimated that the blue:white ratio was 20:80 in 1940; Loughrey (1952), 35:65 in 1952. In 1955 Cooch (1955) estimated that the ratio was 40:60 in a population of 50,000 birds occupying 150 sq miles of habitat. Lemieux (1961) obtained a ratio of 53:47 in 1961 along the south bank of the river, where in 1955 there was a ratio of 45:55 (Cooch, 1955).

Taverner Bay (66°40' N, 72°14' W).—This northern limit of the Baffin Island–Foxe Basin coast breeding area was discovered in 1940 by Manning (1942), who reported a blue:white ratio of 10:90. Loughrey (1952) recorded a ratio of 20:80; and Cooch (1955), a ratio of 25:75 blue:white. Total population in 1955 was estimated at 75,000 (Cooch, 1955).

Cory Bay (65°20' N, 74°40' W).—First noted by Cooch (1955), who recorded a ratio of 70:30 in a population of 3,000. N. G. Smith (pers. comm., 1960) recorded a 75:25 blue:white ratio.

Garnet Bay (65°17' N, 75°10' W).—First noted by Cooch (1955), when 2,500 birds were observed in a ratio of 50:50. N. G. Smith (pers. comm., 1960) recorded a ratio of 60:40.

East Bay (64° N, 82°10' W).—This Southampton Island site was first mentioned by Manning (1942) and later reported by Loughrey (pers. comm., 1953). Cooch (1955) recorded a blue:white ratio of 35:65 in 25,000 birds.

Bear Cove (63°40' N, 84°45' W).—Also on Southampton Island, nesting geese were first reported here by Manning (1944), who quoted Eskimos as saying that the blue:white ratio was 5:95. Loughrey (pers. comm., 1953) found a blue:white ratio of 20:80; Cooch (1955), 30:70; and Elgas (pers. comm., 1960), a 33:67 ratio in a population of 2,000.

Boas River (63°42' N, 85°45' W).—This Southampton Island area was first reported by Sutton (1932) in 1930 on the basis of Eskimo reports and specimens, but was not seen by an ornithologist until 1934 when Manning (1942) visited the area and recorded a blue:white ratio of 5:95. Bray (1943) found a blue:white ratio of 6:94 in 1936. Flock counts of migrating birds made by Gavin (pers. comm., 1953) at Eskimo Point in 1942 indicated that the Boas River colony probably consisted of 10 percent blue-phase birds. Cooch spent the summers of 1952 and 1953 (Cooch, 1953) in the area and recorded blue:white ratios of 20:80 and 22:78, respectively. In 1955 Carrick (pers. comm., 1955) and Cooch (1955) recorded a ratio of 25:75; in 1956 Barry (pers. comm., 1956) recorded 27:73; in 1960 Smith (pers. comm., 1960), 30:70; and in 1961 MacInnes (pers. comm., 1961), 33:67. The population is estimated to be 30,000 adults in 160 sq miles of habitat.

Cape Henrietta Maria (55°10' N, 82°10' W).—This Ontario colony was founded about 1947 (Indian report) and by 1960 had increased to 17,000 adults plus young in an area of 225 sq miles. Blue:white ratios in 1960 are not presently available, but at the time of establishment the ratio was 38:62 (Lumsden, pers. comm., 1961).

Eskimo Point (60° N, 94°50' W).—First noted by Gavin in 1941 (pers. comm., 1953), who recorded 6 blue-phase geese, all white-bellied, male heterozygotes, in a total population of 14,000 geese. The number of blue-phase birds increased slightly each year until 1943, when Gavin left the area. Cooch (1954a) recorded a blue:white ratio of 8:92 in 1954 and in 1959 (unpubl. notes) 14:86. MacInnes (pers. comm., 1960) reported a ratio of 15:85 in a population of 30,000 geese occupying 150 sq miles of habitat, and in 1961 Cooch observed a ratio of 17:83 in 35,000 birds.

Adelaide Peninsula (68° N, 100° W).—Macpherson et al. (1959) reported that 10 percent of the Chen caerulescens seen along the Kakeet River in 1957 were blue-phase.

Perry River east to Adelaide Peninsula (67°50' N, 102° W).—In 1938 Gavin (1947) found 4 white-bellied male, blue-phase birds at Perry River; since local Eskimos did not have a name for the phase, he did not believe that it had occurred in the region previously. In 1949, Hanson et al. (1956) estimated that the population included 6 percent blue-phase birds. Barry (pers. comm., 1960) estimated 12 percent blue-phase in a population of 16,000 adults plus young.

Perry River west to Bathurst Inlet (68° N, 105° W).—Barry (pers. comm., 1960) estimated a blue:white ratio of 5:95 in a population of 5,000 birds (adults plus young).
Victoria Island (Albert Edward Bay) (69° N, 103° W).—Barry (pers. comm., 1961) recorded a blue : white ratio of 20 : 80 in a scattered population of 1,500 individuals.

Banks Island (71°50' N, 124°50' W).—The occurrence of blue-phase birds at Egg River was first reported by Höhn and Robinson (1951). Manning et al. (1957) indicated that as many as 11 were present in 1953. McEwen (1954) observed 4 white-bellied heterozygotes mated to white-phase birds in 1954. Barry (pers. comm., 1960) estimated less than 1 percent blue-phase (1,000) in a population of 116,000 adults plus young.

Anderson River (68°50' N, 129° W).—This colony has been investigated by Soper in 1949 (Soper, 1952), Höhn (1954), and Barry (pers. comm., 1958, 1959, 1960), none of whom recorded blue-phase individuals in a population of 8,000 birds.

Kendall Island (69°10' N, 136° W).—No blue-phase birds were reported in a population of 7,000 investigated by McEwen (1954) and Barry (pers. comm., 1958, 1959, 1960).

Wrangel Island (74° N, 180° W).—No blue-phase geese were reported by Grote (1940). This island has been intensively studied by Uspensky (pers. comm., 1960, 1961), who found large numbers of white-phase birds breeding there in several colonies, but no blue-phase.

Siberian coast to Chutkin Peninsula (70° N, 180° W).—A large scattered population of white-phase birds were reported by Portenko (1937) and Grote (1940). Little is known in the West about this population, which has since been investigated by S. M. Uspensky (pers. comm., 1960, 1961). No blue-phase birds have been reported.

AUTUMNAL DISTRIBUTION IN JAMES BAY

The earliest data on blue : white ratios from southern Hudson Bay and James Bay are those of Hearne (1795), who reported that white-phase geese outnumbered blue-phase geese 100 : 1 at York Factory, Manitoba, but, that near Rupert's House, Quebec, the ratio was reversed. Rae (1888) writes that, in 1840, blue : white ratios at Moose Factory were 1 : 1, and at Albany 1 : 100, but that by 1888 the ratio at Albany was 1 : 1. The first comprehensive assessment of the blue : white cline existing in autumn along the southern coast of Hudson Bay and James Bay was that of Barnston (1860). Publications of that time are in general agreement; east of Moose Factory, Ontario, 95 percent of the birds were blue-phase, but west of there only a trace could be detected.

In 1940, Lewis and Peters (1941) found a 50 : 50 ratio at Attawapiskat, but in 1954 the ratio there had changed to 75 : 25 blue : white (Cooch, 1954b). The most recent complete assessment from York Factory, Manitoba, to Rupert's House, Quebec, was by Cooch (1954b) in 1954. In summary, ratios in 1954 were: Rupert's House to Moose Factory, 95 : 5; Albany, 90 : 10; Attawapiskat, 75 : 25; Lake River, 50 : 50; Winisk, 35 : 65; Fort Severn, 30 : 70; York Factory, 20 : 80. In 1959 the ratio at York Factory was 25 : 75. In some years ratios at any one locality change considerably in one direction or the other, but long-range trends are always toward increasing blue-phase abundance.

