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THE LIVING BIRD

THIRD ANNUAL...............1964

Cornell Laboratory of Ornithology

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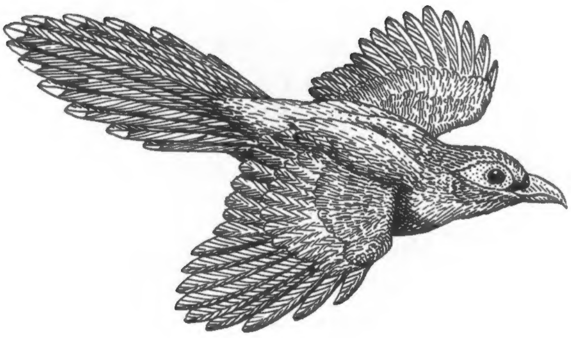

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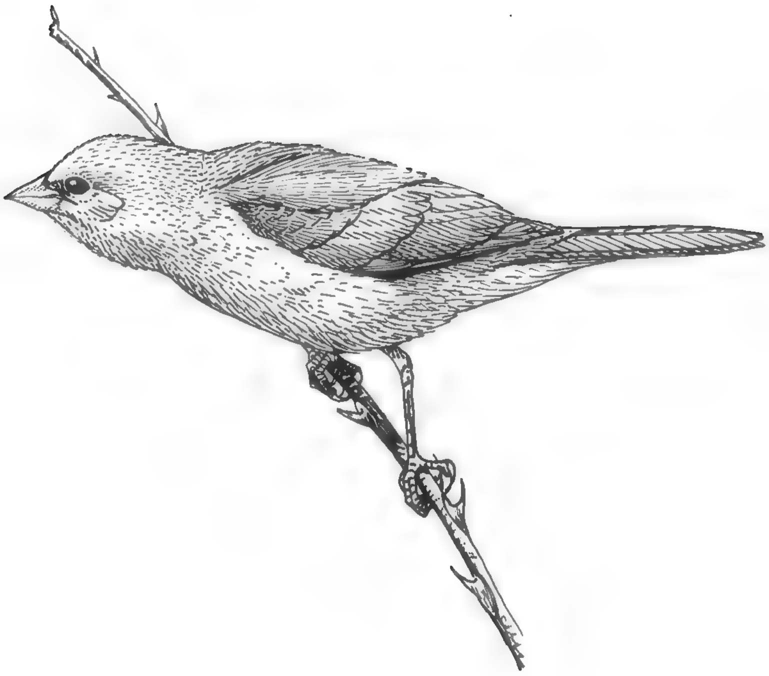

Female Painted Bunting

SURVIVAL IN THE PAINTED BUNTING

DAVID FREELAND PARMELEE

Painted Buntings *(Passerina ciris)* are breeding residents of southern United States from North Carolina, Arkansas, Oklahoma, and New Mexico south into northern Mexico. Within this range the handsome, brilliantly-colored males are often seen along woodland edges and shrub-bordered streams and in the vicinity of thickets. Painted Buntings are so common that we are apt to take them for granted. Rarely do we bother to wonder how they manage to survive.

Anyone who studies the life histories of birds is soon appalled by the enormous destruction of eggs, nests, and young by predators, inclement weather, and other factors too numerous to mention. After seeing nest after nest of one species destroyed, he inevitably asks the question: How can a species, even an abundant species, survive against such odds—against such a high mortality during the critical period of reproduction?

Although I have made intensive studies of a number of different birds in a number of different areas, no bird anywhere — even in the Arctic where climatic conditions are just about as severe as anywhere in the world — has taught me more about matters relating to the success of a species than the little Painted Bunting right in our own temperate environment. While not severe, our environment is nonetheless cluttered with all sorts of physical and biotic ingredients.

I saw my first Painted Bunting among the great oaks that grow so profusely in coastal South Carolina. There, during the spring of 1944, the late E. J. DeCamps and I often watched it and found its nest tucked away in the Spanish moss. Years passed without my seeing another anywhere, and then one day in 1957 my erstwhile major professor, Dr. George Miksch Sutton, asked me to make a special study of the bird. This investigation took me to the University of Oklahoma Biological Station near the banks of Lake Texoma in southern Oklahoma.

Seeing the Painted Bunting in a wholly different habitat was shocking. We do not have to *look* for male Painted Buntings in Oklahoma. They are *there,* perched on telephone wires along roadsides where, open to the sun, they sing throughout the day. Each occupies a certain length of wire for Painted Buntings are highly territorial.

Finding female Buntings was a different matter. Cryptic in coloration and secretive in habits they frequent the forest edge, the thorny hedgerows, the impenetrable smilax tangles. Moreover they build their nests in many different kinds of places.

We worked hard to find the first dozen nests. All were quickly destroyed. Several bird-eating snakes were especially troublesome that year because the flood waters of Texoma had forced them to concentrate in the relatively few high places near the lake. The Buntings, also, were concentrated. So great was the predation on nests that I was about to abandon my proposed study of the species' breeding habits.

Then the impossible happened. A few of the many nests we continued to find somehow survived the onslaught by predators despite the trails we beat to them by our frequent visits. Not only did the broods from these nests fledge successfully, but, within a remarkably short time, the parent birds produced second broods. The ability to produce two broods in one season is true double-broodedness and is the key to the Painted Bunting's success. My interpretation as to how the species accomplishes this feat follows.

Many phases of the breeding cycle of the Bunting are surprisingly short and also precisely timed. For example, the female alone constructs the nest in as little as two days and completes the nest-lining in some cases after laying the first egg. Courtship and mating are similarly brief, taking place during the period immediately preceding and during egg-laying. Shortly after dawn the female leaves her roosting place, goes directly to the nest and lays an egg, usually one each day until there are three or four. Incubation may start after the completion of the clutch but commonly begins with the laying of the next to the last egg, with the result that hatching is spread over a period of two or three days. The period of incubation is short—11.4 days. Even the parasitic Brown-headed Cowbirds *(Molothrus ater),* whose incubation period is 11.5 days, have no advantage over the Buntings in this respect.

I am uncertain as to whether the male Painted Bunting participates in the selection of the nest-site. I do know that he knows where the nest is for I caught marked individuals right beside their nests. Nevertheless, he visits the nest or the nest-tree infrequently and apparently never incubates the eggs. Throughout the whole period of incubation the male sings from his favorite perches and repeatedly drives all males of his kind from the territory. But all female Painted Buntings, mated or otherwise, he tolerates.

The eggs in a Painted Bunting nest may hatch within six hours; or as many as 40 hours may elapse between the hatching of the first and last, depending largely upon when the female started incubating. The female takes full charge of the nestlings; the male pays no heed to them whatever. Between feedings she broods. She may brood them at night for eight consecutive nights and then abandon them on the ninth—the night preceding fledging.

Young Buntings grow at an astonishing rate. Weighing hardly two grams when hatched, they gain about a gram a day until fledging only eight or nine days later. Although the flight feathers develop rapidly, the young Buntings are mostly naked until the seventh day when the body feathers suddenly burst from their sheaths and transform them into well-feathered creatures nearly capable of flight. The eight-day-old chick can fly short distances; a nine-day-old chick can fly strongly, as far as 50 feet or more before alighting.

The female parent continues to attend the fledged brood unassisted. Between feedings she carries fresh nesting material to a new site not far from the old. In practically a single breath she will feed a chick, reach out and pull nesting material from a branch nearby, place the nesting material in her new nest, and then fly off to gather more food.

The new nest may be entirely different from the first. One of our banded females placed her first nest less than two feet off the ground and attached it securely to some vertical stalks of giant ragweed and wild lettuce. This nest was small, compact, deeply-cupped, and durable. She built her second nest some 14 feet from the first and saddled it nearly seven feet up on a horizontal limb of a large persimmon tree. The second nest was large, bulky, and extraordinarily shallow. Not at all durable, it later disintegrated during a light rain. These two nests were so different that, except for the markings on the bird, one would insist that they were the work of two different individuals. In noting nests of other double-brooded Painted Buntings, we concluded that the individual female does not necessarily select a similar site for each nesting, nor does she attach and fashion the nest in the same manner each time.

By the time the female has completed her second nest, the male suddenly shows renewed interest in her and courts. Dramatically, on the very eve of egg-laying, he takes full charge of the first brood which the female thereupon abandons.

It is easy to follow the movements of the bright male—coming and going as he attends his newly-acquired chicks. Hard pressed though he often is to catch enough insects to satisfy them, he still sings from his perches and chases away the trespassing males. The double-brooded female, on the other hand, not only cares for her second brood through the period of fledging, but keeps it through the post-fledging period until the young are 33 to 35 days old and are completely independent.

Most interesting is the unexpectedly short period between fledgings. I studied four cases of double-broodedness. In three instances the interval, from the time the first brood fledged until the second fledged, was precisely 29 days. In the fourth it was 29 to 30 days. The time between fledgings is not only short but it is constant.

Not all breeding female Painted Buntings are double-brooded. To complicate matters further, at least some of these single-brooded females mate with polygamous males which, at the same time, mate with other females that are double-brooded. Presumably there is a selective value in the employment of as many females as possible.

The ability of the polygamous male to care for only a given number of young at any one time may well be the controlling factor and explain why some females proceed with a second nesting and others do not — and why some do not have a third brood. We found no evidence of triple-broodedness.

Of the 45 Painted Bunting nests we found, only 15 survived long enough to produce fledglings—37 in all. More than half of these were produced by four double-brooded females. One of these females produced six of the fledglings. Her polygamous mate sired 10 of them.

Why some females are "favorably" situated or what constitutes a favorable situation are moot questions. As stated above, the double-brooded females do not choose a particular kind of nest-site each time; nor do their nest-sites differ, seemingly, from those chosen by less successful females. A variety of nest types and nest locations produce young. In any event, the Painted Bunting endures and overcomes the high mortality of nests, eggs, and young by virtue of its high breeding potential.

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Wilson's Warbler

THE PROBABLE HISTORY OF SPECIES FORMATION IN SOME NORTHERN WOOD WARBLERS (PARULIDAE)

Robert M. Mengel

Zoologists today are virtually agreed (Mayr, 1963:480, 513) that species formation in warm-blooded vertebrates is a process requiring geographical isolation of stocks ("allopatry") long enough for the development of morphological, physiological, or psychological isolating mechanisms adequate to insure continued genetic separation in case of renewed coexistence, or "sympatry."

How exquisitely complicated, then, must be the history of geographical isolations and distributional changes resulting in the many complex arrays of closely related genera and species of birds found in many parts of the world. But, while the classical examples in certain groups of oceanic islands have invited analysis—Darwin's finches in the Galápagos (Lack, 1947) and the Hawaiian honeycreepers (Amadon, 1950) — continental complexes conspicuously suggesting the history of the formation of numerous species from one or a few ancestral forms seem, at least, to be extremely rare.

This is because the antecedent events, especially due to the oft-lamented deficiencies in the avian fossil record, are usually shrouded in mystery, if not irretrievably lost to knowledge. Unlike the oceanic islands, the ecological "islands," presumably effective in multiplication of species on continents, have appeared, disappeared, and shifted, often leaving no evidence of their existence other than the multiplicity of species itself.

If there are exceptions, it seems logical to seek them among groups of species whose present distributions may be meaningfully interpreted in light of the considerable and rapidly-growing body of fact concerning the Pleistocene (or Ice Age), the most recent and hence best known geological epoch.

Although "the analysis of Pleistocene speciation has just begun" (Mayr, 1963:561), it must be admitted that early findings have been rather meager, especially in Europe, of which it has been said (whether or not too pessimistically) that "it cannot be shown with certainty that even a single glacial isolate . . . reached full species level" (Mayr, 1951; 1963:561). In North America, although a considerable number of pairs of (chiefly) eastern and western species shows clear evidence of resulting from Pleistocene separation of parental stocks (Rand, 1948), almost nothing has been suggested about the evolutionary history of more complex aggregations. It seems, however, that this can be accomplished in the case of many representatives of the American family Parulidae.

My attention was first drawn to these birds in the present connection nearly two decades ago. In considering the distributions in the Appalachian Mountains of various wood warblers, long and then still generally thought of as "typical" of northern coniferous forest, I came upon a statement by Brooks (1947:291, 295) remarking upon supposed changes in the habitat preferences of these species resulting from the destruction of virgin spruce in the Cheat Mountains of West Virginia. What an "amazing power of adaptation," Brooks mused in effect, was shown by those species able to give up "the traditional coniferous forests of their ancestors" and adapt, overnight as it were, to deciduous forest.

At the same time, however, in common with others, I (see Mengel, 1964) was finding some of the same species (for example Blackburnian, Black-throated Green, Black-throated Blue, and Canada Warblers) variously common in deciduous climaxes elsewhere in the Appalachians in places, such as the Cumberland Mountains of Kentucky, where spruce has not occurred in historic times, if ever (Braun, 1950:480). Considering this, together with the virtually certain origin of the Parulidae in the American tropics (Mayr, 1946: 21-22), it struck me forcefully that the true "ancestral homes" of these birds were obviously broad-leaved forests or related life forms and that coniferous forest was necessarily the secondary environment of those species capable of exploiting it.

When it occurred to me further that—because of certain peculiarities in the history of the North American continent—profound evolutionary opportunities would become available to the members of a tropical American forest-adapted group making this exploitation, the distributions and relationships of our northern wood warblers began to take on new significance.

Historical Background

It is essential to review briefly the Cenozoic history of North America. Readers familiar with this should skip this section. For further information, consultation of Flint (1957) on Pleistocene geology, King (1958) on Cenozoic history of the west, Dorf (1959) and MacGinitie (1958) on Cenozoic climates, Axelrod (1958) and Braun (1950, 1955) on vegetational history, Deevey (1949) and Martin (1958) on Pleistocene biogeography, and Kendeigh (1961: 280-339) for a very convenient summary of many pertinent details, should lead to practically all of a vast basic literature. The following capsule summary is based chiefly on the sources just cited.

Tertiary history.—At the beginning of the Tertiary (Paleocene, Eocene, Oligocene, Miocene, Pliocene) the climate of North America, then a continent of average low relief, was much more moderate than today's, with less marked alternation of seasons. Tropical and subtropical climates occurred far north of their present positions and were coextensive with a Neotropical-tertiary forest ancestral to today's tropical forests. North of this and continuously with Eurasia stretched a broad Arcto-tertiary forest consisting of a temperate (chiefly deciduous) element, much like the mixed mesophytic forests of Kentucky and Tennessee today, and a boreal element far to the north which, while richer in coniferous species, bore little resemblance to today's uniform northern coniferous biome. On the Mexican Plateau, probably in the Eocene, there first developed a mixed, woodland, Madro-tertiary flora (for map see Kendeigh, 1961:283, Figure 21–1).

Throughout the Tertiary, but from the Miocene especially, climate deteriorated rather steadily, while simultaneously the western cordilleran mountain system was lifted to its present elevation or nearly so. With these changes:

(1) Floras and climatic zones were depressed southward, bringing the temperate Arcto-tertiary (ancestral deciduous) forest near its final level and driving the tropical forests into Central America.

(2) A broad rain shadow developed in the eastern lee of the rising mountains, forcing the temperate Arcto-tertiary forest eastward before newly developing grasslands and permanently isolating this forest from its Asiatic component and from a depauperate relict in the Pacific northwest.

The areas of the cooler, rising, and more arid west that were vacated by the temperate Arcto-tertiary forest were occupied, in the lower areas (and increasingly far northward), by various elements derived from the Madro-tertiary flora, while simultaneously the higher slopes were gradually colonized by boreal Arcto-tertiary elements. At some time, probably in the Miocene or Pliocene, a sclerophyll woodland and pine element of Madro-tertiary origin invaded the eastern Gulf States and southern Cumberland Plateau, and was ancestral to the southern pine-oak elements of the eastern deciduous forest.

There seems to have been, at the end of the Pliocene, still no real counterpart of today's extensive, uniform, northern and montane coniferous forest formations (Braun, 1950:511). These awaited Pleistocene glaciation for their fullest development.

Pleistocene history.—Gradually, approaching the close of the Pliocene, a long history of climatic deterioration (with increasingly sharp alternation of seasons), aided by mountain building, was culminated by the slow formation of continental and mountain glaciers of dramatic extent. In North America there is a clear record of four major glacial periods, the Nebraskan, Kansan, Illinoian, and Wisconsin (Figure 1). Between these occurred long, warm interglacial periods (Aftonian, Yarmouth, Sangamon) in which recession of ice and climatic amelioration equalled or exceeded today's (Figure 2). In these periods there must have occurred re-expansions of glacially displaced biota in patterns presumably similar to that which seems to have occurred after the last (Wisconsin) glaciation.

Two results of this recurrent glacial flow and ebb were particularly important in the present context.

(1) Upon glacial advance the boreal elements of the Arcto-tertiary forest were more or less separated by prongs of ice (facilitating their differentiation) and were forced far southward—to the Gulf coast, possibly, in the east, and deep into Mexico and Central America in the western mountains. In the southeast these boreal elements either mingled, or were forced into close proximity with, the somewhat compacted temperate (deciduous) Arcto-tertiary forest.

(2) Upon each glacial retreat there was probably established, although doubtless with increasing perfection in succeeding stages, a great, transcontinental, northern coniferous forest and (additionally) extensive montane coniferous forests in the west. This occurred, at least in part, as a result of the peculiar capacity of coniferous (especially spruce) forest rapidly and for a time exclusively to occupy recently glaciated terrain (Braun, 1950:521). Lacking this capacity, the complex remnant of the ancestral deciduous forest remained comparatively static, sending only depauperate "association-segregates" of beech-maple, oak-hickory, etc. (Braun, 1950:522) after the slowly retreating spruce.

Throughout, although varying in extent and position, the grasslands and

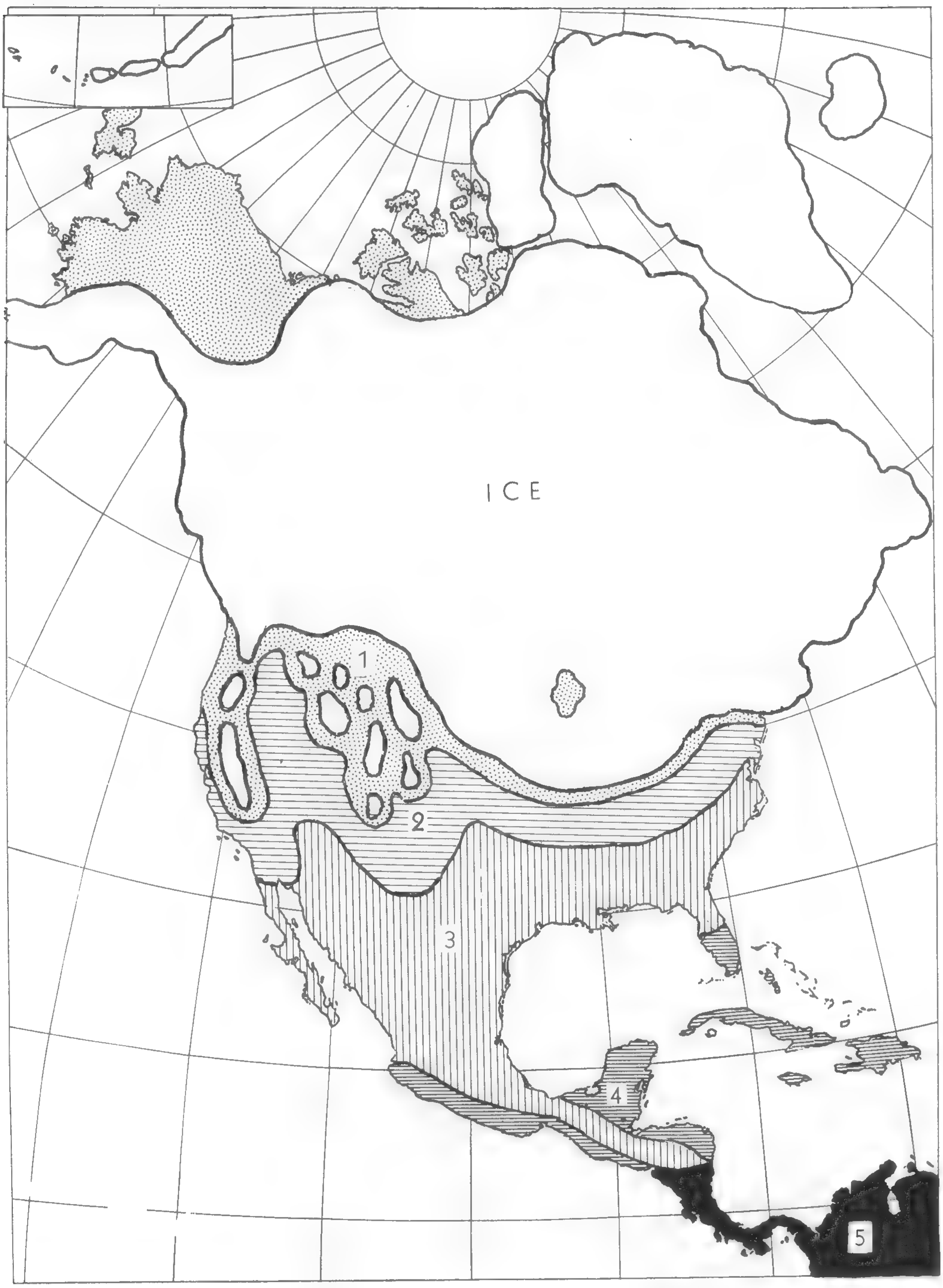

Figure 1. An approximate representation (modified from Dorf, 1959:195, map 5) of climatic conditions and glacial extent in periods of maximum Pleistocene glaciation in North America. The figure is a composite (no single glacier was so extensive, and the margin of each was irregular). The climatic zones are: 1, arctic (tundra); 2, subarctic; 3, temperate; 4, subtropical; 5, tropical.

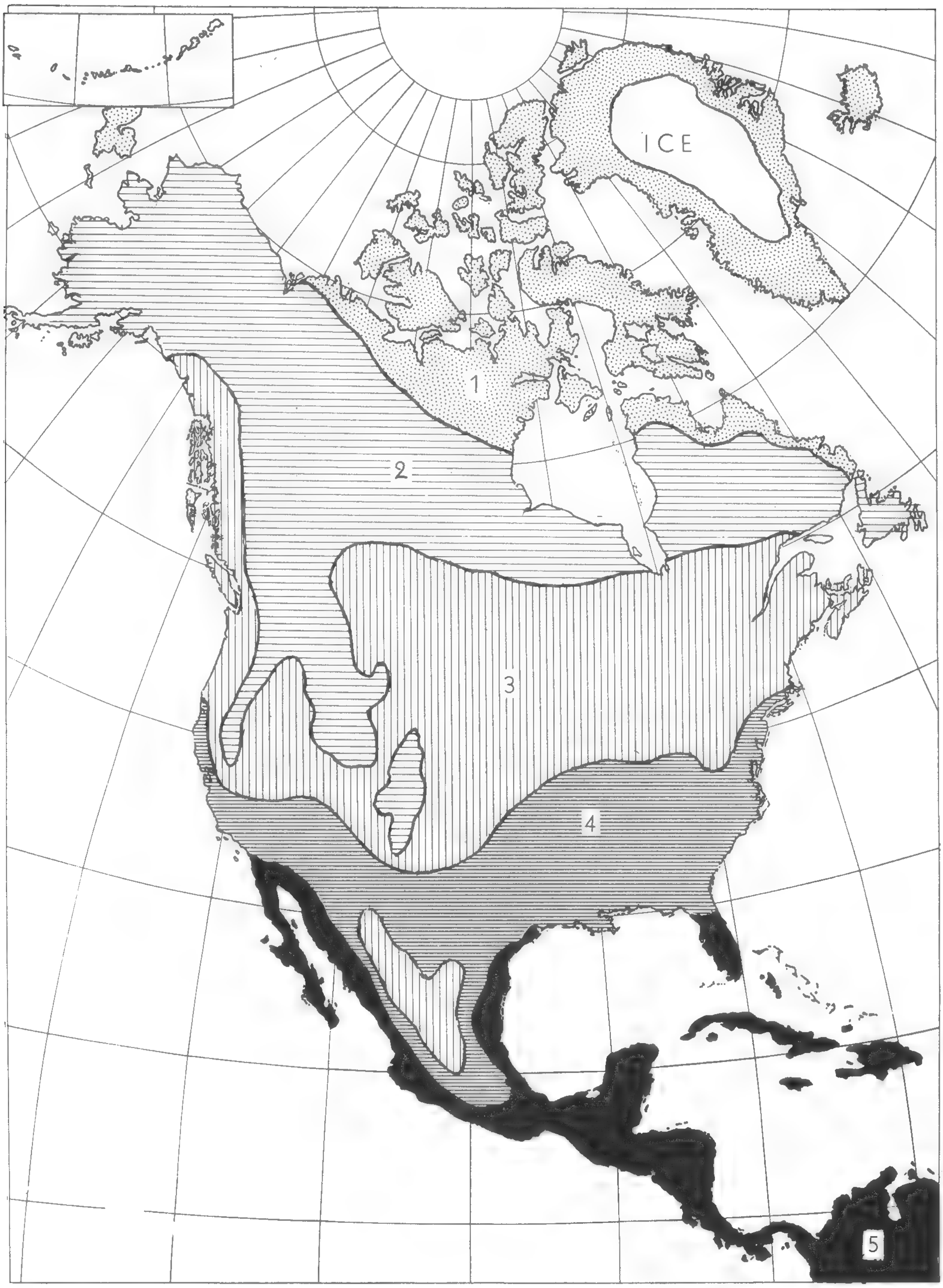

Figure 2. An approximate representation (modified from Dorf, 1959:197, map 6) of climatic conditions during the several interglacial climatic optima of the Pleistocene (save for the ice and the deep southward extent of northern conditions in the mountainous west, the map is also a fair representation of conditions in the late Pliocene; cf. Dorf, op. cit. :193, map 4). The climatic zones are: 1, arctic; 2, subarctic; 3, temperate; 4, subtropical; 5, tropical.

deserts maintained a gap between the deciduous forest of the southeast and the coniferous forests of the mountainous west.

Finally, in the warm, dry interglacials, the western mountain forests must have tended, as they do today, to retreat up the slopes, making forested "islands" of many of the separate mountain masses. Beneath and surrounding these coniferous forest islands were larger pine, oak, and scrub islands of Madro-tertiary origin, isolated from each other by seas of desert and grass. The ultimate disposition of the forest biomes developed through this history is shown in Figure 3.

A Model Sequence

We are now ready to examine the relationships between these events and the wood warblers. Let us begin by imagining a hypothetical ancestral species

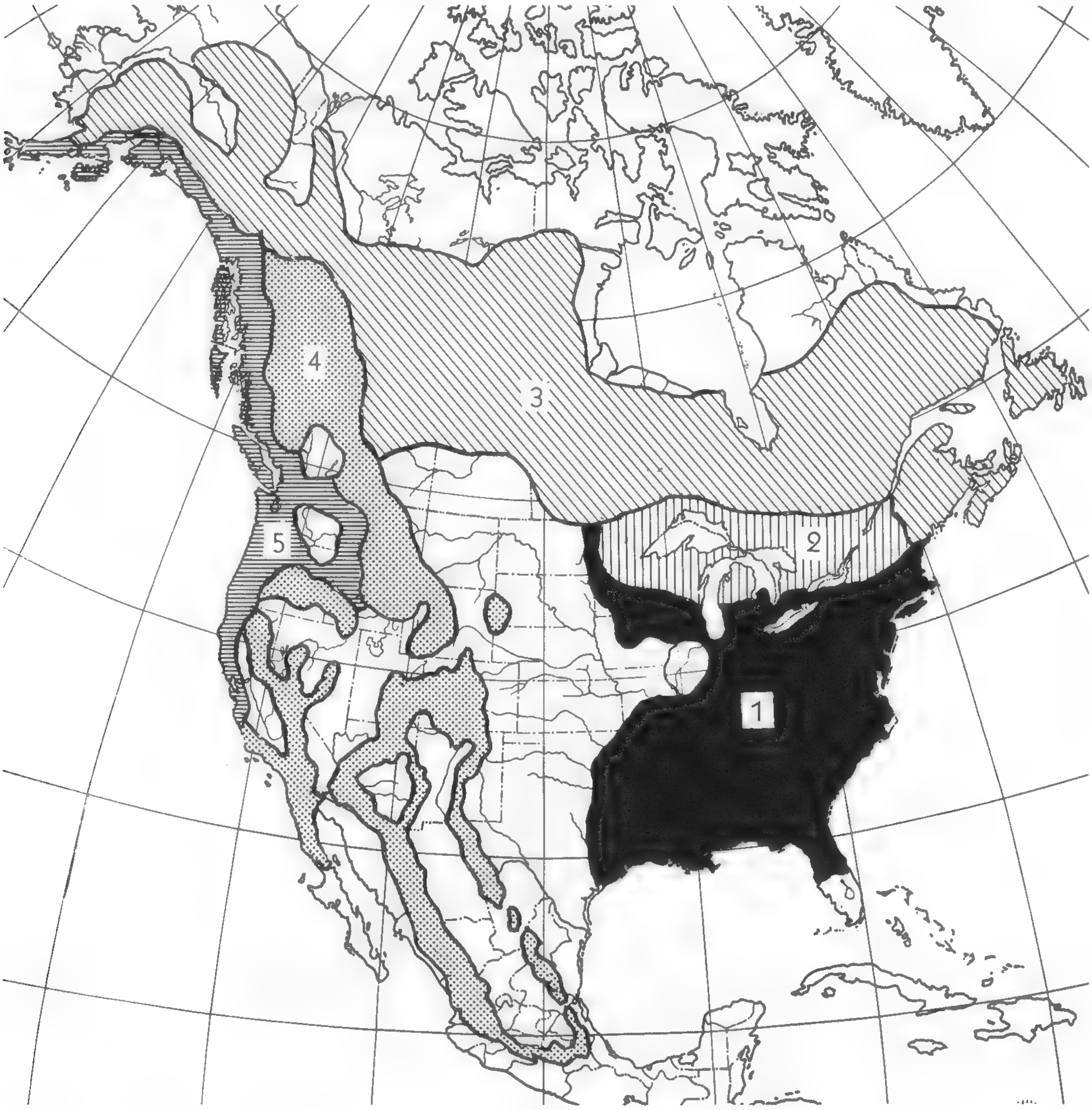

Figure 3. A rough representation of the major North American forest formations of today, modified from Weaver and Clements (1938:frontispiece). We may suppose the formations existing in previous interglacials (with Moreau, 1963:396, I regard distinction between Pleistocene and "Recent" as superfluous) to have been fairly similar. The forest types are: 1, eastern deciduous forest; 2, lake forest (an ecotonal mixed deciduous-coniferous forest); 3, northern coniferous forest (including taiga); 4, western montane (lower) and subalpine (higher) forests; 5, coast (chiefly coniferous) forest. In this paper types 4 and 5, collectively, are usually referred to only as "western montane forests."

of wood warbler adapted to the remnantal, deciduous, Arcto-tertiary forests of southeastern North America at the close of the Pliocene.

With the advent of the Pleistocene and the southward movement of Nebraskan ice, great changes must have occurred at the northern margins of the compacted deciduous forest and to a controversial depth within it. With these changes our ancestral parulid species would have been exposed, for the first time, to the boreal Arcto-tertiary (e.g., northern coniferous) forest elements forced southward by glacial ice. Whether or not, as Brooks conjectured (1947:294), bird populations were "compressed" in the southeastern refugium upon glacial maxima, with an ensuing theoretical increase in competitive pressures (this seems improbable), the ancestral parulid of our model was presented with the opportunity of making, or beginning to make, the adaptation to a completely new and potentially northern coniferous forest environment.