RATE OF INCREASE

It is of interest to estimate the number of years that will elapse under present climatological conditions between the first establishment of predominantly blue-phase birds in a population and the time when predominantly
white-phase birds are reduced to trace numbers. Since the historical record on the breeding grounds extends back only to 1929, it is necessary to derive forecasts by use of a composite curve (Fig. 1). This has been done by combining data from all colonies where a detectable increase in numbers of blue-phase birds has been observed, e.g. Eskimo Point where blue-phase represented a trace in 1941 (18 years later, 8 percent; and 23 years later, 14 percent). The observed changes at Boas River, Eskimo Point, and elsewhere were similarly plotted. The resulting curve appears sigmoid and coincides closely with theoretical rates of increase. The year of first establishment of blue-phase birds is considered to mean the year from which continuous presence of obviously blue-phase birds has been detected, since many unsuccessful immigrations by single birds may have occurred previously. In order to reduce comparisons between populations of varying sizes to a common denominator, the number of years required for a population to reach 1 percent blue-phase is not considered. Thus Table 1 starts at 1 percent.

The rapid increase that occurs between 30 and 70 years after establishment is quite clear-cut. The times required for increases by the various 10-percent stages are given in Table 2.

If the calculations in Tables 1 and 2 and the curve in Fig. 1 are correct, then one can expect that Boas River, which had 20 percent blue-phase birds in 1952, should have 35 percent blue-phase in the autumn of 1961 or spring
### Table 1.—Change in the Percentage of Blue-phase Birds

<table>
<thead>
<tr>
<th>Year after Establishment of 1 Percentile</th>
<th>Percentage of Blue Phase in the Population at End of Period</th>
<th>Net Change in Percent/Annum during Preceding Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1</td>
<td>Trace</td>
</tr>
<tr>
<td>10</td>
<td>5</td>
<td>0.5</td>
</tr>
<tr>
<td>20</td>
<td>13</td>
<td>0.8</td>
</tr>
<tr>
<td>30</td>
<td>23</td>
<td>1.0</td>
</tr>
<tr>
<td>40</td>
<td>40</td>
<td>1.7</td>
</tr>
<tr>
<td>50</td>
<td>60</td>
<td>2.0</td>
</tr>
<tr>
<td>60</td>
<td>77</td>
<td>1.7</td>
</tr>
<tr>
<td>70</td>
<td>87</td>
<td>1.0</td>
</tr>
<tr>
<td>80</td>
<td>94</td>
<td>0.7</td>
</tr>
<tr>
<td>90</td>
<td>96</td>
<td>0.2</td>
</tr>
</tbody>
</table>

*a These are all percentages of the entire population; data derived from Fig. 1.

Table 3 is an attempt to carry the extrapolations to their ultimate end, i.e. give estimates of the situation at selected colonies at 10-year intervals, 1930–80. That some of the forecasts are approximately correct was verified during the 1960 field season by T. W. Barry (Perry River, Banks Island), W. Elgas (Bear Cove), N. G. Smith and Toma (Boas River), and C. D. MacInnes (Eskimo Point) and in 1961 by L. Lemieux (Koukdjuak) and C. D. MacInnes (Boas River).

It will be seen from Table 3 that most Hudson Bay colonies are apparently approaching, or are in, the log phase of blue-phase increase. It is doubtful, however, that anyone now living will see a time when white-phase geese will disappear entirely from the Hudson Bay region, since on the basis of hybrid indices even the Bowman Bay population (97 percent blue-phase) contains at least 50 percent heterozygotes capable of producing some white-

### Table 2.—Years Required for 10 Percent of a Population of *Chen c. caerulescens* to Become Blue-phase Birds

<table>
<thead>
<tr>
<th>Percent Blue Phase in the Population</th>
<th>No. of Years Required for Change</th>
<th>Percentage Changed/Annum</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–10</td>
<td>18</td>
<td>0.56</td>
</tr>
<tr>
<td>10–20</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>20–30</td>
<td>8</td>
<td>1.25</td>
</tr>
<tr>
<td>30–40</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>40–50</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>50–60</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>60–70</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>70–80</td>
<td>8</td>
<td>1.25</td>
</tr>
<tr>
<td>80–90</td>
<td>10</td>
<td>1</td>
</tr>
</tbody>
</table>

*a As derived from Fig. 1.

*b Percentages refer to the entire population of white- + blue-phase birds.
Table 3.—Predicted Percentage Occurrence of Blue-phase Geese at Selected Breeding Colonies

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Bowman Bay</td>
<td>95</td>
<td>96</td>
<td>97</td>
<td>98</td>
<td>99</td>
<td>99</td>
</tr>
<tr>
<td>Cape Dominion</td>
<td>50</td>
<td>50</td>
<td>70</td>
<td>82</td>
<td>91</td>
<td>95</td>
</tr>
<tr>
<td>Koukdjuak</td>
<td>3</td>
<td>8</td>
<td>18</td>
<td>33</td>
<td>52</td>
<td>72</td>
</tr>
<tr>
<td>Boas River</td>
<td>-</td>
<td>tr.</td>
<td>7</td>
<td>15</td>
<td>27</td>
<td>45</td>
</tr>
<tr>
<td>Eskimo Point</td>
<td>-</td>
<td>-</td>
<td>5.5</td>
<td>12</td>
<td>22</td>
<td>38</td>
</tr>
<tr>
<td>Banks Island</td>
<td>-</td>
<td>-</td>
<td>tr.</td>
<td>1</td>
<td>5</td>
<td>13</td>
</tr>
</tbody>
</table>

a As calculated from Fig. 1; tr. = trace.
b Verified in 1960 and 1961 by independent estimate on the breeding areas.

phase birds. The number of years required before all white genes work out of that population is presently unknown.

Records available since 1949 indicate that, on the average, 30 percent (range: 25–35 percent) of the Hudson Bay Chen caerulescens populations are replaced each year. With the Boas River colony used as an example, it can be shown that in mixed blue–white populations the annual replacement cohort contains an increased proportion of predominantly blue-phase birds. Population predictions based on probable pairings (Table 4 and Appendix A) compare quite favorably with those derived from Fig. 1. Adult figures represent results to be expected in the autumn of a given year or the following spring. Flock counts on migrating birds made at Eskimo Point in the

Table 4.—Observed and Predicted Percentages of Predominantly Blue-phase Birds in the Boas River Population

(An Annual Replacement of 30 Percent of the Adult Cohort and a Stable Population Size Being Assumed; for Explanation of Calculated Values, see Appendix A)

<table>
<thead>
<tr>
<th>Year</th>
<th>Number</th>
<th>Percent Blue</th>
<th>Percent of Progeny in Blue Phase</th>
<th>Percent of Replacement Cohort in Blue Phase</th>
<th>Percent of Adults by Pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Blue</td>
<td>White</td>
<td>Observed</td>
<td>Theoretical</td>
</tr>
<tr>
<td>1952</td>
<td>6,000</td>
<td>24,000</td>
<td>20.0ᵃ</td>
<td>20.0</td>
<td>23.8</td>
</tr>
<tr>
<td>1953</td>
<td>6,180</td>
<td>23,820</td>
<td>20.9ᵇ</td>
<td>20.6</td>
<td>24.8</td>
</tr>
<tr>
<td>1954</td>
<td>6,418</td>
<td>23,582</td>
<td>21.6ᵇ</td>
<td>21.9</td>
<td>26.2</td>
</tr>
<tr>
<td>1955</td>
<td>6,725</td>
<td>23,275</td>
<td>23.5ᵃ</td>
<td>22.5</td>
<td>28.8</td>
</tr>
<tr>
<td>1956</td>
<td>7,066</td>
<td>22,934</td>
<td>24.6ᵇ</td>
<td>23.6</td>
<td>29.8</td>
</tr>
<tr>
<td>1957</td>
<td>7,538</td>
<td>22,462</td>
<td>25.7ᵇ</td>
<td>25.1</td>
<td>30.8</td>
</tr>
<tr>
<td>1958</td>
<td>7,959</td>
<td>22,041</td>
<td>26.9ᵇ</td>
<td>26.5</td>
<td>31.8</td>
</tr>
<tr>
<td>1959</td>
<td>8,344</td>
<td>21,656</td>
<td>28.6ᵇ</td>
<td>27.8</td>
<td>34.3</td>
</tr>
<tr>
<td>1960</td>
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<td>21,297</td>
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<td>29.1</td>
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<td>20,821</td>
<td>33.0ᵇ</td>
<td>30.8</td>
<td>39.5</td>
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<tr>
<td>1962</td>
<td>9,665</td>
<td>20,335</td>
<td>34.8ᵇ</td>
<td>32.2</td>
<td>43.3</td>
</tr>
</tbody>
</table>

ᵃ Observations made at Boas River, or on flocks migrating over Eskimo Point.
b Estimated by plotting survey data for other years and reading the intermediate results directly from a graph.
F. G. Cooch: Color Phases of *Chen c. caerulescens*

Spring of 1959 indicated that the Boas River population contained approximately 30 percent blue-phase birds of all age classes. This corresponds favorably with the 30.7 percent predicted in Fig. 1. N. G. Smith (pers. comm., 1960) visited Boas River in August 1960, and reported 30 percent blue-phase adults. MacInnes (pers. comm., 1961) visited the area in June and August 1961, and recorded 33 percent blue-phase birds among nesting adults.