Now consider the advantages open to a species or population making this adaptation. Upon retreat of glacial ice and the subsequent establishment of coniferous forest in its place, this species would possess the key to *exclusive occupancy of a vast transcontinental range.* Our hypothetical warbler having accepted this opportunity, we have arrived at the situation shown in Figure 4, C.

This transcontinental distribution introduces a new and vital possibility, because the species is vulnerable to disjunction upon the next glacial advance (Figure 4, D). Geographical isolation would then be realized and differentiation could begin, not only in the refugia of the Nebraskan glaciation but continuing through the following warm interglacial — given isolation in western mountain forests then restricted to separate mountain masses (Figure 4, E).

At this point, moreover, the whole process could be repeated. That is, the original ancestral parulid (or, more properly, its modified descendant) during the Kansan maximum (Figure 4, D) would be renewing, perfecting, or maintaining its coniferous forest adaptations, and would again re-advance through the expanding coniferous forests of the second interglacial (Figure 4, E), again to achieve a transcontinental distribution and renewed vulnerability to disjunction.

It is unnecessary to follow the sequence to its logical conclusion as shown in Figure 4, F-I. If the process outlined be repeated successfully (that is, with differentiation to the species level in each case) through four glaciations and into the present fourth "interglacial," there would be one modified "parental" species in the east and three "derivative" species in the west (why four derivatives are shown in Figure 4, I, will become clear shortly).

There is, further, the possibility of additional derivative species being formed, if western differentiates should re-invade the northern coniferous forest (a possibility indicated by the dotted arrows of Figure 4), again to achieve a transcontinental distribution but from the opposite direction. This seems likely to have occurred, although rarely.

Analysis of Wood Warbler Distributions

A few preliminary remarks should precede consideration of concrete cases. Most importantly, it seems too much to expect that the descendants of any particular ancestral parulid would actually have pursued in full the precise course of the model, and, if they did, it is perhaps equally unlikely that all of the resulting forms would survive. Various ancestors probably did not begin at the beginning of the course; others, so starting, did not successfully complete all stages; still others, running all or part of the course, may have left an imperfect record through extinction of descendants. And there is, finally, the excellent possibility that two or more derivative species sometimes resulted from isolated remnants of a single invasion.

Here also I must caution the reader against too ready acceptance of chronological indications. If, here and there, I suggest that two related events occurred in the Illinoian and Wisconsin times, respectively, what is more definitely indicated is only "earlier" and "later," such indications being based on an assumption (probably valid more often than not) that greater differences take longer to develop than lesser ones. Definite times are offered only as appealing possibilities.

These various qualifications do not detract from the instructive value of the model. Let us now turn to the living wood warblers in search of support for the hypothesis.

The Black-throated Green Warbler Group

This group (Plate I) is most intriguing in the present connection. It consists of five species of obviously very close relationship. Four of them, the Black-throated Green Warbler *(Dendroica virens),* Townsend's Warbler *(D. townsendi),* Hermit Warbler *(D. occidentalis),* and Golden-cheeked Warbler *(D. chrysoparia),* are extremely similar in many basic respects. High-ranging, high-nesting species of coniferous or partly coniferous forest, they are essentially allopatric and form a classical superspecies *sensu* Mayr (1942:169). The lower-nesting, lower-ranging Black-throated Gray Warbler *(D. nigrescens)* is smaller than the rest, slightly different in proportions and pigmentation, and somewhat aberrant ecologically; it is sympatric to some extent with *D. townsendi* and broadly sympatric with *D. occidentalis* (Figure 5).

A convenient summary of the habitat preferences of the group by Stein (1962) is brief but still more extensive than can be attempted here. This should be consulted, together with those general treatments (Griscom, Sprunt, et al., 1957; Bent, 1953; Chapman, 1907) which apply to all warbler species here discussed.

Since the remarkable similarity of the distributions of the group (Figure 5) with the terminal stage of the model (Figure 4, I) will probably be noted, I hasten to confess that Figure 4 was constructed precisely as it was for dramatic effect. If, however, the drama is diminished by the confession, inspection of Figure 6, showing the distribution of another species group, will reveal that nature has provided a sufficiently dramatic resemblance on her own!

The Black-throated Green Warbler.—This species has a wide range in the northern coniferous forest, the ecotonal lake forest, and the mixed forests of the Appalachian Mountains, where it tends to occupy various but rather circumscribed niches. Its present, nearly continent-wide distribution places it in jeopardy of disjunction upon another glacial advance. Although it no longer enjoys a very wide distribution in the eastern deciduous forest, there is evidence that it may once have done so, since it maintains marginal populations in cool, upland deciduous climaxes and extensive populations wherever hemlock is an important dominant of the mixed mesophytic forests. A morphologically poorly-marked race *(D. v. waynei)* occupies pure deciduous growth near the central Atlantic coast. Descent with modification from an

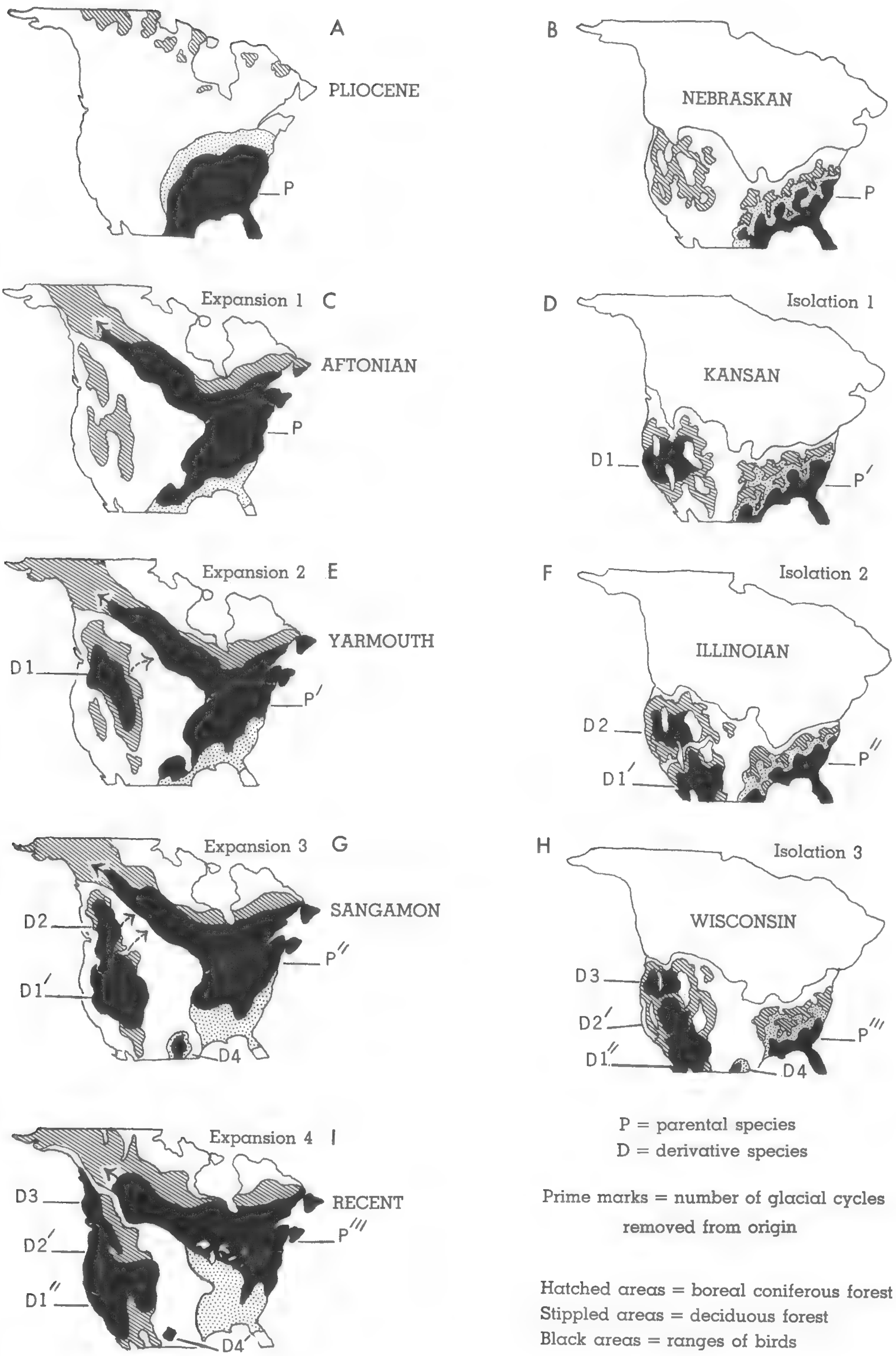

Figure 4. A model sequence showing the effects of glacial flow and ebb on the adaptation and evolution of a hypothetical ancestral wood warbler and its descendants (see text for explanation). The details of glacial boundaries are not meant to be accurate.

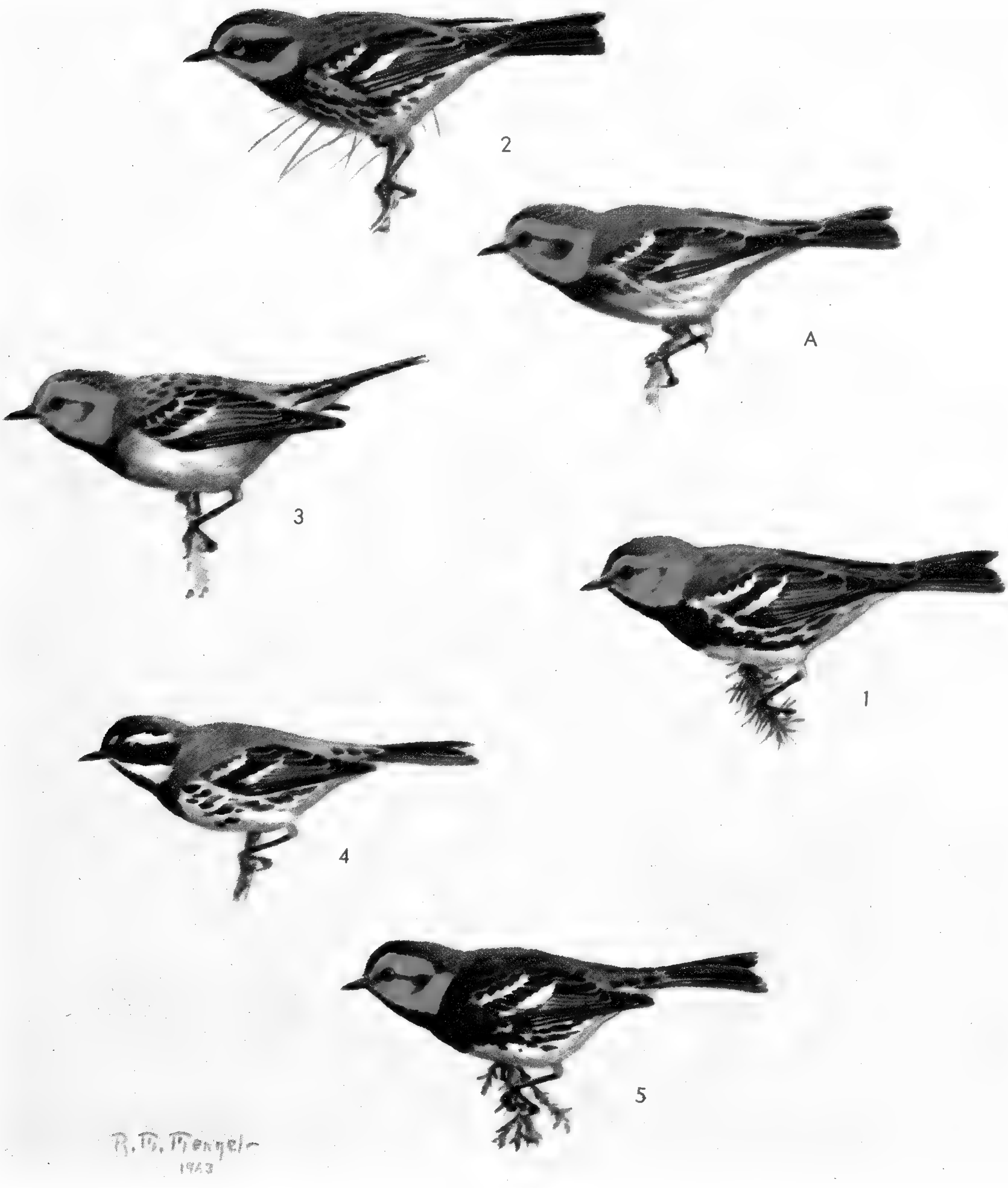

Plate I. The Black-throated Green Warbler Group

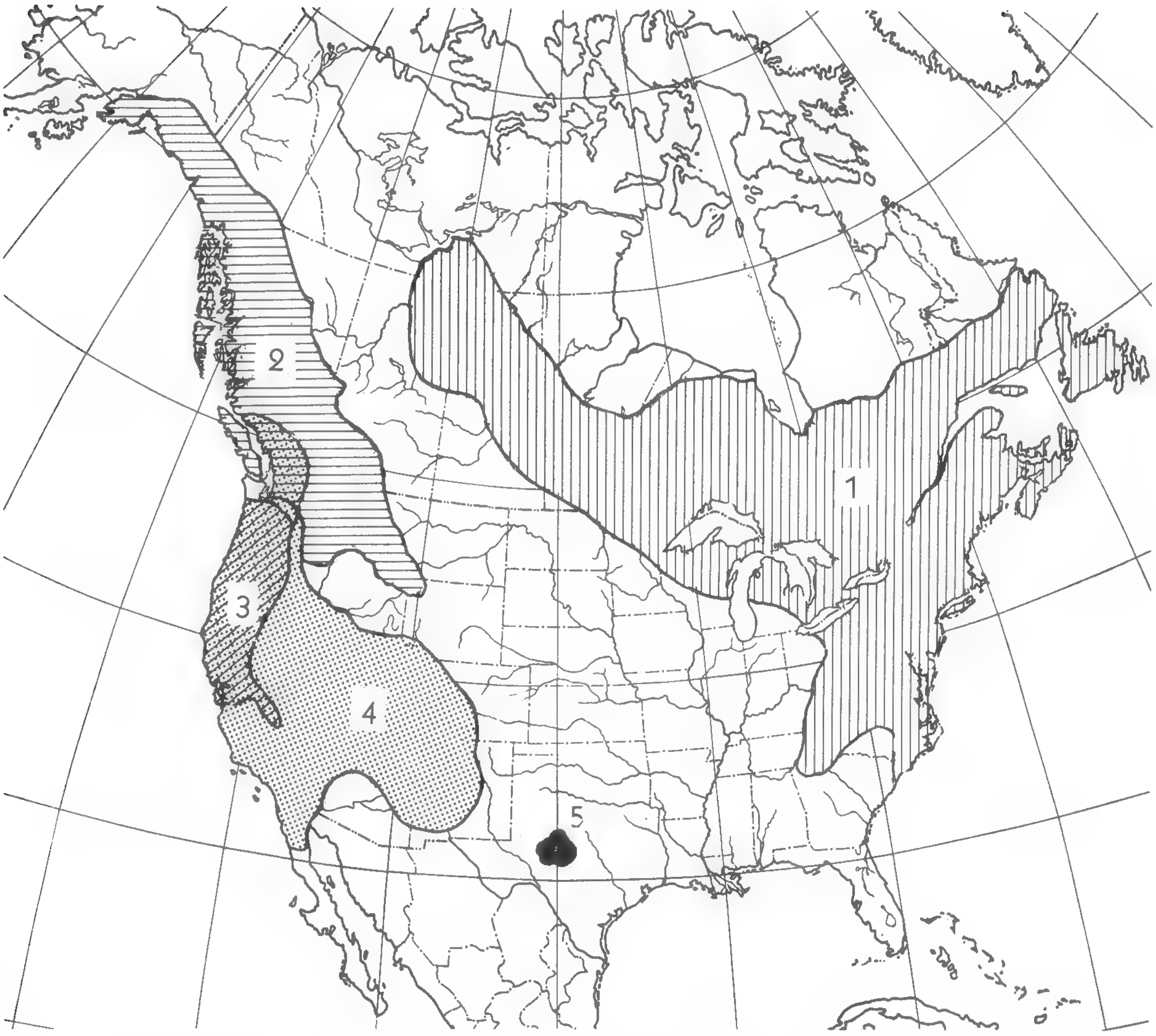

Figure 5. Approximate breeding distributions of the Black-throated Green Warbler group. 1. Black-throated Green Warbler; 2, Townsend's Warbler; 3, Hermit Warbler; 4, Black-throated Gray Warbler; 5, Golden-cheeked Warbler. The numbers and positional relationships of the ranges are reflected by those of the birds of Plate I (opposite) and will identify them, save for the extra bird of the plate (A), which is a hybrid Townsend's × Hermit Warbler. The birds are adult males in fresh to somewhat worn autumn plumage except the hybrid, which is a first-year male in the same plumage.

ancestor of long deciduous forest history (see also under Golden-winged Warbler) seems very likely, although in its present form the species has nearly relinquished its deciduous forest affiliations in favor of mixed and purely coniferous forests. Its song, appropriately for a species occurring sympatrically with many other wood warblers, is markedly stereotyped, although displaying two patterns (Stein, 1962:64).