It is probable that most "white" populations contain blue genes at low level and that from time to time "blues" have been produced (cf. Cooch, 1961b; Hanson et al., 1956). For reasons explained elsewhere, it is doubtful that selection pressure (Cooch, 1961b) would permit the blue phase to maintain itself with progeny from that source.

The ecological aspects of the present increase of blue-phase birds have been discussed elsewhere (cf. Cooch, 1961b), as have some of the physical and ethological barriers to the spread of the blue genes. This paper attempts to document recent changes and to derive estimates of the speed at which the increase can be expected to occur. If present climatic conditions and hunting pressure continue, then most Hudson Bay populations can be expected to exceed 75 percent blue-phase birds by 1980 (Table 3).

The data would indicate that a continuing westward extension in distribution of blue genes can be expected and that, if present ecological trends persist, blue genes will eventually predominate in all known *Chen c. caerulescens* breeding colonies. Two major physical barriers, reinforced by tradition and assortative mating, have impeded massive, westward gene-flow. The first barrier was the hiatus between Baffin Island and Southampton Island populations, both on the breeding and wintering areas (Cooch, 1961b), and the second was a similar hiatus between Eskimo Point and Perry River. The latter was especially important, since most birds from Perry River probably winter in California and central Mexico (Hanson et al., 1956) and those from Eskimo Point (the nearest colony containing an appreciable proportion of blue-phase individuals) in east Texas. A few individuals from Eskimo Point and Boas River also winter in Mexico and presumably some drift into the Perry River population. To date, 21 recoveries from 34,138 birds banded at Eskimo Point and Boas River have been obtained in Mexico (all white-phase) and 7 recoveries from the Perry River–Adelaide Peninsula area (again white-phase). Since pairing is assortative, it is not unexpected that within every migration corridor blues tend to move east, and whites west, toward areas of respective color abundance. It would thus seem that the probability of blue-phase birds moving westward would be low until an appreciable proportion of the "donor" population was blue-phase.

It has been observed that "immigrant blues" are always obvious heterozygous males. The bulk of these birds are produced by mixed pairing (B×W) or from a pair of predominantly white-phase geese having dark alulae and some dark secondaries (cf. Cooch, 1961b). It is postulated that, since 60 percent of females in mixed pairs are white-phase birds (Cooch and Beard-
more, 1959), progeny are imprinted to that color or are at least more tolerant to it. These progeny are therefore the most likely candidates for moving westward in any given migration corridor, and pairing with a bird from an adjacent breeding colony. Because pairing is assortative, the number of potential emigrants remains low until at least 5 percent of the birds in a given colony are predominantly blue-phase individuals. Only then can successful emigration be expected. For example, in 1940 the number of blue-phase birds at Boas River reached 8 percent, and at the same time blue-phase birds were detected at Eskimo Point and Perry River. The number of blue-phase birds at Perry River probably reached 5 percent about 1949, and in 1951 blue-phase birds were recorded on Banks Island. If the 5 percent estimate is correct, then blue-phase birds should establish themselves in an adjacent colony within 20 years. Thus, predominantly blue-phase birds should be established at Anderson River before 1970 and Kendall Island before 1990. Not considered in the calculations has been the effect of population size or continuums of breeding habitat, such as that occurring between Adelaide Peninsula and Kent Peninsula, with regard to the interval between establishment of blue-phase birds and the attainment of a 1 percent level. Once a level of 1 percent has been reached, then direct comparisons can be made between populations independent of size. A rapid increase of blue-phase birds in a small scattered population (Perry River) may not provide a sufficient number of potential emigrants until the proportion of blue-phase birds is very great.

Most blue-phase birds presently found at Perry River probably migrate southeast and winter on the Gulf of Mexico along with the Eskimo Point populations, whereas most of the white-phase cohort filter westward toward Mexico and California. An increasing number of migrant blue-phase birds are reported each year in Alberta and California. However, they are not yet present in sufficient numbers to account for all of the Perry River population. Banding of large numbers of birds is needed in order to solve the problem of divergent migration from Perry River. Until more blue-phase birds enter the segment of the Perry River population migrating to the west coast of North America, the last physical barrier to their spread cannot be considered to have been overcome. Once that occurs, however, one can anticipate a rapid increase in the proportion of predominantly blue-phase birds wintering in California. Introgression of blue genes on a large scale may already be occurring, but no data are available on changes in frequency of adult white-phase birds with dark alulae (heterozygotes) from the Pacific Flyway. Limited data on alula color from Anderson River (Barry, pers. comm., 1960) based on 13 adult birds, indicated that 9 had white and 4 had partially dark alulae. No birds were recorded with totally dark alulae. Comparable data from Eskimo Point (15 percent blue-phase) based on 300 birds, were 53 percent white, 29 percent partially dark, and 18 percent dark alulae. Data are not presently available from Perry River or any other intermediate area.
ACKNOWLEDGMENTS

Grateful acknowledgment is made to the Office of Naval Research and the Arctic Institute of North America for grants-in-aid for 1952 and 1953. Acknowledgment is also made of the assistance and generosity of T. W. Barry, G. M. Stirrett, G. F. Boyer, and A. H. Macpherson, Canadian Wildlife Service; N. G. Smith and C. D. MacInnes, Cornell University; T. H. Manning and W. E. Godfrey, National Museum of Canada; and Angus Gavin, Ducks Unlimited (Canada), for permission to use their unpublished observations. I am indebted to Frank McKinney, Delta Waterfowl Research Station; D. A. Munro, Canadian Wildlife Service; and Kenneth C. Parkes, Carnegie Museum, Pittsburgh, Pa., for critical comments on earlier drafts of this manuscript.

SUMMARY

Recent warming of the eastern Canadian Arctic has produced notable changes in the distribution of some avian species; blue-phase Chen caerulescens have dispersed rapidly in recent years, especially since 1930, and most populations of this color phase in the Hudson Bay drainage are approaching, or are in, a period of very rapid increase. The nature of the increase is sigmoidal, with the log phase between 20 and 80 percent involving a change of 2 percent of the population per annum. If present conditions prevail, most Hudson Bay colonies should exceed 75 percent blue-phase birds by 1980. That does not mean that 75 percent of the birds will show no indication of white genes, but merely that it will be possible to assign 75 percent of all individuals to a general (nonwhite) blue-phase category. Approximately 15–20 years after blue-phase birds become established in a population, a sufficiently large donor population results, and successful westward emigration becomes possible. Notable increases in numbers of blue-phase birds can be expected in California, probably within the next 20 years.

REFERENCES CITED

APPENDIX A

Derivations of Columns 5, 6, and 7 of Table 4

Columns 5, 6, and 7 are interdependent of one another and were derived as follows: If one takes the 1952 Boas Bay population as an example, 30,000 adults containing 20 percent that can be assigned to a blue (nonwhite) category would produce pairing in the following manner per 100 pairs:

\[
\begin{align*}
B \times B & : 11 \\
(B \times W) & \text{ or } (W \times B) : 17 \\
W \times W & : 72
\end{align*}
\]
A pairing arrangement of this nature produces young in the following ratios, assuming an average production of four goslings per pair:

<table>
<thead>
<tr>
<th>Pairing</th>
<th>Progeny</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>B</td>
</tr>
<tr>
<td>11</td>
<td>44</td>
</tr>
<tr>
<td>17</td>
<td>51</td>
</tr>
<tr>
<td>72</td>
<td>288</td>
</tr>
<tr>
<td>100</td>
<td>95B</td>
</tr>
</tbody>
</table>

Since we started with a ratio of 20B : 80W, which had an observed pairing arrangement as given above, progeny are produced in the ratio of 23.8B : 76.2W.