The Townsend's Warbler.—This species occupies various specialized coniferous climaxes in the giant trees of the humid northwestern coast forests, and seems to have no overlap with the preceding species, although the gap (in Alberta) between their present breeding ranges is not great. Its similarity with the Black-throated Green Warbler is obvious (Plate I) and has been noted by many. The song, while differing in phraseology from that of the Black-throated Green (and more variable, befitting a species with few sympatric congeners) is still more similar to it in quality than those of the next two species (Stein, 1962:65). It seems very probable that Townsend's Warbler was derived from a western invasion of the ancestors of the Black-throated Green

Warbler (I shall henceforth use the prefix "pro"—e.g., in the present case "pro-*D. virens*"—to avoid the unwieldly "ancestors of the . . . ").

The Hermit Warbler.—The last statement applies equally to this species, whose differences from the Black-throated Green, while slightly disparate in kind, are little if any greater in degree. The species, which occupies tall, coniferous Cascade and Sierra Nevadan montane forests (hence occurring at higher elevations than Townsend's Warbler), slightly approaches the Black-throated Gray Warbler in its diminution of xanthic pigments. Its song shows patterns difficult to distinguish both from the Townsend's Warbler on one hand and the Black-throated Gray on the other (Stein, 1962:68).

The Hermit Warbler may be an earlier differentiate than the Townsend's, but it is perhaps easier to conceive of the two as descending simultaneously from isolated differentiates resulting from the same western invasion of pro-*D. virens*. In either case their differences from each other and from the Black-throated Green Warbler suggest the possibility, if not the probability, of differentiation of one or both in a time earlier than Wisconsin, perhaps Illinoian. (This is indicated by comparison of their differences with those displayed by various species—or near-species—such as Audubon's and Myrtle Warblers, thought more clearly to represent very recent, probably Wisconsin, differentiation.)

Within their narrow zone of sympatry Hermit and Townsend's Warblers are known to hybridize (Jewett, 1944), and of several migrant hybrids taken in Arizona by Allan R. Phillips, one served as the model for the hybrid shown in Plate I, A. Although, as Jewett pointed out, various assortments of characters are shown by hybrids (possibly of second or later generations), at least some, like the one figured, interestingly display a combination of characters nearly reconstituting the Black-throated Green Warbler. This certainly suggests that various of the genes possessed by each are much like those of the Black-throated Green Warbler and tends to indicate a common ancestor much like that species.

The Black-throated Gray Warbler.—This comparatively minute species, nearly devoid of xanthic pigments but remarkably like Townsend's Warbler in pattern, enjoys a widespread distribution geographically overlapping both of the foregoing species but nearly if not quite separate ecologically. As Stein (1962:67) has summarized (from Chapman, 1907): "Its habitat in the northwest is mainly shrubby openings in coniferous forests, but elsewhere it varies from shrubby openings in mixed woods to dry slopes covered with oaks, junipers, and pinyon pine, and even chaparral." Relatively speaking, its geographic position, morphological differences (reduction in yellows, minute size), and addiction to comparatively xerophytic deciduous habitats are comparable to those of *Vermivora luciae* of the next group. It seems certainly to have descended from a western colonization more remote in time than that postulated for the Townsend's and Hermit Warblers. This may have been the colonization of an early pro-*D. virens* across an early northern route. Alternatively, its descent may be from a still earlier ancestor of Madro-tertiary affiliations which simultaneously or later gave rise to earliest pro-*D. virens* later to follow the northern route of the model. Its choice of habitat may suggest the second alternative, although, on the other side of the ledger, the early "northern routes" may have involved coniferous forests less highly evolved and less uniformly coniferous than today's.

In song also—"about the most variable and the least stylized" (Stein, 1962:68)—it seems to stand at the extreme with reference to the group at large.

The Golden-cheeked Warbler.—Like the Kirtland's and Colima Warblers, this species appears to be a relict and in danger of extinction. Its geographic position, on the Edwards Plateau of central Texas, is intriguing. Are these birds, as I once thought, the now restricted remnants of a once widespread early western differentiate? The song of the species, in which Stein (1962:67) detects resemblance to the Hermit Warbler (but which also suggests the Black-throated Green), might suggest this, but several considerations lead me now to think not.

First, the species seems to me strikingly like a somewhat melanistic Black-throated Green Warbler, an opinion shared by Lester L. Short, Jr. (letter, 29 August 1963), who has written me as follows: "*Dendroica chrysoparia* appears to be a strongly differentiated disjunct form of *D. virens*. . . . The Golden-cheeked Warbler sings very much like the Black-throated Green. . . . [the] characters of *chrysoparia* are observable to some extent in *virens*. Individuals of the latter may show considerable black on the back and crown. Young and even adult male *virens* frequently exhibit moderate to strong development of a transocular stripe. Finally, the race *waynei* of *D. virens* is similar to *chrysoparia* in having a more restricted black patch on the throat and breast."

Second, the distributional relationship between *D. virens* and *chrysoparia* is remarkably suggestive of a number of plant and animal distributions ably analyzed by Blair (1958), strongly indicated to be Wisconsin in origin, and thought to mark the presence on the Edwards Plateau of a postclimax relict of the eastern deciduous forest community.

This, with the bird's habitat — cedar brakes containing miscellaneous deciduous growth—seems to me to be evidence of an originally broad deciduous forest range of late pro-*D. virens* in the not-too-distant past. Whether or not this is so, a hypothetical pinching off of this relict species explains the presence of four (rather than the "expected" three) western differentiates in Figure 4, I.

Finally, the Golden-cheeked Warbler, unlike other members of the group, still migrates to a winter home largely coextensive with that of *Dendroica virens*.

Remarks.—This group, of all to be considered, has a conformation most closely resembling that of the "ideal" model, and in fact may have come fairly close to the "ideal" history. It appears to consist of an eastern form *(D. virens)*, modified by long descent from an old deciduous forest ancestor (pro-*D. virens*); of a disjunct, relict descendant quite recently separated from the same ancestral line *(D. chrysoparia)*; and of three western differentiates representing the descendants of (probably) one earlier *(D. nigrescens)* and one or two later *(D. townsendi, D. occidentalis)* western invasions, the latter two probably and the first possibly by pro-D. *virens*.

Earlier I (see Mengel, 1963:394) have indicated without discussion disagreement with Stein's conclusions (1962:69) that in this complex the Black-throated Gray is closest to Townsend's Warbler and the Townsend's and Black-throated Green and the Hermit and Golden-cheeked Warblers are "counterparts."

Although Stein seemed by the use of this word to imply descent from an immediate common ancestor, perhaps he meant only resemblance, rather than phylogenetic equality. His conclusions were based, in any event, as all such conclusions to some extent must be, upon resemblances, particularly between plumage patterns and song spectrograms (the significance of which is still little known). Evaluation of resemblances, of course, is largely subjective, and I have already admitted to interpretative differences with Stein. I agree with Lester Short (letter) that "there is a great plasticity of color pattern in this warbler group, so that one can on this basis make a case for almost any arrangement of relationships among the various forms."

Still more importantly, I agree with Udvardy (1963:1147), that consideration of community histories and zoogeographic evidence — with their suggestions of the probable and the possible—must also be given significant weight in the evaluation of present conditions. It is comparatively difficult to reconcile Stein's suggestions with current indications of the biogeographic history of the late Cenozoic.

The Nashville Warbler Group

This group (Plate II) consists of four obviously closely related species, the Nashville Warbler *(Vermivora ruficapilla),* Virginia's Warbler *(V. virginiae),* Lucy's Warbler *(V. luciae),* and Colima Warbler *(V. crissalis).* Possibly the Nashville, Virginia's, and Colima Warblers should be thought of as a superspecies, although this may strain the definition a bit. From this complex Lucy's Warbler stands apart in much the same ways as does the Black-throated Gray Warbler from the Black-throated Green complex, but somewhat more sharply.

The distributions of the group (Figure 6) are almost as striking in their apparent illustration of the theoretical model as those of the foregoing one, and the similarities stimulate the imagination. This group differs from the last in that its members are low-ranging, chiefly ground-nesting birds tending to inhabit shrubby deciduous seral stages in the coniferous forests and comparable shrubby situations elsewhere. A difference from the last group is that two *races* of the Nashville Warbler occupy geographic positions relatively (though not absolutely) comparable to those of two *species* (Black-throated Green and Townsend's Warblers) of the previous group. Each of the five forms, nonetheless, has a geographic counterpart in the last group.

The Nashville Warbler.—This species inhabits shrubby growth at the edges of deciduous, mixed, or coniferous forest. It retains a somewhat smaller present distribution within the northern part of the deciduous forest region than does the Black-throated Green Warbler of the last group, but its habitat preferences strongly suggest either an origin in the eastern deciduous forest region or a long history there. Two subspecies are recognized: *Vermivora ruficapilla ruficapilla* in the east and north, and *V. r. ridgwayi* (the "Calaveras" Warbler) with a fairly wide distribution in the mountains west of the Rockies. The latter utilizes various habitats of shrubby nature including chaparral, oak-scrub, piñon and juniper, and willows, sometimes at the edges of coniferous forest. The species stands in jeopardy of disjunction in case of further glaciation, even the eastern subspecies having a range sufficiently wide to make this a possibility.

The two races, which are not well differentiated, are unique among the unequivocal subspecies of wood warblers here considered in being separated by an (apparently) considerable gap extending from eastern Saskatchewan to central British Columbia. These facts suggest a wide western colonization, with subsequent imperfect or intermittent isolation of stocks, either in Sangamon time or (perhaps more probably) in very late Wisconsin time. The position of the present separation, in any case, and the slight distinction of the forms, suggests that the disjunction may date only from the Valders re-advance of Wisconsin ice some 11,000 years ago.

The Virginia's Warbler.—A somberly handsome little warbler, this one, like the foregoing, is a ground nester. It inhabits oak scrub (especially), oak mingled with pine, juniper, piñon, and similar communities at moderate elevations in the south-central Rocky Mountains and is essentially allopatric with *Vermivora ruficapilla ridgwayi.* Its choice of habitat is compatible with a descent from pro-*V. ruficapilla* ancestors of seral stages and edge situations like those occupied by the Nashville Warbler today. The song, as nearly as can be told from descriptions in the literature, is typically "Vermivoran" and not greatly unlike the Nashville's. The considerable distinctness of this species from the Nashville Warbler in various ways (I think greater than that of the Townsend's from the Black-throated Green Warbler) may suggest differentiation from a pro-*V. ruficapilla* of considerable remoteness, perhaps in Illinoian time. Marked resemblances to the Colima Warbler will be taken up under that species.

The Lucy's Warbler.—This is one of the most diminutive of wood warblers. In size and pallid coloration it exhibits superficial convergence with some of the bushtits, verdins, etc. of similar desert and semi-desert habitat. While it seems definitely to belong with the present group, it must be admitted that it is quite aberrant. Its plumage totally lacks xanthic pigments; its song (said to resemble a Yellow Warbler's) is distinctive; its rump, instead of the usual yellow, is chestnut like that of the striking Mexican species *Vermivora superciliosa;* and its choice of nest-sites (in crevices and cavities above ground) is unique. Additionally, it inhabits hot, dry desert regions in southwestern United States and northern Mexico that are home to no other wood warbler. These things place this species in the same relation to its group that the Black-throated Gray Warbler occupies in the preceding one.

Remote descent from a pro-*V. ruficapilla* crossing from the east by an early northern route is possible, but it seems equally if not more likely that this species descends from the isolated western population of an old, once widespread form of Madro-tertiary connections, whose eastern population became pro-*V. ruficapilla.*

The Colima Warbler. — A little-known species, this *Vermivora* is as remarkably large as Lucy's Warbler is small. Aside from size, its resemblance to Virginia's Warbler is marked. Its comparatively small breeding range is restricted, so far as known, to the Chisos Mountains of southwestern Texas and to mountainous parts of the Mexican states just to the south—Coahuila and Tamaulipas (probably), Michoacan and Colima (doubtfully). Its habitat and habits seem much like those of Virginia's Warbler, but its Pine Warbler-like song is distinctive. Its over-all morphological and ecological resemblance to Virginia's Warbler, however, suggests to me, as to Lester Short (letter), a close relationship and I think it likely that the two species stem from disjunct colonies from the same invasion of pro-*V. ruficapilla* in (probably) Illinoian time or earlier.

While the possibly coincidental but striking similarity of the distributions of the Colima and Golden-cheeked Warblers (Figure 5, 5; Figure 6, 5) tempts one to postulate similar origins, this seems unlikely, despite the recent sweeping pronouncement by Phillips (1962:364-365) that the Colima, Virginia's, and Nashville Warblers are conspecific. (In this connection I think the

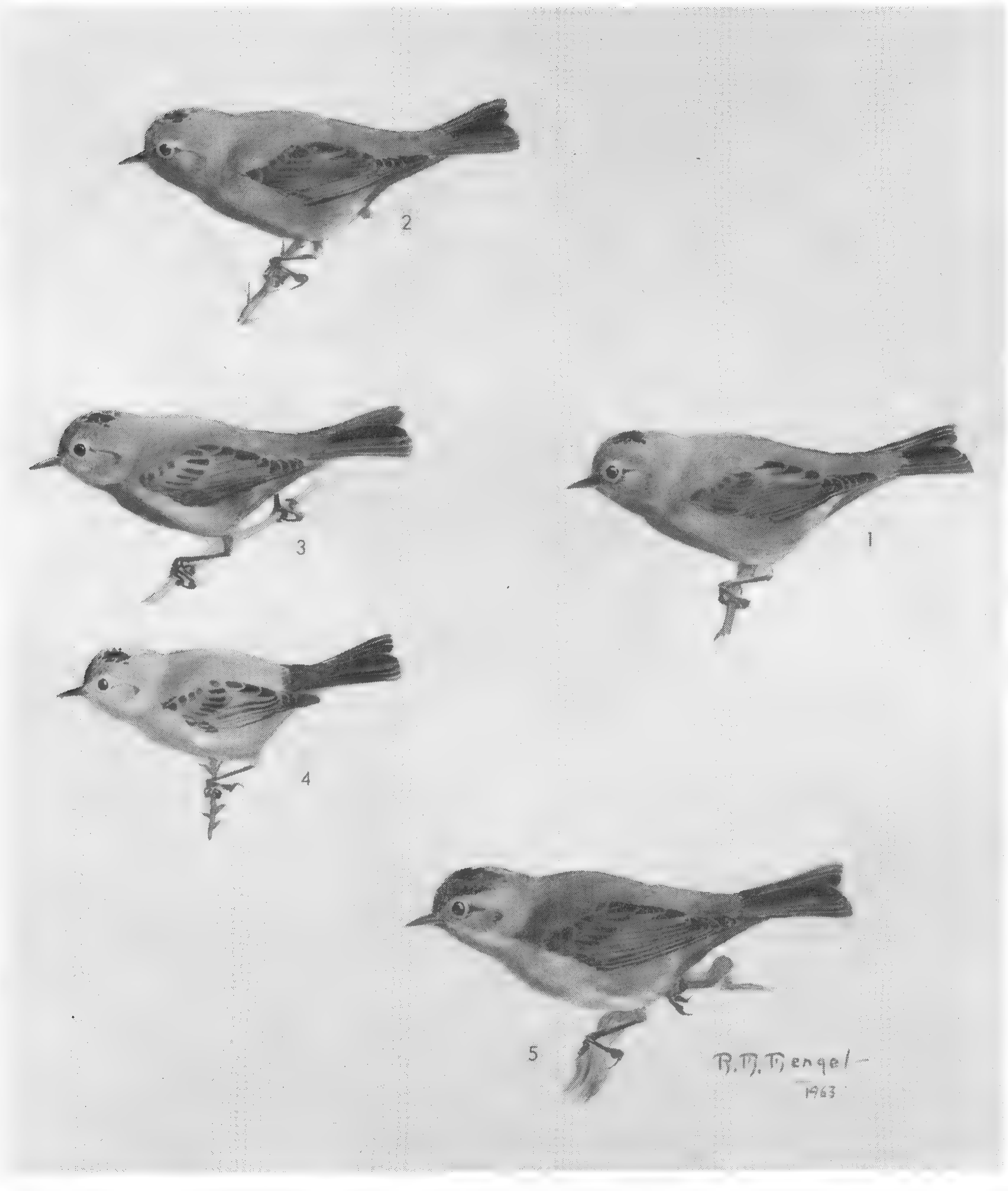

Plate II. The Nashville Warbler Group

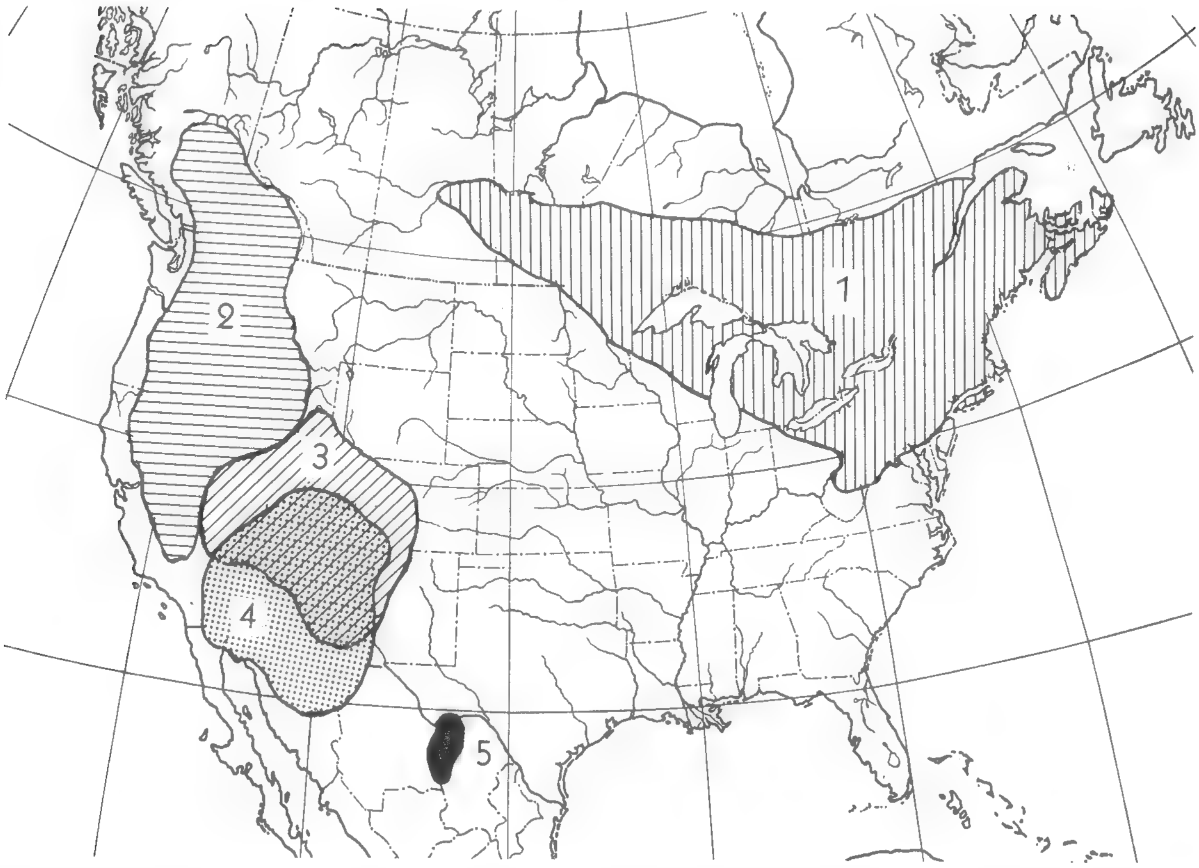

Figure 6. Approximate breeding distributions of the Nashville Warbler group. 1, eastern race of the Nashville Warbler; 2, western race of the Nashville Warbler; 3, Virginia's Warbler; 4, Lucy's Warbler; 5, Colima Warbler. The numbers and positional relationships of the ranges are reflected by those of the birds of Plate II (opposite) and will identify them. The birds are adult males in fresh autumn plumage.

statement of Mayr, 1942:170-171, concerning the value of the concept superspecies should be strongly urged as relevant.) If Phillips' contention were valid, and if the Colima Warbler's origin were similar to that postulated above for the Golden-cheeked, I should expect to find both of them on the Edwards Plateau; to find considerably greater similarity between *V. crissalis* and *V. ruficapilla* than is evident to my eyes; and perhaps also to find *V. crissalis* performing a longer migration than it seems to, like most essentially eastern warblers and similar to that of *D. chrysoparia.*

The Connecticut Warbler Group

This group displays features which may be meaningfully interpreted in relation to the model, but which tax the power of imagination more than those of the foregoing groups. This is because the situation is probably "imperfect," in the sense of providing fewer species, or fewer surviving species, for analysis.

The group (Plate III) consists of only three species: the Connecticut Warbler *(Oporornis agilis),* which stands a bit apart, and the exceedingly similar Mourning Warbler *(O. philadelphia)* and MacGillivray's Warbler *(O. tolmiei),* which are doubtfully distinct at the species level but which, if so, form a superspecies. These are furtive, ground-nesting, low-ranging, large-eyed, long-legged birds adapted to gleaning foliage insects and turning leaves on the ground and in the low levels of the understory, in openings of mixed and coniferous forests. Their ranges are shown in Figure 7, A.

The Connecticut Warbler.—The oblong, rather restricted breeding range of the Connecticut Warbler is nearly central in North America, but extends a little more westward (northeastern British Columbia) than eastward (James Bay) in the northern coniferous forest. The species has, however, a markedly eastern migration route of great length, suggesting an eastern deciduous forest origin. It is questionable, considering its present distribution, whether it would be divided in the event of another glaciation or forced into an eastern or western refugium. Its distribution suggests that it is not now an ascendant species, and it may be on its way to reliction and ultimate extinction. It seems to be less numerous than the extensively sympatric Mourning Warbler. Its resemblance to the Mourning and MacGillivray's Warblers is great, but considerable differences in size, proportions, coloration, and song suggest a comparatively early divergence.

The MacGillivray's Warbler.—While differing in various ways from the Connecticut Warbler, this form is only dubiously distinct from the Mourning Warbler at the specific level, as already suggested by Phillips (1947:296) and Hofslund (1962:44). The morphological differences are limited to slight distinctions in size and coloration, the most conspicuous of which is the interrupted eye-ring of males, while behavioral differences, including song, and ecological differences are indeed slight so far as known. Two alleged hybrids considered by some to be evidence of limited sympatry (Hofslund, 1962:44) are of controversial identity as indicated in the original report on them (Peterson, 1958). In all, very recent differentiation is suggested.

The Mourning Warbler.—Almost restricted to edge situations in northeastern coniferous forests (south to West Virginia) and west in the north to Alberta, this is scarcely more than an eastern MacGillivray's Warbler. It has been claimed (Hofslund, 1962:44) that in song and perhaps other characters the Mourning Warbler shows increasing convergence with MacGillivray's Warbler as it approaches that form in the west. This is reminiscent of comparable convergence found in the sibling species of the meadowlarks *Sturnella magna* and *neglecta* (Lanyon, 1962:189).

Remarks.—I propose as a hypothesis that a pro-*O. agilis* stock originally derived in the eastern deciduous forest (where a congener, the quite distinct *Oporornis formosus,* the Kentucky Warbler, is still exclusively found), and gradually adapting to seral stages of the northern coniferous forest, early (perhaps in the Yarmouth interglacial, if not before) accomplished an invasion of the western mountain forests. It was disjuncted by subsequent glaciation, and differentiated into two forms, the western one of which was pro-*O. tolmiei.* While pro-*O. agilis* was losing its roots in the deciduous forest, pro-*O. tolmiei* differentiated fully and (I propose tentatively in Sangamon interglacial time) successfully accomplished a reverse invasion of the northern coniferous forest. This is suggested by the very large western range and geographic differentiation of several races within this range (Phillips, 1947) of *O. tolmiei* (the 1957 A.O.U. Check-list recognizes only subspecies *tolmiei* and *monticola).* Wisconsin glaciation, driving a wedge through this re-expanded range, permitted the isolation and comparatively slight differentiation resulting in the present, variable, western *O. tolmiei* and the homogeneous, eastern *O. philadelphia.* The migration route of the Mourning Warbler, more westerly and shorter than that of the Connecticut and to a winter range partly coextensive with that of MacGillivray's Warbler, may be further evidence of the origin here suggested for the Mourning Warbler.

Any alternative explanation seems to require more assumptions. The most obvious one would require the presence in the original eastern deciduous forest of *both* pro-*O. agilis* and pro-*O. philadelphia* (with no clue as to their differentiation from a common stock), and would further require us to assume that the ancestors of the form that is now most exclusively restricted to northern coniferous forest *(O. agilis)* never accomplished a sufficiently extensive westward colonization therein to permit isolation by glaciation (as evidenced, anyway, by a surviving differentiate).

The Yellow-throated Warbler Group

This group consists of four species which may constitute a superspecies. Only two of them, the southeastern Yellow-throated Warbler *(Dendroica dominica)* and the southwestern Grace's Warbler *(D. graciae)* are figured here (Plate III). Completing the group (Figure 7, B) are the West Indian Olive-capped Warbler *(D. pityophila)* and Adelaide's Warbler *(D. adelaidi)*. These species have been figured in Griscom, Sprunt et al. (1957: pl. 32). Kirtland's Warbler *(D. kirtlandii),* the most thoroughly studied member of the family (see Mayfield, 1960), has been figured with the group, for reasons to be explained, but does not belong with it immediately. (Note, however, that Ridgway, 1902:603-605, placed it next to *D. pityophila* in his systematic order.)

The Yellow-throated Warbler.—This is a southeastern species with interesting variability in habitat; regionally it may almost exclusively occupy live oaks, pine, cypress, or sycamore, so long as the trees are tall. Its appearance, general habits, and choice of habitat clearly ally it with Grace's Warbler, but the differences between the two (in song, size, details of pattern) are sufficiently great to make pre-Pleistocene separation seem reasonably probable. Certainly I cannot concur with Hellmayr (1935:400) that the Yellow-throated and Grace's Warblers are probably conspecific. Three continental races and one insular race additionally suggest some degree of antiquity for *D. dominica,* although the continental races *(D. d. dominica, albilora,* and *stoddardi)* are not very well marked. The soft, slurred song suggests that of an Indigo Bunting *(Passerina cyanea).*

The Grace's Warbler.—A southwestern mountain species, Grace's Warbler reaches Central America. It frequents tall pines, both in pure stands and in oak woodland (Phillips and Webster, 1961:551), sings something like a Chipping Sparrow *(Spizella passerina),* and has differentiated slightly (Webster, 1961) into four races *(D. g. graciae, yaegeri, remota,* and *decora).* Ranging north only to Utah, the species shows no indication of affiliations, past or present, with northern coniferous forest.

The Adelaide's Warbler.—Long placed next to Grace's Warbler in systematic lists, the species was suggested by Hellmayr (1935:400) to be probably conspecific with it, an extreme view in my opinion. Bond (in Griscom, Sprunt et al., 1957:265) seems to suggest that it is more disparate from Grace's Warbler than is the next species, both in appearance ("completely lacks the black streaking on both upperparts and underparts and the entire breast and abdomen are yellow") and habitat (mostly thickets, but occurs in mountain forests and tall trees on St. Lucia), although perhaps not in song. To me the combinations of characters displayed by the Adelaide's and Olive-capped Warblers, in comparison with Grace's Warbler, suggests the comparison of