Those progeny from 1952 do not, however, enter directly into the breeding population, but do so when the birds are 23 months old. The replacement cohort in the autumn of 1952 or spring of 1953 consisted of progeny hatched in 1951. The population at that time was 19 percent blue-phase, but produced progeny in the ratio of 22B : 78W.

In order to derive the blue : white ratio for the 1953 breeding season, the following calculations were made:

<table>
<thead>
<tr>
<th>Blue</th>
<th>White</th>
</tr>
</thead>
<tbody>
<tr>
<td>23.8B</td>
<td>76.2W</td>
</tr>
</tbody>
</table>

APPENDIX B

**Theoretical Development of Blue-phase Population Following Introduction of One Blue-phase Bird into a Population of 1,000 Whites**

The calculated increase of blue-phase birds over a 25-year period (Table 5) is necessarily based on several assumptions:

a) that the first immigrant will live for at least 5 years or be immediately replaced by another immigrant;

b) that progeny will suffer a 60 percent loss in their first and a 25 percent loss in their second year;

c) that adults will suffer an annual loss of 30 percent;

d) that half of the potential pairs breed each year; and

e) that annual production will be four goslings per pair.

Mortality assumptions have been derived from an analysis of banded birds, and reproductive success from midwinter inventories conducted by the U.S. Fish and Wildlife Service (pers. comm., J. J. Lynch).

The table has been derived on the basis of a single introduction of one blue-phase bird. Observations at colonies where blue-phase birds were just getting established (Eskimo Point, Perry River, Banks Island) indicate that the first occurrence of blue-phase birds may have consisted of a family group of four, and that all of them subsequently mated with white-phase individuals. In addition, it is logical to expect that if one immigration
As a result, the actual rate of blue increase is greater than that presented in Table 5, immigration. There is some circumstantial evidence that successful immigrations occur ever, a reasonable representation of events.

In years following a very successful breeding season. Since 1950 such seasons have occurred most impressive in the first few years after establishment. Once the number of blues accelerate the rate of increase of blue-phase birds. The result of such introductions would have a greater longevity and lower mean annual mortality than do white-phase birds. If the number of blues is increasing in the donor population, there will be increasing opportunity for a wave occurs, others will follow in subsequent years. It also follows that if the number of blues is increasing in the donor population, there will be increasing opportunity for immigration. There is some circumstantial evidence that successful immigrations occur in years following a very successful breeding season. Since 1950 such seasons have occurred at roughly 4-year intervals.

Examination of mortality data based on banded birds indicates that blue-phase birds have a greater longevity and lower mean annual mortality than do white-phase birds. As a result, the actual rate of blue increase is greater than that presented in Table 5, where mortality is presented as being equal. The manner in which blue increase is, however, a reasonable representation of events.

Repeated introductions of one or two birds even at 4-year intervals would greatly accelerate the rate of increase of blue-phase birds. The result of such introductions would be most impressive in the first few years after establishment. Once the number of blues became very large (in excess of 10 percent) the addition of one or two immigrants would not appreciably change the sequence as given in Table 5. Some examples follow:

a) Two additional birds added at each 4-year interval would yield 58 blues at year 25 vs. year 15 if no introductions occurred.

b) If the first introduction consisted of four birds, but there were no subsequent introductions, there would be 66 blue-phase adults in 25 years.

c) Two additional birds added at 4-year intervals and following an initial immigration by four individuals would yield 86 blue-phase birds in 25 years.

The last example c closely follows the situation as observed at Boas River during the increase from 5 to 10 percent.

Table 5.—Theoretical Development of Blue-phase Population Following Introduction of One Bird into a Population of 1,000 Whites

<table>
<thead>
<tr>
<th>YEAR</th>
<th>NUMBER OF BIRDS</th>
<th>NUMBER OF PAIRS</th>
<th>NUMBER OF PROGENY</th>
<th>NUMBER OF SUBADULTS</th>
<th>POTENTIAL REPLACEMENT</th>
<th>ACTUAL REPLACEMENT</th>
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<tr>
<td></td>
<td>Blue</td>
<td>White</td>
<td>B×B</td>
<td>B×W</td>
<td>W×W</td>
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<tr>
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<td>1</td>
<td>999</td>
<td>0</td>
<td>1</td>
<td>499</td>
<td>3</td>
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<td>72</td>
<td></td>
</tr>
<tr>
<td>111</td>
<td></td>
</tr>
</tbody>
</table>

The result of such introductions would be most impressive in the first few years after establishment. Once the number of blues became very large (in excess of 10 percent) the addition of one or two immigrants would not appreciably change the sequence as given in Table 5. Some examples follow:

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Anpassungen und geographische Isolation bei Vögeln der peruanischen Küstenlomas

MARIA KOEPCKE

Museo de Historia Natural “Javier Prado,” Lima, Peru

KLIMA UND LANDSCHAFT


Das Klima der peruanischen Wüstenküste zeichnet sich vor allem aus durch eine niedrig liegende Wolkendecke, die etwa sieben Monate lang über weiten Küstengebieten liegt, das Fehlen bzw. die Seltenheit von Regenfällen, Gewittern und stärkeren Winden, die relativ niedrig liegenden Temperaturen, die im Südwinter bis auf 12°C heruntergehen können, sowie durch hohe Luftfeuchtigkeit. Nach dem zuletzt genannten Klimafaktor wird dieses Küstengebiet auch als Bereich der Feuchtluftwüsten bezeichnet. Trotz der hohen Luftfeuchtigkeit kommt es jedoch nicht zu normalen Regenfällen, sondern nur zu dem als Garua bezeichneten Nieselregen, der z.B. in Lima einen Jahresniederschlag von etwa 4 cm ergibt.

Der auffälligste Klimafaktor dieser Feuchtluftwüsten ist die tiefliegende Wolkendecke, deren Untergrenze sich meist bei 400 bis 600 m und deren Obergrenze sich etwa bei 1 000 m befindet. An denjenigen Stellen, an denen die Wolkendecke die Küstenberge berührt oder der Wüste aufliegt, befinden sich die Gebiete der Nebelvegetation, die sogenannten Lomas. Wo die Garua- und Nebelniederschläge eine gewisse Menge überschreiten, die bei 10 cm (im Jahre) liegen mag, findet man schon einen niedrigen Pflanzenbewuchs aus Blaualgen, Flechten und wurzellosen Tillandsien (Fig. 1). Nach der Art des Erdreichs kann man Sand-, Stein- und Felsloma unterscheiden, während die Menge der Niederschläge die Höhe und Dichte der Vegetation bestimmt, so dass wir in den Lomagebieten alle Zwischenstufen von Halbwüsten über Steppen bis zu parkähnlichen Landschaften oder sogar kleinen immergrünen Wäldern antreffen.

Fig. 1. Lomas von Pasamayo bei Ancón (Küste in Mittelperu). Der obere Bereich der Düne ist durch Flechtenbewuchs dunkel gefärbt. Nach H.-W. Koepcke, 1961.

Fig. 2. Phanerogamen-Sandloma zur Trockenzeit. Lomas von Chala (Südperu).
Der Anblick eines solchen Lomagebietes in der Garuazeit ist überraschend, denn der Erdboden ist bedeckt mit zartblättrigen Pflanzen, die die Landschaft zur Blütezeit in ein wahres Blumenmeer verwandeln können und die an die Bodenvegetation eines holarktischen Waldes im Frühling erinnern. Die Vegetation ist meist triefend nass. Trotz des nebligen und trüben Wetters hört man überall Vogelrufe und Vogelgesang. Während der Trockenzeit bieten die Lomas ein völlig andersartiges Bild, indem jetzt diese Landschaft grösstenteils einen halbwüstenartigen Charakter besitzt und dann dort nur verhältnismässig wenige Vögel anzutreffen sind. (M. Koepcke, 1954). Die Lomas der Küste gehören also zu den wenigen Landschaften in Peru, die einen ausgeprägten Jahreszeitenwechsel besitzen (Fig. 2 und 3). Da in Mittelperu die Nebelzeit normalerweise etwa zwei Monate früher beginnt als im Süden des Landes, sind die Jahreszeiten von Norden nach Süden etwas verschoben.
Es gibt an der peruanischen Küste etwa 25 Lomagebiete, die durch Wüstenbereiche und Flusstäler von einander isoliert sind. Jede dieser "Loma-Inseln" ist von Wüste umgeben, denn unterhalb der Wolkendecke fallen nur so geringe Niederschläge, dass das Gelände eine Wüste ist. Ebenfalls wür-
stenhaft sind die aus der Wolkendecke herausragenden Bergspitzen, und schliesslich ist auch das Hinterland eine Wüste, und zwar eine besonders extreme, weil hier weder die Garua-Wolkendecke noch die Sommerregen der Anden hinreichen. Es gibt nur wenige Stellen, wo die Lomas die Gebiete der Flussoasen berühren oder wo sie sogar bis an das Meeresufer herabreichen, wie z.B. bei Atico in Südperu. Es muss besonders darauf hingewiesen werden, dass die Lomagebiete von den Regensteppen des westlichen Andenabhanges durch einen meist ziemlich breiten Wüstenstreifen isoliert sind. Weil die Lomas sich wie eine Kette von Inseln an der peruanischen Küste entlangziehen, eignen sie sich besonders gut zum Studium der Probleme der graphischen Isolation und damit der Rassen- und Artbildung.