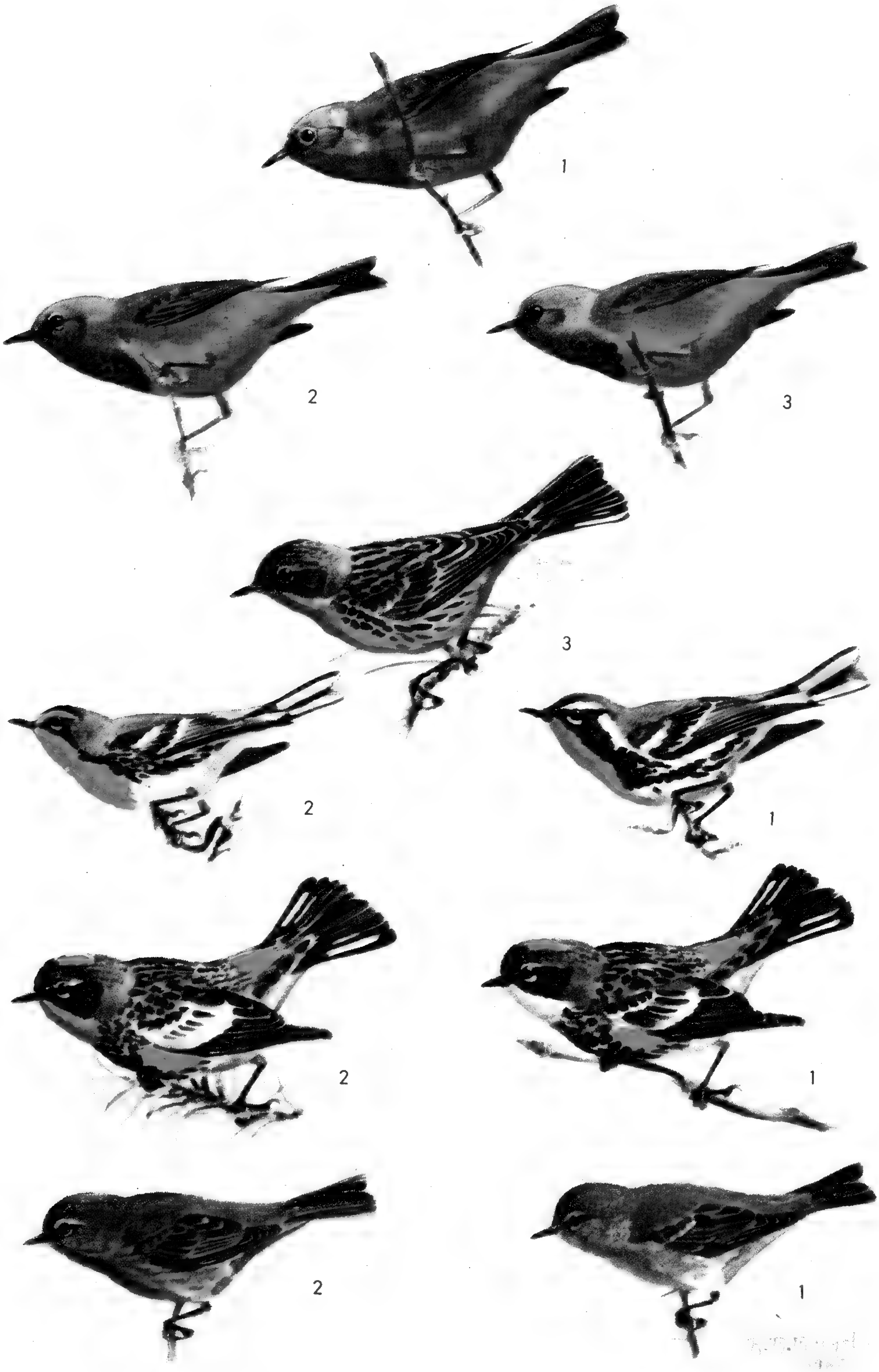

Plate III. Four Wood Warbler Groups

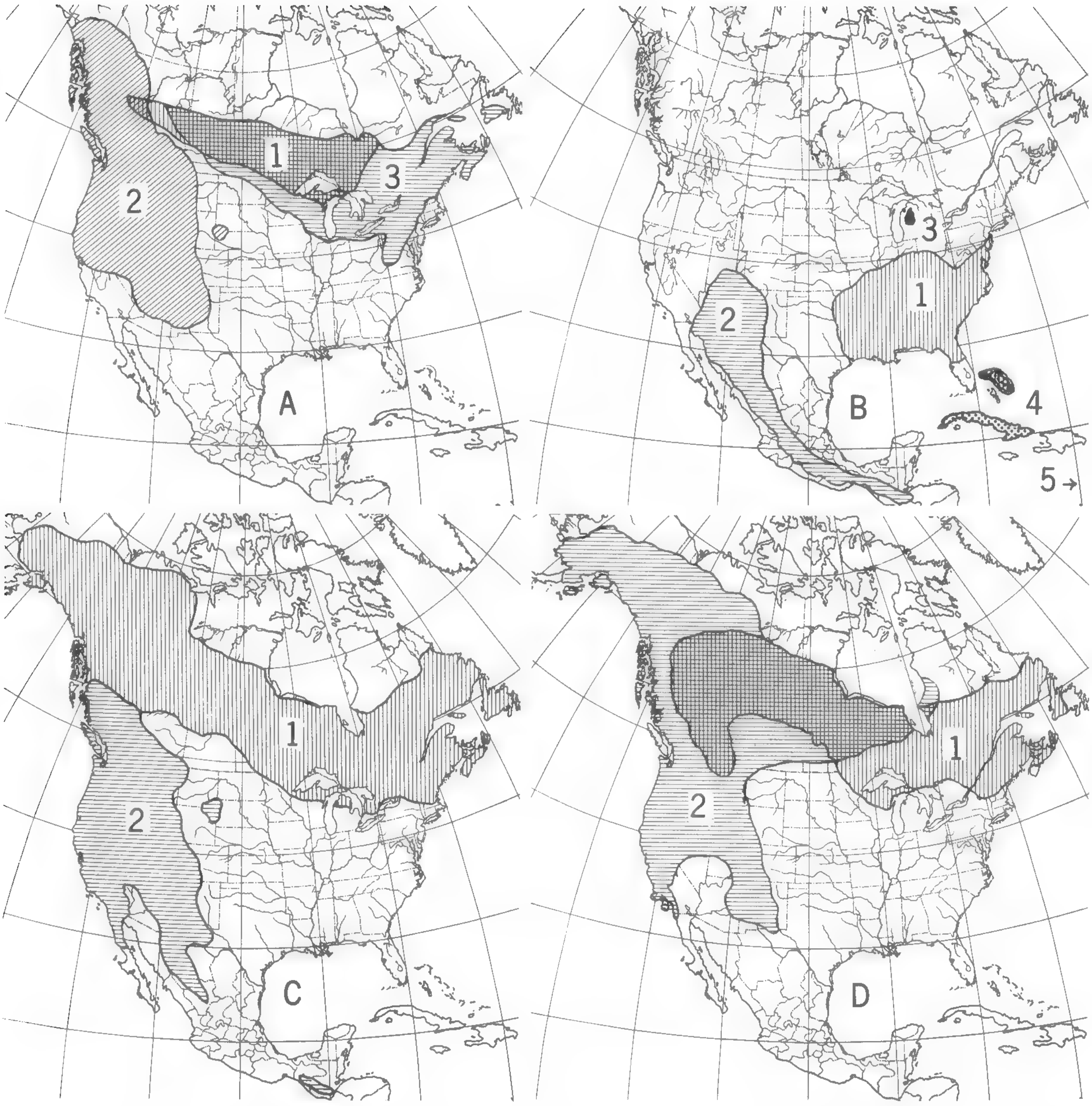

Figure 7. Approximate breeding distributions of the four warbler groups shown on Plate III (opposite). The numbers and positional relationships of the ranges are reflected by those of the birds in the plate and will identify them. A. Connecticut Warbler group (top three birds): 1, Connecticut Warbler; 2, MacGillivray's Warbler; 3, Mourning Warbler. B. Yellow-throated Warbler group (part) and Kirtland's Warbler (next three birds): 1, Yellow-throated Warbler; 2, Grace's Warbler; 3, Kirtland's Warbler (see text). The West Indian Olive-capped Warbler (4) and Adelaide's Warbler (5) are not figured. C. Myrtle Warbler group (next two birds): 1, Myrtle Warbler; 2, Audubon's Warbler. D. Tennessee Warbler group (bottom two birds): 1, Tennessee Warbler; 2, Orange-crowned Warbler. The birds are males in fresh autumn plumage, except for Kirtland's and Yellow-throated Warblers which are in somewhat worn breeding dress.

Townsend's and Hermit Warblers in their relationship with the Black-throated Green. The existence of three races in the present species suggests considerable duration of residence in the West Indies.

The Olive-capped Warbler.—This species, which differs from Grace's Warbler largely "by having a yellowish olive-green crown and by lacking the conspicuous black streaks on the sides and flanks" likewise inhabits pines, although at intermediate instead of upper strata (Bond, loc. cit.). As nearly as I can tell from Bond's written accounts, its song is not greatly different from that of Grace's Warbler.

It is perhaps worth noting that this species has probably been derived from its mainland ancestor in much the same way as *Dendroica vitellina* from the Prairie Warbler, another alleged member (Kendeigh, 1961:298) of the old Madro-tertiary sclerophyllous woodland assemblage.

[*The Kirtland's Warbler.*—This celebrated species is included here chiefly because of its interest, and its strikingly relictual distribution, but also to mention that both its appearance and its habitat (jack-pine reproduction in burned areas) suggest it may be a remnant of an ancestor also related to the old Madro-tertiary sclerophyll woodland element. Its West Indian winter range, in the Bahamas, is reminiscent of those of other species thought (Kendeigh, 1961) to belong with this element, e.g., Prairie, Pine, and Yellow-throated Warblers.]

Remarks.—Although the distributions of *D. dominica* and *D. graciae* might at first suggest it, there is little doubt that the history of this group has slight resemblance to that of the model. This is evidenced by the lack of adaptation of any of the forms to northern coniferous forest or seral stages thereof, and by their generally southern present distributions. Rather, it seems likely that the members of this group have been part of a fauna associated with vegetational elements—sclerophyll woodland, etc. (see Kendeigh, 1961:298)—derived from the Madro-tertiary flora, which may in the late Miocene and early Pliocene have been more or less continuously distributed around the Gulf of Mexico (see Pitelka, 1951:383-384). Towards the close of the Tertiary, this flora (with its attendant animals) was disjuncted into southeastern and western components by a combination of influences in which climatic change and expanding grassland were evidently predominant.

Thus an ancestral pine or pine-oak woodland parulid probably differentiated into two forms, pro-*D. dominica* and pro-*D. graciae*. Further multiplication of species was permitted when members of the ancestral form (doubtless isolated migrants or strays remaining to establish breeding populations; see Bond, 1948:208-210) became established at least twice in the West Indies and differentiated in truly insular isolation. Thus in Puerto Rico, Vieques Island, Barbuda, and St. Lucia, Adelaide's Warbler occurs today, with the Olive-capped Warbler occupying Cuba and the northern Bahamas (Grand Bahama, Abaco), in the latter of which it is sympatric with a well-marked, presently-differentiating race *(D. dominica flavescens)* of the Yellow-throated Warbler. Interestingly, both West Indian species rather more resemble the geographically remote Grace's Warbler than the proximal Yellow-throated Warbler (Bond, loc. cit.), so that the ancestral form was perhaps rather more like Grace's Warbler than like the Yellow-throated. This seems also to indicate considerable, probably pre-Pleistocene, antiquity of the insular forms.

The Myrtle Warbler Group

The two species of this group (Plate III), the Myrtle Warbler *(Dendroica coronata)* and Audubon's Warbler *(D. auduboni),* if truly distinct as species, form a superspecies and seem to represent a recent differentiation, probably in Wisconsin time. Hybridization seems to be frequent (Packard, 1945; Alexander, 1945; and others), probably in a narrow zone of sympatry in British Columbia or Alaska.

The Myrtle Warbler.—Fully adapted to northern coniferous forest, this species has virtually no roots in the eastern deciduous forest. Its currently broad distribution places it in clear danger of disjunction in case of further glaciation. The northwestern population *(D. c. hooveri)* constitutes a poorly marked race, doubtless of post-Wisconsin differentiation. Like the following form, the Myrtle Warbler is remarkable in the family for its cold-hardiness and short migrations, wintering almost wholly in warm-temperate latitudes.

The Audubon's Warbler.—Much like the Myrtle Warbler, this mountain form occupies a very wide range from southeastern Alaska to Guatemala in western montane coniferous forests, where it has differentiated into four rather well-marked races *(D. a. auduboni, memorabilis, nigrifrons,* and *goldmani).*

In standard references the breeding range of the species is still given as south only to southern Durango. There is, however, a well-marked race, *D. a. goldmani* Nelson, breeding in the mountains of Guatemala and possibly Chiapas (van Rossem, 1934:402-403; Phillips, 1960:352; K. C. Parkes, pers. com.).

Remarks.—The history of the evolution of these two forms seems likely to be similar to that of the model, but only a fragmentary record exists.

The full adaptation of the two forms to coniferous forest, the absence of any remnantal deciduous forest affiliations of the Myrtle Warbler in the east, the absence of any clear relatives there, and the wide western distribution and considerable geographic variability of Audubon's Warbler all combine to suggest a long history largely obscured by extinction of critical forms. Two tentative hypotheses seem possible.

(1) The Myrtle Warbler descends directly from an eastern ancestor (pro-*D. coronata)* of early and long coniferous forest adaptations, whose deciduous forest affiliations were abandoned some time in the past. The Audubon's Warbler descends from a western differentiate resulting from the last western expansion of pro-*D. coronata,* the earlier differentiates that ought to exist either (a) having become extinct or (b) never having achieved full specific status (which seems less probable). Arguing against this hypothesis are the unique cold-hardiness and short migrations of the two forms, which qualities set the Myrtle Warbler sharply off from other eastern parulids.

(2) The Audubon's Warbler descends from an early differentiate resulting from the western invasion of an eastern ancestor now extinct, while the Myrtle Warbler is a recent (Wisconsin) differentiate resulting from eastward re-expansion of this pro-*D. auduboni.* In this case, it is not inconceivable that something much like today's Magnolia Warbler (adapted to northeastern mixed and coniferous forests) was the chronologically remote eastern ancestor. I favor the second hypothesis.

The Tennessee Warbler Group

Here, again, we have only two species (Plate III; Figure 7, D), the Tennessee Warbler *(Vermivora peregrina)* and Orange-crowned Warbler *(V. celata)* which, while clearly close relatives, are distinct well beyond the point of representing a superspecies (a possibility also precluded by their partial sympatry).

The Tennessee Warbler.—Thoroughly adapted to northern coniferous forest, the Tennessee Warbler, while breeding on the ground in *Vermivora* fashion, forages in the middle layers. Its staccato song is much like the Orange-crowned's but more emphatic and definite in form. It retains no appreciable connections in the eastern deciduous forest but its extremely long, presumably conservative, eastern migration route suggests a long eastern history. It shows no tendency toward geographic differentiation. Today, with its broad northern distribution, the species is in position to be disjuncted by subsequent glaciation. While it differs from the Orange-crowned in possessing a breeding dress modestly altered from the plumage assumed in autumn, the two birds in the latter plumage are remarkably similar. They differ slightly in proportions, the Orange-crowned having a relatively shorter wing and longer tail (appropriate to its much shorter migration). The Tennessee, unlike the Orange-crowned, lacks the orange patch typical of many of the genus.

The Orange-crowned Warbler.—In contrast to the Tennessee Warbler, this species inhabits brush and shrubby seral stages, sometimes riparian, in coniferous or mixed forest regions. A low ranger and, usually, a ground nester (occasionally nests in small trees up to 15 feet), it has a wide western range with four moderately distinct subspecies *(V. c. celata* in the north, east of Alaska and British Columbia; *V. c. lutescens, orestora,* and *sordida* in the west), suggesting a comparatively long western tenure. Eastward in the northern coniferous forest the species appears to be re-invading and has reached around James Bay. A western origin of these northern birds seems to be indicated not only by their distribution but also by their migration pattern (rather misleadingly stated by Bent, 1953:89). While some *Vermivora celata celata* do migrate through the east to winter homes in the Gulf States, as Bent says, they are a trickle in comparison with the flow that passes through the central and western states—here in Kansas, where I write, they are probably the most numerous migrant wood warbler — to winter in the southwest, Mexico, and Central America. In the north the species is broadly sympatric with the Tennessee Warbler.

Remarks.—No forms exist to suggest an early history relating the present group to the somewhat similar Nashville Warbler group. Neither are there enough species to permit a strong hypothetical reconstruction of past events. Nevertheless, the two species again recall the model.

Since their considerable differences suggest some remoteness of differentiation, I suggest that pro-*V. peregrina* early, perhaps in Yarmouth time, established by way of northern forests a western stock which upon isolation by Illinoian glaciation differentiated into pro-*V. celata. V. celata* now, perhaps for the first time, is accomplishing a re-invasion of the northern coniferous forest that is already sufficiently extensive to permit isolation by glaciation.

Any additional derivative species have been lost by extinction.

Other Northern Wood Warblers

A few species should be mentioned whose present distributions, adaptations, and similarities, while suggesting very little when the birds are considered singly, may assume some significance in light of all that has been said here.

There are morphological, behavioral, and ecological similarities between the Blackpoll Warbler *(Dendroica striata),* Bay-breasted Warbler *(D. castanea),* and Cape May Warbler *(D. tigrina)* that suggest they may be quite closely related (the resemblance, particularly of the first two, in autumn plumages is well known to banders, bird watchers, and others), and a hybrid between the first two is known (Brodkorb, 1934). Also, the celebrated "Carbonated Warbler" of Audubon has been thought to represent a hybrid Blackpoll × Cape May (for references see Cockrum, 1952:148). All are today restricted and highly adapted to northern coniferous forests, hence broadly sympatric. They are high rangers with thin, wiry songs dissimilar in form more than in quality. They nest variously from the ground (Blackpoll, occasionally) to very high (Cape May).

In terms of the model, it is conceivable that these species descended from a single eastern ancestor (could the Chestnut-sided Warbler, *Dendroica pensylvanica,* resemble this bird?) of the deciduous forest. Needed is only a history of adaptation, expansion, differentiation, re-expansion, etc., together with extinction of critical western differentiates and loss of eastern deciduous affiliations. We have seen evidence that all of these processes have occurred in various groups, and their occurrence in the right combination could account for the descent of the species here considered from a common ancestor.

Wilson's Warbler *(Wilsonia pusilla)* should be mentioned here also, because of its novel distribution. This distribution is unique in the family in embracing northern coniferous and western montane forests with no eastern vicariant species or well-marked subspecies. The northern race, *Wilsonia p. pusilla,* and the western montane *W. pusilla pileolata* are faintly marked and probably represent post-Wisconsin differentiation. The comparatively short migration route of the eastern race (no longer than that of the western one) and the distribution suggest that the northern range has been re-invaded from a western center of differentiation while the descendants of an eastern ancestral form are extinct. Neither congener *(Wilsonia citrina, W. canadensis)* seems close enough to qualify as such an ancestor.

Some General Considerations

It is further instructive to examine simultaneously the distributions of all the forms occurring in the areas considered, excluding a few kinds which are associated with grassy and shrubby environments, and whose distributions are unrelated to the thesis of this paper (e.g., the Yellow Warbler, *Dendroica petechia;* the Yellowthroat, *Geothlypis trichas;* the Yellow-breasted Chat, *Icteria virens,* which last may not be a warbler at all—Ficken and Ficken, 1962; and various southwestern, essentially Mexican forms such as the Red-faced Warbler, *Cardellina rubrifrons).*

Figure 8 shows graphically and Table 1 summarizes numerically the broad distributional relationships of the 46 wood warblers here considered, to the eastern deciduous, northern coniferous, and western montane forest regions. The figure illustrates a trend beginning with exclusive occupancy of eastern deciduous forest and ending with exclusive occupancy of western

TABLE 1

Summary of the Distributions of 46 Forest-adapted Wood Warblers

Distribution type	*Regions occupied**	*Number of species*	*Per cent of total*	*Number of species indigenous**		
				I	*II*	*III*
1	I	11	23.9	11		
2	I-II	14	30.4	14	14	1
3	I-II-III	1	2.2	1	1	
4	II	8	17.4		8	
5	III	10	21.7			10
6	III-II	2	4.4		2	2
Totals		46	100.0	26	25	13

*I = eastern deciduous forest; II = nothern coniferous forest; III = western montane forest.

montane forest, with many intermediate situations and a few (those representing probable eastward re-expansions) situations suggesting a weak reciprocal trend.

It is of particular interest to note (1) that 11 deciduous forest species, potentially eligible for coniferous forest adaptation, have not yet exercised their franchises; (2) the gradual apparent loss of deciduous forest distribution and (presumably) adaptation in at least 15 species now attaining coniferous forest distributions and adaptations; and (3), particularly, the distributions of those birds whose occurrence across the northern coniferous forest eminently qualifies them for disjunction should another glaciation occur and thus begin a sequence of events like that of the model. At least 14 species certainly (those occurring all the way across the northern forest), and some 10 more possibly (those occurring more or less half way across), are now "waiting in the wings," so to speak, for the opening curtain of the next glaciation.

Two additional points are emphasized by Figure 8.

(1) No endemic genus occurs anywhere except exclusively or almost exclusively in the eastern deciduous forest which has no less than four (I am aware of course that these "genera" are no better than our taxonomy, but they do stand for special degrees of distinctness). This seems surely to indicate antiquity of the formation—and to a lesser extent of the region itself—as a center of distribution of the family.

(2) *Only one of the 12 endemic and/or probably autochthonous species of wood warblers of the western montane forests is without an obvious vicariant* (e.g., modified descendant of a probable common ancestor) *in the eastern deciduous and/or northern coniferous forest.* (Only Wilson's Warbler, discussed above, provides an exception.) Conversely, *not a single eastern form that has not acquired extensive coniferous forest adaptations possesses a vicariant or vicariants in the western montane forests,* except the Yellow-throated Warbler. The peculiar circumstances concerning the last have been discussed above.

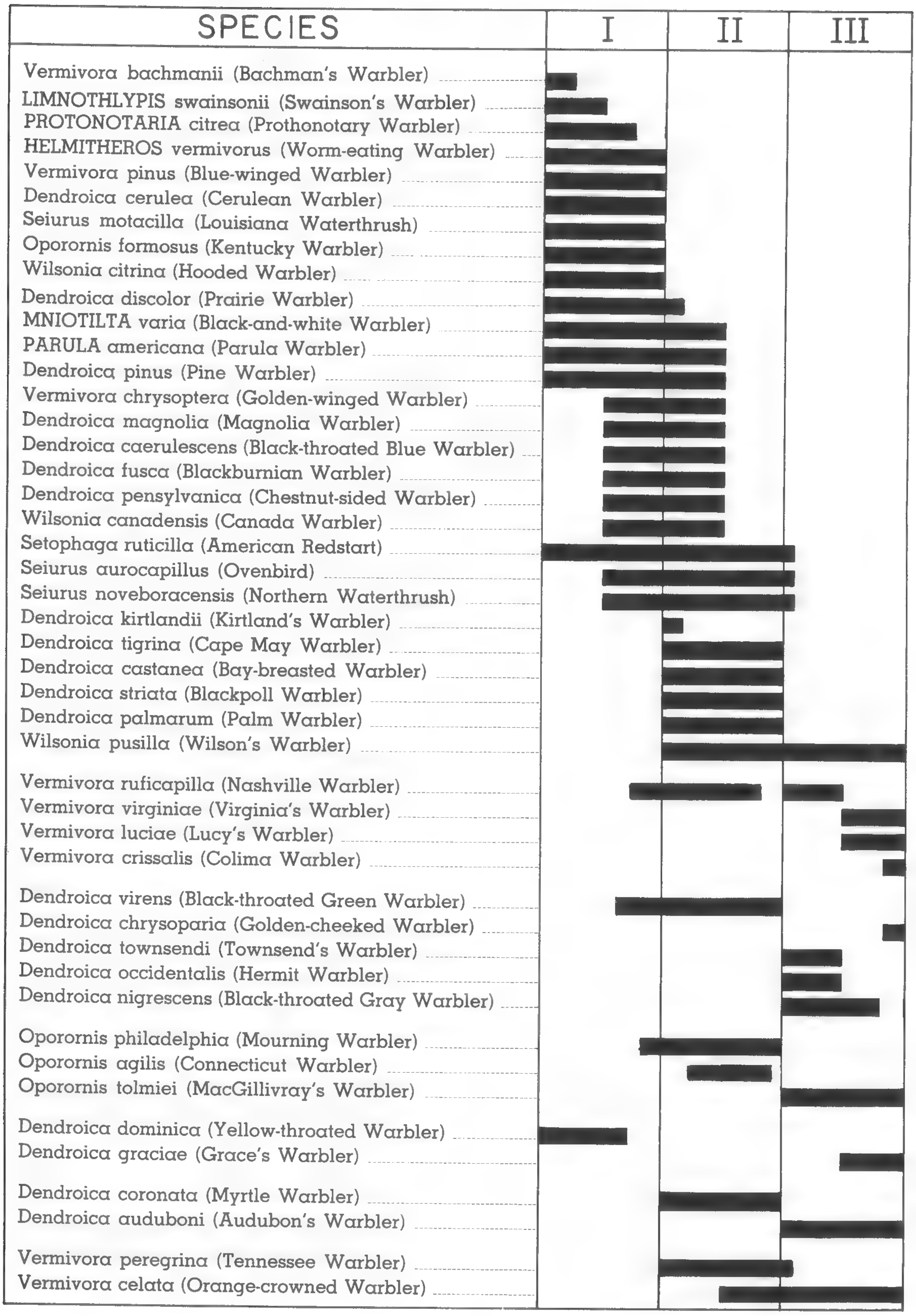

Figure 8. Generalized breeding distributions of 46 North American forest-adapted wood warblers in relation to the three great forest types of temperate and boreal North America (I, eastern deciduous forest; II, northern coniferous forest; III, western montane forests). Extension of a bar across a full column indicates occurrence through most or all of the region concerned; extension across part of a column indicates occurrence in part of the region, proximity to adjacent regions being indicated by the position of the bar. Genera set in capitals are endemic or nearly endemic to the eastern deciduous forest region. *Parula* is "endemic" only in the immediate context of the figure. The several species groups here discussed in detail are treated at the bottom and separated by spaces.

These are, then, additional indications of a broad, continental, historical pattern whose elements consist of (1) the eastern deciduous forest as an ancient center of wood warbler distribution and differentiation, (2) the northern coniferous forest as a recurrent corridor for expansion of species pioneering outward therefrom, (3) the western montane forests as a secondary center of distribution and (through glacial isolation) differentiation, and (4) the northern coniferous forest (more rarely) as a secondary center of differentiation for such western differentiates as again invade it only to be disjuncted once more by glacial advance.

Discussion

The model and some alternatives.—While this paper has been devoted particularly to suggesting the importance of the model and its northern route for western colonization, it would be a mistake, as already indicated, to explain all distributions in those terms. We have seen, in the case of the Yellow-throated-Grace's Warbler complex, species seemingly related historically not to northern forests but to woodlands derived from the old southern Madro-tertiary flora. Other wood warblers seem also to be related historically to this element.

The Parula Warbler *(Parula americana),* with both tropical *(P. pitiayumi)* and southwestern *(P. graysoni)* representatives, belongs here also, evidently. Other species that seem to belong with this group, although leaving no western representatives, are the pine and pine-oak inhabiting Pine, Prairie, and Kirtland's Warblers.

Numerous other members of the Madro-tertiary faunal element seem to have suffered disjunction as the once-widespread, southern woodland flora to which they were adapted was fractionated in the late Tertiary. For example, the Ivory-billed-Imperial Woodpecker group *(Campephilus principalis-C. imperialis),* with a West Indian representative of its own, is marvellously similar in distributional pattern to the Yellow-throated Warbler group, while less perfect parallels are offered by the scrub jays (Pitelka, 1951) and the pine-inhabiting pygmy nuthatches *(Sitta pygmaea, S. pusilla)* and certain ladder-backed woodpeckers *(Dendrocopos borealis, D. scalaris-D. nuttalli).*

In general, the more likely descendants of this Madro-tertiary fauna (for a list of some see Kendeigh, 1961:298) seem to have shown little tendency toward adaptation to northern coniferous or western montane coniferous forest, and the fauna has consequently had little success in northern colonization (Parula, Pine, and Kirtland's Warblers have done comparatively well in this direction).

It is probable, however, that not all species originally stemming from Madro-tertiary associated faunas have yet been identified. Some, perhaps early arrivals in the southeast, may early have been incorporated into the Arcto-tertiary forest community.

I have already indicated that Lucy's Warbler in the Nashville Warbler group and the Black-throated Gray Warbler in the Black-throated Green Warbler group may indeed be relicts resulting from the early (probably pre-Pleistocene) disjunction of a Madro-tertiary ancestor. The eastern differentiates, pro-*V. ruficapilla* and pro-*D. virens,* in such case, proceeding thereafter to follow the course of the model, would seem to be unique among descendants of the Madro-tertiary faunas in their exploitation of northern coniferous forest environments.

Some evidence in support of this line of thought may be that the Nashville

Warbler (like others of its group) is adapted to seral stages *in,* but not really *to,* northern coniferous or montane forests as such, as well as to edge situations in mixed deciduous-coniferous forest in the northeast. Likewise, the comparatively narrow niches (especially hemlock growth but including pine and pine-oak in some areas) occupied by the Black-throated Green Warbler in the eastern deciduous forest region may lend some support to this theory, as does the peculiar cedar brake, oak-scrub habitat of the very similar Golden-cheeked Warbler.

We must, further, not suppose that even both of the above-mentioned processes (Arcto-tertiary origins, northern route; Madro-tertiary origins, disjunction of a southern ancestor), singly or in combination, account for all northern, late Cenozoic wood warbler differentiation. Various cases seem to fall wholly outside the framework of the present discussion. For example, Short (1963) has provided a tempting hypothesis for Pleistocene isolation and differentiation, in the *east alone,* of the Blue-winged and Golden-winged Warblers, and similar processes, even if obscure, may have accounted for additional speciation.

(It is, finally, not inconceivable that one or two species have made the adaptation *directly* from western Madro-tertiary woodland affiliations to western montane coniferous forest environments—the strange little Red-faced Warbler of southwestern mountains is a likely candidate—but indications are that this must have happened very rarely indeed and with limited success.)

Ecological considerations.—Emphasis thus far has been zoogeographical, that is, upon the trends and distributions of species. It should not be overlooked, however, that the zoogeographical trends of expansion and adaptation of species from deciduous to coniferous forest, hence northward and westward, is reflected ecologically by a marked gradient in population densities. As individuals, wood warblers, among the most numerous birds in typical eastern forests (including the northern coniferous climax in its eastern portion), are comparatively scarce in western coniferous forests, and progressively so with increase in elevation. There is thus a clear gradient in their population densities across the northern coniferous forests. This is inversely correlated with a trend in the densities of the cold-adapted Eurasian autochthones such as the tits, nuthatches, cardueline finches, and kinglets (Snyder, 1950), which historically may have been competitors for space in these coniferous forests.

In this connection, it may be supposed also, as more and more wood warblers have made the postulated adaptations and ventured with varying success across the northern route, that the process would become increasingly difficult when new pioneers encountered more and more well-entrenched predecessors. Thus we may well marvel at the capacity of the group at subtle niche diversification permitting extensive sympatry of nearly related forms, as shown specifically by MacArthur (1958) and demonstrated generally by the presence in some Appalachian regions of as many as 17 breeding species in a few square miles of comparable elevation (pers. obs.).

Equally, it seems that the tasks of western differentiates recrossing the northern route eastward would be especially difficult for the same reasons, since more and more potential competitors would be encountered in progressing toward the east. This may account in part for the apparent rarity of the event. Also, it should be recalled that (a) the supply of western species is much smaller; (b) they tend to be isolated by elevation during interglacial optima; and (c) their adaptations to the comparatively specialized montane environments may have unfitted them for recolonization of northern coniferous forest. It is perhaps significant that those forms which seem most likely to have accomplished eastward re-invasion (Orange-crowned, Wilson's, and Mourning Warblers) are adapted to seral stages, which are well known (Pitelka, 1941:131; Odum, 1945:198) to be more uniform in type than are climaxes, and which likewise are less liable to interglacial, montane isolation.

The origin of the Parulidae.—A few remarks on the history of the family may be ventured. The origin of the family in the North American tropics was postulated by Lönnberg (1927) and reaffirmed by Mayr (1946:21-22). Characteristics of the group here brought into focus support this hypothesis and, additionally, suggest a little about the timing of this origin.

If the Parulidae had been in existence and very early adapted to the temperate or (especially) boreal elements of the Arcto-tertiary forests, it would be remarkable not to find some of them in Asia, and many more than we do in western North America. We must, therefore, suppose that the group, arising from Neotropical-tertiary and Madro-tertiary forests, began its adaptations to the temperate Arcto-tertiary forests after these forests had been fractionated by climatic deterioration and mountain-building. This process of fractionation began in the Miocene and gained impetus through the Pliocene.

At the same time, however, a comparatively early appearance (e.g., probably by the early Pliocene) of the group, in considerable force, in the temperate Arcto-tertiary forests is still indicated. Otherwise it is difficult to account for the abundance of species and genera restricted today and exclusively adapted to the remnantal eastern deciduous forest; invasion of this forest from more tropical formations would have become increasingly difficult for tropical forms and, by late Pliocene time, highly improbable as the deciduous forest became isolated by broad grasslands and other xerophytic formations extending to the Gulf of Mexico.

All of this seems to point to an early mid-Tertiary origin of the group (perhaps in the late Oligocene or early Miocene) in Neotropical-tertiary and perhaps Madro-tertiary forests of southern North America, with the more progressive and rapidly evolving members invading the shrinking Arcto-tertiary forests in the later part of the mid-Tertiary (late Miocene, early Pliocene), where they were to await the advent of the Pleistocene before embarking upon the radiation postulated in this paper.

Here it is tempting to theorize, invoking "Matthew's hypothesis" (Matthew, 1939: many pp., but see especially 140-144), that it is just in these Arcto-tertiary forests, near the end of the Tertiary, that we should look for those progressive and adaptable members of the group most capable of evolving in the face of changing conditions and of capitalizing upon the evolutionary opportunities stressed in this paper. The less plastic and more primitive members of the group would have retreated deep to the south where, perhaps, we find them today in the form of such genera as *Basileuterus, Euthlypis, Granatellus, Myioborus,* etc.