ÜBER DIE VÖGEL DER LOMAGEBIETE

Liste der beobachteten Arten

Es wurden bisher 77 Arten und Rassen von Vögeln in den Lomas beobachtet, die in der folgenden Liste zusammengestellt sind:

<table>
<thead>
<tr>
<th>TINAMIDAE</th>
<th>Nothoprocta pentlandii ssp. 1*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N. pentlandii ssp. 2*</td>
</tr>
<tr>
<td>COLUMBIDAE</td>
<td>Zenaida auriculata hypoleuca (Bonaparte)</td>
</tr>
<tr>
<td></td>
<td>Gymnopelia c. ceciliae (Lesson)</td>
</tr>
<tr>
<td></td>
<td>Columbigallina m. minuta (Linnaeus)</td>
</tr>
<tr>
<td></td>
<td>Eupelia cruziana (Knip &amp; Prévost)</td>
</tr>
<tr>
<td>THRESKIONITHIDAE</td>
<td>Theristicus caudatus melanopis (Gmelin)</td>
</tr>
<tr>
<td>ANATIDAE</td>
<td>Sarkidiornis sylvicola Ihering &amp; Ihering</td>
</tr>
<tr>
<td>CHARADRIDAE</td>
<td>Oreopholus r. ruficollis (Wagler)</td>
</tr>
<tr>
<td></td>
<td>O. r. pallidus (Carricker)</td>
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<tr>
<td>SCOLIOPACIDAE</td>
<td>Numenius phaeopus hudsonicus</td>
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<tr>
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<td>Crocethia alba (Pallas)</td>
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<tr>
<td>BURHINIDAE</td>
<td>Burhinus superciliaris (Tschudi)</td>
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<td>Thinocorus rumicivorus cuneicauda (Peale)</td>
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<td>Coragyps atratus (Bechstein)</td>
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<td>Cathartes aura jota (Molina)</td>
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<td>ACCIPITRIDAE</td>
<td>Chondrohierax u. uncinatus (Temminck)</td>
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<td>PANDIONIDAE</td>
<td>Pandion haliaetus carolinensis Gmelin</td>
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<tr>
<td>FALCONIDAE</td>
<td>Buteo p. polyosoma (Quoy &amp; Gaimard)</td>
</tr>
<tr>
<td></td>
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<td>Parabuteo uncinatus harri (Audubon)</td>
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<td>Circus cyaneus cinereus Vieillot</td>
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<td>Pandion haliaetus carolinensis Gmelin</td>
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<td>CHARADRIDAE</td>
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<td>F. sparverius peruvianus (Cory)</td>
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<td>STRIGIDAE</td>
<td>Bubo virginianus nacurutu (Vieillot)</td>
</tr>
<tr>
<td></td>
<td>Speotyto cunicularia nanodes Berlepsch &amp; Stolzmann</td>
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<tr>
<td>PSITTACIDAE</td>
<td>Psilopsiagon a. aurifrons (Lesson)</td>
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<td>CAPRIMULGIDAE</td>
<td>Caprimulgus longirostris decussatus Tschudi</td>
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<td>APODIDAE</td>
<td>Chaetura pelagica (Linnaeus)</td>
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<td>Apus andulus parvulus (Berlepsch &amp; Stolzmann)</td>
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<td>R. v. tertia Hellmayr</td>
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<td></td>
<td>Thaumastura cora (Lesson &amp; Garnot)</td>
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<tr>
<td></td>
<td>Myrtilis f. janny (Lesson)</td>
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</tbody>
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* Die Originalbeschreibung folgt in einer späteren Arbeit.
Einteilung der Lomavögel nach Ihrer Herkunft


* Die Originalbeschreibung folgt in einer späteren Arbeit.
** Nachtrag bei der Korrektur: Inzwischen wurden noch die folgenden Arten für die Lomas nachgewiesen: Erithilda babiti (Coues), Coccyzus lansbergi Bonaparte, Spizitornis flavirostris arequipae Chapman, Streptoprocne zonaris ssp. und Petrochelidon fulva rufocollaris (Peale).
Die in den Lomagebieten beobachteten Vögel können in der folgenden Weise eingeteilt werden:

A. Standvögel der Lomas
   1. Endemische Lomavögel.
   2. Arten, die sowohl in den Lomas als auch in anderen Lebensgemeinschaften der Küste vorkommen.
   3. Arten, die sowohl in den Lomas als auch in anderen ähnlichen Lebensgemeinschaften am westlichen Andenabhang vorkommen.
   4. Arten, die im peruanischen Küstenland und am westlichen Andenabhang weit verbreitet sind.

B. Vögel, die nur zeitweilig in den Lomas auftreten
   1. Arten der Fluss- und Grundwasseroasen sowie der Bergsteppen des westlichen Andenabhanges, die zum Brüten in die Lomas einwandern.
   2. Arten, die im peruanischen Küstenland und am westlichen Andenabhang weit verbreitet sind, und die nur zur Nahrungssuche in die Lomas kommen.
   3. Zugvögel, die in den Lomas überwintern.
   4. Ausnahmeerscheinungen.

Standvögel

ten flachen Lomaboden und gehören zur typischen Sandloma-Landschaft (Fig. 6). *G. paytensis* ähneln in ihrer Lebensform bis zu einem gewissen Grade einer Lerche, nicht zuletzt auch dadurch, dass sie einen Balzflug mit Gesang ausführt.

Eine weitere *Geositta*-Art, *G. maritima*, bevorzugt das steinigere mehr oder weniger ebene Gelände im Hinterland der Lomas. Sie dürfte, zumindest in Mittelperu, ein Vogel des zwischen Lomagebieten und Regensteppen des westlichen Andenabhanges liegenden Wüstenstreifens sein, ist also kein so typischer Lomavogel. *G. crassirostris* schliesslich ist eine Art, die nur in den Lomas und an ähnlichen Stellen des westlichen Andenabhanges auftritt. Sie lebt an Felswänden und grossen Felsblöcken mit einiger Tillandsien- oder Buschvegetation (Fig. 7).

Ein weiterer Charaktervogel der Lomas und zwar der nur manchen Lomagebieten eigenen Kakteenbestände ist *Asthenes cactorum*, ein Furnariide, der auch am westlichen Andenabhang in einer weiteren, schwach unterschiedenen Form vorkommt. Dieser Vogel lebt an steinigen Hängen und benötigt Blocksteine und Säulenkakteen. Das etwa kopfgrosse weithin sichtbare Nest wird zwischen Kakteenäulen gebaut. Es wird aus Stöckchen und Kakteenstacheln hergestellt mit einer inneren Auskleidung von Kakteenwolle, Spinnweben und einigen Federn und besitzt einen seitlichen Eingang (Fig. 8). *Asthenes* ähneln in der Lebensform sehr einem Zaunkönig.

Die vorstehend behandelten fünf Arten von Furnariiden sind hochgradig
auf bestimmte Lebensstätten spezialisiert, so findet man z.B. *Asthenes cactorum* oder *Geositta crassirostris* niemals auf den flachen Sandlomas, während *G. paytensis* und *G. cunicularia* umgekehrt nur selten zwischen Kakteen und Felsblöcken anzutreffen sind. Diese vier soeben genannten typischen Loma-Furnariiden können das ganze Jahr über in den Lomas bleiben, weil sie besondere Anpassungen an das Leben in diesen zeitweilig extremen Lebensstätten besitzen. Zunächst ist ihre mit der Allgemeinfärbung des Untergrundes harmonierende Gefiederfärbung zu erwähnen, ferner müssen sie die Fähigkeit besitzen, zeitweilig statt der für Furnariiden sonst typischen Insektennahrung auch pflanzliche Kost zu sich zu nehmen (so ernährt sich *Asthenes cactorum* in der an Insekten armen Trockenzeit weitgehend von Kakteenfrüchten), und schliesslich benötigen sie in dem vegetationsarmen Gelände geschützte Schlaf- und Brutplätze (Erdbaue bzw. grosses geschlossenes, von Stacheln geschütztes Nest). Es scheint, dass die Familie der Fur-
nariiden zur Besiedlung von extremen Lebensstätten besonders prädestiniert ist, denn man findet auch ausserhalb der Lomas (z.B. hochandine Halbwüsten und Steppen, Felsufer des Meeres) Furnariiden als Charakterarten extremer Biotope, und ausserdem findet man in dieser Familie eine ungewöhnlich grosse Anzahl von verschiedenen Anpassungstypen an die Umwelt (Lebensformen).

Ein anderer bemerkenswerter Standvogel mancher Lomagebiete, der allerdings nur an vegetations- und steinreichen Stellen (Parkloma) vorkommt, ist das Steisshuhn *Nothoprocta pentlandii*. Diese Art lebt in Peru hauptsächlich in den Bergsteppen der Andenabhänge und fehlt den Flusstätern. Es scheint,
dass es berechtigt ist, mittel- und südperuanische Küstenpopulationen als besondere geographischen Rassen zu unterscheiden und von den Andenabhangstieren abzutrennen. *Nothoprocta* besitzt eine ausserordentlich gute Schutzfärbung an den steppenhaften Untergrund zur Trockenzeit (Fig. 9 und 10). Ihren Wasserbedarf scheinen sie zum Teil durch Aufnehmen von Wassertropfen (Garuaniederschlag und Tau) zu decken. Nach Gefangenschaftsbeobachtungen nehmen sie lieber Wassertropfen von Blättern auf, als

![Fig. 9. *Nothoprocta pentlandii ousaleti* Berlepsch & Stolzmann. Foto eines zahmen Tieres.](image)


Es gibt nur wenige Standvögel der Lomas, die sonst nur noch in den Flussoasen vorkommen, wie z.B. *Pyrocephalus rubinus* und *Anthus chii*. Standvögel, die die Lomas nur mit den Bergsteppen des westlichen Andenabhanges gemeinsam haben, d.h. die in den Flussoasen fehlen, sind die schon genannten *Nothoprocta pentlandii*, *Asthene cactorum* und *Geositta crassirostris*, denen noch die Nachtschwalbe *Caprimulgus decussatus* hinzugefügt werden kann. Zahlreicher scheinen solche Arten zu sein, die in den Lomas Standvögel
sind und sowohl in den Flussoasen als auch am westlichen Andenabhang vorkommen, wie Speotyto cunicularia, Gymnopelia ceciliae, Trogodytes musculus, Turdus chiguano und Pheucticus chrysopeplus. Es soll noch hervorgehoben werden, dass eine Reihe der Arten der Flussoasen bisher in den Lomagebieten nicht angetroffen wurden, d.h. also die Nebeloasen zu meiden scheinen, wie z.B. Zenaida asiatica, Crotophaga sulkirostris und Myiophobus rufescens.

Fig. 10. Nothoprocta pentlandii oustaleti Berlepsch & Stolzmann; Aufsicht, um die kryptische Färbung zu zeigen. Foto eines zahmen Tieres.

Zweitweilig auftretende Arten und Ausnahmeerscheinungen

Unter den Vögeln, die wohl vor allem von den Fluss- und Grundwasseroasen her zeitweilig in die Lomagebiete einwandern, fällt Zonotrichia capensis peruviensis besonders auf. Diese Art erscheint, ebenso wie Volatinia jacarina, Spinus magellanicus, Sicalis luteola und andere zu Beginn der Nebelzeit in den Lomas, wo sie vorher in der Trockenzeit selten war oder auch völlig fehlte. Zunächst trifft man kleine umherstreifende Trupps an; später, wenn sich die Lomas zu begrünen beginnen, ist Zonotrichia paarweise, vor allem in den Parklomas und in den Weidelomas mit Büschen anzutreffen. Schon von weitem hört man den Gesang der zahlreichen Männchen, der zu einem Dauergäusch zusammenfließen kann. Während der Trockenzeit der Lomas, also im Südsommer, wenn Zonotrichia in den Lomas selten ist, brütet die Art
in den Flussoasen (vor allem in der Kulturlandschaft) und ihr Gesang ist nun dort häufig zu hören. Mit Hilfe der Beringung müssten diese Verhältnisse noch eingehender untersucht werden.

Ein auffälliger Brutvogel mancher Lomagebiete ist der Höhenläufer *Thinocorus rumicivorus cuneicauda*, der z.B. in den Lomas von Lachay (etwa 90 km nördlich von Lima) zu Ende der Trockenzeit in grossen Schwärmen bis zu 2 000 Exemplaren in den flachen Sandlomas auftritt. Sobald sich die Lomas zu begrünen beginnen, lösen sich die Schwärme auf und die Paare verteilen sich über ein grosses Gebiet. Überall hört man dann die charakte-

![a. Vom Vogel zugedecktes Nest. b. Das aufgedeckte Nest.](image)

Fig. 11. Nest von *Thinocorus rumicivorus cuneicauda*. Lomas von Lachay (Mittel-peru).

ristischen Balzrufe aus der Luft. Als Vogel des offenen Geländes hat *T. rumicivorus* eine gute kryptische Färbung, die es bewirkt, dass der sitzende Vogel leicht mit einem Erdklumpen verwechselt werden kann. Bemerkenswert ist ferner, dass das Gelege beim Verlassen des Nestes vollständig mit kleinen trockenen Pflanzenteilen zugedeckt wird, so dass es schwer ist, die Nester zu finden (Fig. 11). Der Regenpfeifer *Oreopholus ruficollis*, der in denselben Sandlomagebieten brütet, deckt sein Gelege nicht zu, das statt dessen eine mit dem Untergrund besonders gut übereinstimmende kryptische Färbung besitzt (Goodall, Johnson, und Philippi, 1951). Ebenso wie *Thinocorus* tritt auch *Oreopholus* am Ende der Trockenzeit in Trupps in den Lomas auf, die jedoch meist hundert Exemplare nicht überschreiten. Bisher ist es noch unbekannt, wo sich *Thinocorus* und *Oreopholus* ausserhalb der Brutzeit aufhalten. *Thinocorus rumicivorus cuneicauda* ist nur vom Küstengebiet bekannt, während *Oreopholus* auch im Gebiet der Hochanden brütet. Der Ibis *Theristicus caudatus melanopis* ist ein weiterer Brutvogel der Lomas, der vorwiegend im Küstengebiet umherwandert und durch die Verfolgung durch den Menschen selten geworden ist. Auch die in den Lomas brütenden *Pezites*


Ein in den Lomagebieten regelmässig anzutreffender Zugvogel aus dem südlichen Südamerika ist Muscisaxicola macloviana mentalis, die man meist in lockeren Trupps antrifft. Aus Nordamerika kommen ausser den oben schon erwähnten Falco peregrinus und Chaetura pelagica noch gelegentlich einige Küstenwanderer hinzu, wie Numenius phaeopus hudsonicus und Crocethia alba, die man auf dürftigen Sandlomas antreffen kann.

Eine Gruppe weiterer Vögel scheint nur ausnahmsweise in den Lomas aufzutreten. Der Fischadler, Pandion haliaetus carolinensis, ist ein Zugvogel aus Nordamerika, der regelmässig die peruanische Meeresküste besucht und manchmal die Bäume meeresnaher Lomagebiete als Ruheplätze benutzt, da er sich offenbar ungern auf Felsen setzt. Eine Reihe weiterer Raubvögel

**GEOGRAPHISCHE ISOLATION UND DIE HERAUSBILDUNG GEGENPOLISCHER RASSEN**

Wie schon im ersten Abschnitt dieser Arbeit gesagt wurde, sind die Lomagebiete wie eine Kette von grünen Inseln in der Wüste entlang der peruanischen Küste angeordnet. Damit ist hier die Voraussetzung zur geographischen Isolation und damit zur Rassen- und Artbildung gegeben.


Lomainseln. Die Unterschiede zwischen den beiden Grossbereichen sind üb- rigens nicht nur in der Lomafauna ausgeprägt, sondern zeigen sich auch in der Fauna der Fluss- und Grundwasseroasen. So werden z.B. *Pyrocephalus rubinus obscurus* an der südperuanischen Küste durch *P. r. cocachacrae* und *Troglohytes musculus audax* durch *T. m. tecellatus* abgelöst.


Bei dem Furnariiden *Asthenes cactorum* findet man ebenfalls Unterschiede in der Färbung zwischen den mittel- und südperuanischen Küstenpopula- tionen. Auch diese Art kommt ausserdem noch am westlichen Andenab- hang (bisher bekannt von Lachay bis Arequipa) vor, wo sie wiederum eine, wenn auch nur sehr schwach unterscheidbare Form bildet.

lebende *G. cunicularia* ssp. dunkler gefärbt ist als die beiden Wüstenformen der *G. paytensis*.


**SUMMARY**

*Adaptations and Geographical Isolation of the Birds of the Peruvian Coastal Lomas*

The lomas are areas of fog-vegetation which exist along the Peruvian desert coast. Much of the Peruvian coast is characterized by a special climate caused by the cold Humboldt Current. The most characteristic feature of the climate is a low cap of clouds which stays continually over the coast region for about 7 months of the year. Where it touches the ground or the coastal hills, there are areas of fog-vegetation. In the winter
of the Southern Hemisphere, these areas are green and rich in flowers, and birds are abundant there; however, in the summer when the clouds are lacking, the landscape has a semidesert-like aspect, and bird life is scarce. The lomas are one of the few landscapes of Peru that have a pronounced seasonal change. About 25 such areas are known in Peru. Most of them are strictly isolated from each other by extreme desert and by river valleys. The lomas are also well separated from the rain-vegetation of the western slope of the Andes by large districts of extreme desert. The lomas may be sandy, stony, or even composed of boulders; and their vegetation consists of all types of landscapes between semideserts and even small evergreen forests.

A list of birds known from the Peruvian coastal lomas is presented, and the birds are subdivided and treated in the following manner:

A. Permanent Residents

1) Endemic lomas birds (e.g. subspecies of *Asthenes cactorum* and *Nothoprocta pentlandii*),
2) Species that live in the lomas as well as in other life communities of the coast (as *Geositta paytensis peruviana* and *Anthus chii peruvianus*),
3) Species that live in the lomas as well as in other similar life communities of the western slope of the Andes (as *Nothoprocta pentlandii* and *Geositta crassirostris*),
4) Species that are widely distributed along the Peruvian coast and the western slope of the Andes (as *Gymnopelia c. ceciliae* and *Troglodytes musculus audax*).

B. Temporary Visitors

1) Species of the river valleys or of the steppes of the western Andean slope that come to the lomas to breed (as *Zonotrichia capensis peruviensis* and *Volatinia jacarina peruviensis*),
2) Species widely distributed along the Peruvian coast and the western slope of the lomas that visit the lomas seemingly in search of food only (as *Vultur gryphus* and *Pygochelidon cyanoleuca peruviensis*),
3) True migratory birds that winter in the lomas (as *Muscisaxicola macloviana mentalis* and *Falco peregrinus anatum*),
4) Accidental birds (as *Columbi gallina m. minuta* and *Sarkidiornis sylvicola*).

The different groups of birds are discussed, particularly the endemic forms and those permanent residents that, although they live in other similar places of the coast or on the western Andean slope, are typical of the lomas and find optimal life conditions there. We discuss in some detail the five species of Furnariidae: *Geositta paytensis*, *G. cunicularia*, *G. maritima*, *G. crassirostris*, and *Asthenes cactorum*. Each one inhabits a special niche in the semidesert and steppe-like parts of the lomas, and possesses special adaptations for living the year around in these places. Of the temporary birds, some are discussed in detail, including the seed snipe, *Thinocorus rumicivorus cuneicauda*, and *Zonotrichia capensis peruviensis*. The latter breeds in the lomas in large numbers during the southern winter, although they also breed in the river valleys during the southern summer.

The plants and the nonflying invertebrates of the lomas show a number of geographical forms. In birds, endemic forms are rare and only subspecific in character. The relatively few endemic forms of birds in the lomas, as well as the paucity of species of true desert animals along the Peruvian coast, can be explained by the fact that the coastal deserts of western South America are relatively young (as compared with those of Africa and Australia). But the steppe fauna of the northwest Peruvian coastal steppes, and that of the dry part of the Marañón valley, are surely older and longer isolated, as indicated by their relatively greater number of endemic forms, including even endemic species and genera.

The most isolated loma is that of Cerro Illescas at about 6° S on the western side of the Sechura Desert. Here *Zonotrichia capensis* forms a special subspecies which lives completely isolated in an area about 40 km long. The other lomas fall into two sections divided by the Desert of Ica. This division is reflected not only in the plants and nonflying invertebrates but also in the birds, several species of which possess a northern and a southern lomas form, as *Nothoprocta pentlandii* and *Asthenes cactorum*. The most
pronounced splitting into subspecies is shown by *Geositta paytensis*. In the middle Peruvian lomas lives the subspecies *peruviana*, the color of which harmonizes with the grayish ground of the sandy lomas. In the north as well as in the region of Ica, where sandy deserts predominate and lomas are nearly lacking, occur the pale sand-colored forms *paytensis* and *rostrata*, the color of which is similar to the pale ground of those areas. In southern Peru finally, south of the Desert of Ica, where lomas are common, there is another somewhat dark-colored miner, *Geositta cunicularia* ssp. Thus, the color of these four miners harmonizes with the general ground color of their niches.

Thus, the lomas present an excellent opportunity to study geographical isolation. Because they are relatively newly formed and are separated in varying degrees from each other and from other habitats, the beginning of the development of geographical forms and species of plants and animals can be studied there.

LITERATUR


Tern Colonies in Aruba, Curaçao, and Bonaire, South Carribean Sea

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The Netherlands Antilles island group of Aruba, Curaçao, and Bonaire is situated in the semidesert climatic zone at about 12° N latitude, at distances of 17-55 miles from the northern coast of Venezuela. At least six species of terns have been found nesting in these islands, as well as one species of gull. The geographic origin of these species is extremely different. Hence, it is interesting to know in what numbers and how regularly the species nest in these islands. The presently known status of these birds is described below, partly based on previously published records (Voous, 1957). As some of the species do not seem to nest each year, at least not in constant numbers, observations made by the author during a census of tern colonies in the islands in one breeding season (1961) have been given separately. Breeding cases are documented by study skins, eggs, photographs, color slides, and color motion pictures assembled by F. H. Ansingh, Brother Arnoldo, H. J. Koelers, K. Mayer, P. A. van der Werf, and the author.

*Sterna h. hirundo* Linnaeus (Common Tern).—This Holarctic species nests only very exceptionally in the tropics. The first record of its thus nesting was published by Hartert (1893, 1902) for Bonaire in 1892, but this record unfortunately failed to convince American ornithologists. Additional breeding records and photographs of nests and downy chicks in Curaçao in 1955 have been published by Voous (1957). At present the species has been found nesting in at least 2 localities in Aruba, 3 in Curaçao, and 2 in Bonaire. It nests either in solitary pairs or in small colonies of its own species, up to approximately 10 pairs. It has been definitely found to be associated with other species of terns only once, viz. in Curaçao in 1961 on a small coral-rock island together with *S. dougallii* and *S. sandvicensis*.

In 1961 we found it nesting in Aruba (2 or 3 localities), Curaçao (3 localities), and Bonaire (2 localities).

Eggs have been found from May to early August. The clutch size recorded is 1–3, most frequently 2.

*Sterna d. dougallii* Montagu (Roseate Tern).—This cosmopolitan species was first found nesting on Aruba in 1892 by Hartert (1893, 1902). The species subsequently remained unnoticed on this island until 1961. At present the species has been found nesting in 1 locality in Aruba, 2 in Curaçao, and 2 in Bonaire. It does not form breeding colonies of its own, but has always been found in association with other nesting terns, viz. with *S. sandvicensis* and *S. albifrons*. The largest colony found was in Curaçao in 1955 (about 40 pairs; Voous, 1957). The color of the bill is deep coral red with a broad black tip; once a wholly black bill was noticed (at Bonaire, 1961).

In 1961 we found these terns nesting in Aruba (1 locality), Curaçao (2 localities), and Bonaire (1 locality).

Eggs have been found in May–July. The clutch size recorded is 1–2, occurring in about equal frequencies.

*Sterna anaethetus melanoptera* Swainson (Bridled Tern).—This circumtropical species is only known from Aruba, in one locality. First recorded nesting there by Hartert (1893, 1902) in 1892, it was not found nesting again until 1961, when we discovered two breeding colonies, each of approximately 5–10 pairs. One of these colonies was apparently in the same locality on the coral shingle reef wall as it was nearly 60 years before. This part of the reef wall is now opposite the big oil harbor of Sint Nicolaas, which in Hartert’s days did not yet exist. The reef water on the land side is now seriously polluted with black oil residue. Both Hartert and I found these terns nesting in company with *S. dougallii* and possibly with *S. albifrons*.

Eggs have been found in June and July. The clutch size recorded is 1.

*Sterna albifrons antillarum* (Lesson) (Least Tern).—This semicomopolitan species is widely spread in all three islands, its nesting having been recorded from 3 localities in Aruba, at least 5 in Curaçao, and 4 in Bonaire. It nests in colonies of varying numbers and in varying densities. The largest colony known consisted of approximately 100 pairs (Island of Klein-Curaçao; Voous, 1957). In the densest colonies, nests were about 2 or 3 m apart. These terns have been found nesting in association with *S. sandvicensis* and *S. dougallii*. Nests have also been found on top of deserted flamingo nests in Bonaire (fide J. Rooth, and personal observation).

In 1961 we found it nesting in 3 localities in Aruba, 1 locality in Curaçao, and 3 in Bonaire.

Eggs have been found in May–July. The clutch size recorded is 1–4, most frequently 1 and 2.

*Sterna m. maxima* Boddaert (Royal Tern).—This pantropical Atlantic species, although to be seen the whole year round, has only been found nesting in single pairs on three occasions, viz. in 1955 in Curaçao and Bonaire (Voous, 1957), and in 1958 in Curaçao (Ansingh et al., 1960). In all three cases the nests were found among nesting *S. sandvicensis*.

No nests were found in 1961.

Eggs have been found in May and June. The clutch size recorded is 1–2.

*Sterna sandvicensis eurygnatha* Saunders (Yellow-billed Sandwich Tern or Cayenne Tern).—This Atlantic–Mediterranean or perhaps semicomopolitan species apparently is represented on the islands by a variable hybrid population of yellow- and black-billed terns, the yellow-billed individuals predominating (Junge and Voous, 1955; Ansingh et al., 1960). It was first found nesting in Curaçao in 1952 and 1954 (Voous, 1957). Breeding colonies are now known from 2 localities in Curaçao and from 2 in Bonaire. They nest in large and dense colonies. The largest one known was at Curaçao in 1958 (about 1,200 nests; Ansingh et al., 1960). The average distance
between nests (eggs) in Curaçao in 1958 was 35–40 cm and in 1961 26 cm. In 1961 we found 1 colony in Curaçao (about 130 nests) and 1 in Bonaire (about 350 nests).

Eggs have been found in May–July. The clutch size recorded is 1–2; two eggs occurred in less than 4 percent of the nests.

The frequency distribution of the coloration of the bill in the 1961 colonies compared with previous records is given in Table 1 (see also Ansingh et al., 1960:55).

<table>
<thead>
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<th>Table 1.—Bill Color in Sterna sandvicensis eurygnatha</th>
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<td>Year No. of birds sampled</td>
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<td>-----------------------------------------------</td>
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<tr>
<td>Bill Color</td>
</tr>
<tr>
<td>Yellow</td>
</tr>
<tr>
<td>Yellow with black</td>
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<tr>
<td>Black with yellow tip</td>
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<td>Red</td>
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Larus a. atricilla Linnaeus (Laughing Gull).—This warm-temperate to tropical, eastern North American and West Indian species is known to be breeding only on Bonaire in our region in one locality. It was first found nesting in 1960 by Brother Arnoldo and J. Rooth. In 1961 Brother Arnoldo showed us a colony in exactly the same place as in 1960. The colony consisted in 1961 of no more than 10 breeding pairs, with nests several meters apart and Least Terns nesting all around.

Eggs have been found in July. The clutch size recorded is 1.

SUMMARY

The presently known status of terns and gulls breeding in Aruba, Curaçao, and Bonaire off the northern coast of Venezuela is described. Six species of terns and one species of gull have been recorded breeding. Probably not all of these species nest regularly in the islands. The geographic origin of the tern species differs widely. Sterna hirundo probably has here its only regular tropical breeding population. S. sandvicensis is represented by a mixed yellow- and black-billed population, probably of hybrid origin.

LITERATURE CITED


Late-Pleistocene Vicissitudes of the African Avifaunas

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SUMMARY

From geological evidence of changes in African climates during the Late Pleistocene and up to the present time, it follows that vast changes have occurred in the geographical ranges of avifaunas in Africa, especially:

1) Birds at present confined to montane areas (above 1,500 m) were able to occupy all areas in the tropics above about 500 m above sea level, for the last time as recently as 20,000 years ago—with reciprocal limitation of lowland birds.

2) Fluctuations in the southern edge of the Sahara between 300 miles south of its present position and 300 miles north (the latter only 7,000 years ago) involved great vicissitudes of the West African birds. At one stage the evergreen forest must have been almost eliminated; and at another stage Lake Chad projected 500 miles into the Sahara.

3) The Palaearctic avifauna extended at least 400 miles south from Barbary into the Sahara.

4) Over most of the Congo a Kalahari avifauna replaced that of the forest about the end of the Middle Pleistocene and extended considerably to the northeast of its present range only 10,000 years ago.

1 The paper presented under this title by the author at Ithaca was subsequently published as follows:


List of Films and Additional Papers Presented at the Congress

ALLEN, TED T. Myological Evidence of the Phylogeny of Limpkins, Cranes and Rails

AUSTIN, OLIVER L., JR. Comparative Demographies of *Sterna hirundo* and *Sterna fuscata*

BERGMAN, G. Radar Studies on Migrating Ducks in Finland

BOULTON, RUDYERD. Ecological Studies in Central Africa (film)

BROEKHUYSEN, G. J. Some Interesting Birds from Bredasdorp in the Cape, South Africa (film)

BRUNS, HERBERT. Color Preference in Birds and Its Significance for Practical Ornithology

DE VOS, A. Possible Causes for Range Extensions of Birds in the Holarctic Region

DEXTER, RALPH W. The Pattern of Returns and Fluctuation of Abundance of Banded Chimney Swifts at Kent, Ohio, 1944–1961

DRIVER, P. M. Observations on Hatching Behaviour in Nidifugous Birds (by title only)

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Waldhoer, E. The Wall Creeper (film)

Errata

Page 84, line 9  For Philherodius read Pilherodius
Page 116, line 17  For Raritae read Ratitae
Page 494, line 12  For Actitis hypoleuca read Actitis hypoleucus
Page 584, table 1, line 13  For Volatina splendens read Volatina splendens
Page 593, col. 1, line 6  For Meleagridae read Meleagrididae
Page 630, line 17  For Francolinus swainsonii read Francolinus swainsoni
Page 663, line 18  For Colaptes caffer read Colaptes cafer
Page 854, col. 2, line 11  For Chlidonias nigra read Xema sabini
Page 1136, table, col. 2, line 3  For Emberiza pallasi read Emberiza pallasi

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The subject headings in this index have been set in boldface for the convenience of the reader. About 70 percent of the headings follow those found in the Aves section of The Zoological Record as of about 1960. Some headings have been used simply because the compilers of the index felt more comfortable in using them (Anatomy, Ethology, Evolution, Sensory System, Systematics, Zoogeography) or because the materials in the present volumes lent themselves to a slightly more detailed breakdown. These, however, have cross references leading to them from the usual Record categories. A few misspelled scientific names, which were undetected in authors' manuscripts, appear here with their correct spelling.

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