Miscellaneous observations.—Various elements of the evidence here considered provide indications of possible significance to other aspects of Pleistocene biogeography.

For instance, while I readily grant that circularity of reasoning is being skirted, the pattern of western differentiates here indicated (in which several degrees of distinctness are discernible, suggesting varying antiquities of disjunction and hence repeated use of the northern route of the model) seems to argue that the northern coniferous forest as we know it today, or nearly so, may in fact be considerably older than the Wisconsin glacial retreat. This is a logical enough assumption and one made by many authors but, because of the tendency of each glacier to eradicate the underlying tills of its predecessors, there is still little concrete evidence for it (Braun, 1950:511).

Likewise, the survival of a comparatively unmodified array of Arcto-tertiary temperate elements over much of the southeastern glacial refugium throughout the Pleistocene is strongly suggested by the number of surviving parulids fully adapted and solely or largely restricted to the eastern deciduous forest of today. While a whole essay could and should be devoted to this subject, it is here possible only to say that it is extremely difficult to imagine this large, diverse, and closely-adapted fauna gaining its present distribution and degree of adaptation since the Wisconsin, much less regaining these three or four times. Thus Deevey's view (1949:1371-1375) *contra* Braun (1947; 1950: 512-520; 1955) that the Arcto-tertiary temperate (=mixed mesophytic forest of today *sensu* Braun, 1950:39-121) was radically altered throughout, if not essentially obliterated as an integral community, by invasion of northern floral elements during glacial maxima seems less plausible than the slightly more moderate view of Martin (1958:383, Figure 2), and than the still more moderate compromise indicated by Kendeigh (1961:285, Figure 21–2).

Antiquity of speciation.—Finally, all of the evidence presented suggests that Wetmore's statement (1959:21-22) that most modern bird species were probably already in existence at the beginning of the Pleistocene needs modification, at least with reference to the higher passerines, and especially those of northern distribution. In the present case the suggestions are that at least 10 (22 per cent) and possibly as many as 17 (37 per cent) of the 46 species of continental wood warblers here considered have achieved their specific distinctness directly as a result of Pleistocene events.

This number might well be greater were it not for the probability of many extinctions. We see that today four species of wood warblers considered are relicts liable to extinction with the slightest unfavorable turn of events (Kirtland's, Golden-cheeked, and Colima Warblers, and the previously-unmentioned Bachman's Warbler, *Vermivora bachmanii*). Allowing four extinctions per glacial cycle, it is possible that there are today no less than 12 ghosts in the parulid fauna of North America; how much the distributions and characters of these spirits might tell us, if they were living birds!

In Summary

The distributions and relationships of 46 continental and 2 insular species of forest-adapted wood warblers are considered in relation to the Tertiary and Pleistocene history of North America, and the implications to Pleistocene biogeography in general are briefly discussed. The following hypothesis is developed and defended.

At the close of the Pliocene there were two elements in that part of the family Parulidae occurring in North America: A large, more northern element adapted to the remnantal temperate (deciduous) Arcto-tertiary forest in eastern North America and a smaller, more southern element adapted to recently disjuncted western and eastern sclerophyll woodlands derived from the Madro-tertiary (relatively xerophytic deciduous) flora. Some species, notably Grace's Warbler and possibly the Black-throated Gray and Lucy's Warblers owe their differentiation from eastern stocks to the latter disjunction.

With the advent of Pleistocene glaciation, boreal (northern coniferous) elements of the Arcto-tertiary forest were forced deep into the southeast, invading a compacted temperate Arcto-tertiary forest (henceforth equated with today's eastern deciduous forest) and permitting development of adaptations to coniferous forest or its seral stages by some of the wood warblers living there.

Upon glacial recessions, broad, transcontinental bands of boreal Arcto-tertiary forest (henceforth equated with northern coniferous forest) were established in the wake of the retreating ice (western montane coniferous forests similarly replaced the mountain glaciers) and these were occupied by the newly-adapted wood warblers. These birds thereby achieved immense, continent-spanning ranges (comparable to many seen today) that permitted disjunction of the stocks into separate eastern and western refugia upon subsequent glacial advance. Differentiation occurred in these refugia, and some western differentiates were further isolated, during the warm interglacial periods, in western montane coniferous forests as these withdrew up the mountain slopes into separate "islands." Other, though fewer, western differentiates re-invaded the northern coniferous forest and again achieved wide distributions, only to be disjuncted once more.

Repetition of this process through four glacial cycles resulted in the differentiation of all or nearly all of the endemic and/or autochthonous western species of wood warblers (aside from Grace's Warbler) of which 12 survive (others have probably become extinct). These are: the Townsend's, Hermit, and possibly Black-throated Gray Warblers of the Black-throated Green Warbler group; the western race of the Nashville Warbler, and the Virginia's, Colima, and possibly Lucy's Warblers of the Nashville Warbler group; the MacGillivray's Warbler of the Connecticut Warbler group; Audubon's Warbler of the Myrtle Warbler group; the Orange-crowned Warbler of the Tennessee Warbler group; and the Wilson's Warbler. The Golden-cheeked Warbler of Texas was separated and differentiated from the ancestors of the Black-throated Green Warbler recently, probably since the Wisconsin (most recent) glaciation.

Possibly the Blackpoll, Bay-breasted, and Cape May Warblers are products of similar processes, but descendants of very probable ancestors adapted to eastern deciduous forest are lacking and possibly extinct.

The eastern Mourning Warbler seems likely to be descended from a western differentiate (e.g., the fore-runner of MacGillivray's Warbler) re-invading eastward, and the Myrtle Warbler may be also. The Orange-crowned and Wilson's Warblers are today evidently re-invading eastward from western centers of differentiation, but the latter leaves no eastern vicariant, being, in this respect, unique among western wood warblers.

The eastern forms descending directly from the eastern ancestral stocks responsible for the several westward invasions (Black-throated Green, Nashville, Connecticut, possibly Myrtle, and Tennessee Warblers) have tended progressively to lose their original deciduous forest adaptations and distributions. This is true also, to usually lesser but varying degrees, of at least 15 species currently invading the northern coniferous forest and liable themselves to disjunction and differentiation in case of subsequent glaciation.

The differentiation of between 10 (22 per cent) and 17 (37 per cent) out of 46 species indicates a high rate of Pleistocene speciation in the northern Parulidae and suggests that higher passerine species formation may have been more extensive in the Pleistocene than has heretofore been thought.

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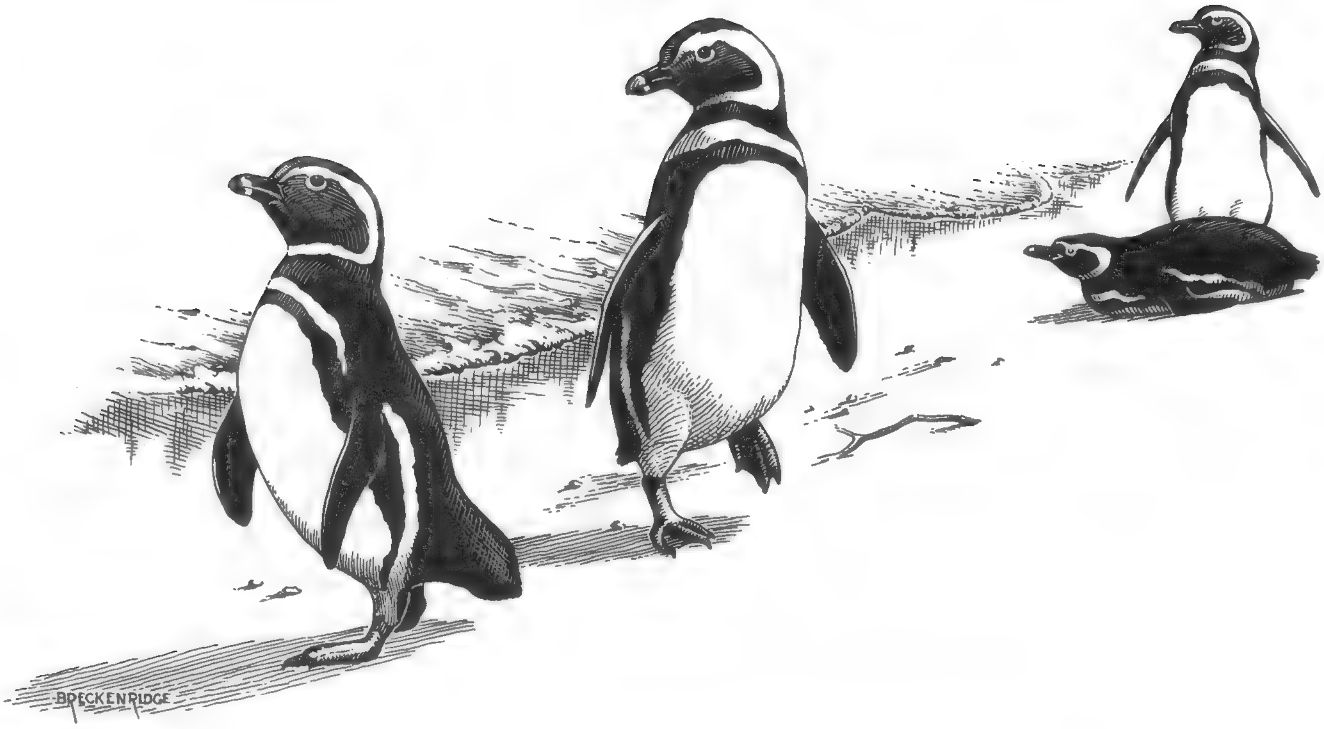

Jackass Penguins. Drawing by W. J. Breckenridge

PENGUINS ASHORE AT THE FALKLAND ISLANDS

OLIN SEWALL PETTINGILL, JR.

Photographs by the author, courtesy of WALT DISNEY PRODUCTIONS

Penguins are dual personalities. In the sea they are the most supremely aquatic of all birds. Their bodies, densely and uniformly covered with sleek, scale-like feathers, are the shape of torpedoes. Their wings, reduced to strong flippers, are efficient and powerful propellers. Their short tails and their legs set far back on their bodies are steering devices. Thus equipped, penguins not only swim under water at speeds estimated at 25 miles an hour but, unlike other aquatic birds, they "porpoise" by alternately shooting above the surface to breathe and diving below to swim.

On land penguins are among the most awkward of all birds. The shape of their bodies and the position of their short, stubby legs compel them either to stand upright like a man and walk with a clumsy gait or, when in a hurry, to "toboggan" by dropping on their bellies and using "all fours"—kicking with their feet and "rowing" with their flippers. Their near-sightedness, the result of a vision better suited to water than to air, tends to accentuate these movements to the point of comedy.

The presently-existing 17 or 18 species of the family of penguins (Spheniscidae) are generally uniform with respect to body form and locomotion. Nevertheless they show varying adaptations in action and behavior to the land environments they choose for nesting purposes. This is clearly the case with the three species of penguins breeding in the Falkland Islands.

The Falkland Islands and Three Species of Penguins

The Falkland Islands lie in the South Atlantic, 800 miles north of the Palmer Peninsula of Antarctica and 300 miles northeast of the southern tip of South America. Two main islands, East Falkland and West Falkland, and well over 100 smaller islands and islets comprise the 4,618 square miles of land surface. The shores of the larger islands vary from broad beaches rising to meet an undulating, grassy interior where sheep graze to bold, rocky headlands and steep, sometimes perpendicular, cliffs. Except in the many fiord-like harbors and narrow, inter-island channels, these shores are continually lashed by winds and pounded by mountainous surf.

Reaching these exposed shores, landing and loitering, proceeding inland to nest, and returning to the sea are three species of penguins, the Gentoo *(Pygoscelis papua)*, the Rockhopper *(Eudyptes crestatus)* and the Jackass or Magellanic *(Spheniscus magellanicus)*. The Gentoos come ashore principally

Figure 1. Gentoo Penguin. A bird-of-the-year photographed in early March.

on the sandy beaches—in any case, on shores of moderate incline from the surf—that adjoin grassy slopes over which they pass to the nesting colonies. The Rockhoppers, whose colonies are on the face and brows of cliffs, or on steep talus slopes—all rising directly from the sea—come ashore on those adjacent rocks or ledges that provide access to their nests. The Jackass Penguins come ashore on sandy or pebbly beaches leading up to peat-blanketed slopes in which they have excavated their nesting burrows. The nesting season for all three species extends from early October to March with the Jackass Penguin nesting a little earlier than the other two.

During our five months in the Falkland Islands, October 1953 to March 1954, Mrs. Pettingill and I spent many hours watching and filming these three species of penguins as they emerged from the sea and proceeded to and from their nests. The purpose of this article is to report some of our observations on their actions and behavior in this phase of their lives ashore.

The Gentoo Penguins

The Gentoos, standing about 30 inches high, are not only the largest of the three species of penguins in the Falklands, but they are by their very nature the closest to the penguin stereotype (Figure 1). On level ground they walk deliberately with short strides, lifting their feet high and swaying lumberingly with each step, the head forward and flippers up and far back as a counterbalance. They can jump—if they have to—across a ditch or up or down a cut in an embankment, provided the distance is no greater than 12 to 15 inches. However, before making any such jump, regardless of how often they have jumped before in the identical spot, they hesitate and inspect the situation carefully by bending forward and peering down—far down—to accommodate their near-sightedness. (After viewing my movies of Gentoos jumping across a small ditch, a middle-aged woman remarked that she now knew just how she looked while using her new bifocals to guide her steps on the stairs.) The jump itself, once undertaken, is a matter of jerking upright, springing with both feet together, and coming down "flat-footed." This is the total extent of the agility of the Gentoos on land and accounts for their avoiding as much as possible any rough terrain.

We found the Gentoos consistently gregarious throughout the nesting season, one bird rarely being separated from its fellows by more than a few feet at any time. This was true at Rabbit Cove on East Falkland (Figure 2) where we watched groups arriving from the sea and moving along the trail to the colony of about 300 breeding pairs on Sparrow Point (Figure 3). The birds, now and then alone but more often in loose groups of from several individuals to a dozen or even more, first appeared out in the cove, porpoising shoreward. Once within 50 feet of the beach and just outside the breaking waves, they dived below the surface; if we saw them at all, they were merely black streaks between waves until they literally exploded out of the surf, a foot or more clear of the water, and landed on the beach, sometimes upright, sometimes on their bellies, occasionally tumbling and somersaulting. They recovered their composure quickly and hurried — tobogganing when alarmed — to a very special section of the broad beach where others of their kind were standing and where they almost invariably stopped to rest.

Whenever a Gentoo found itself alone because it landed on the "wrong" section of the beach or if it had dozed and the others had walked off to the nesting colony without it, the bird, obviously disconcerted, hastened to find company somewhere or returned to the sea.

Figure 2 (*above*). Gentoo Penguins arriving at Rabbit Cove prior to moving along the trail to the nesting colony on Sparrow Point.

Figure 3 (*below*). The nesting colony of Gentoo Penguins at Sparrow Point. The town of Stanley is in the background, extreme left.

The duration of the rest period varied from a few minutes to half an hour or even longer. Nearly always the birds preened; some of them slumped, sleeping on their feet; occasionally, in the middle of the day, a few lay down on their bellies and slept while the sand, driven by the constant wind, drifted across them. In general the birds were docile and showed little if any hostility toward one another although each bird was careful to keep its "individual distance." Once in a while a bird trumpeted; otherwise the gathering was quiet. At times it seemed that a single trumpet was a signal for the start of the long trek to the colony.

The departure on the trail to the colony appeared to depend on the size of the resting group. When the number of birds on the beach reached about 30, and more were arriving steadily, a minimum of from 10 to 12 broke away and started up the trail. Between 4:30 and 5:30 PM on 28 October, 115 birds came ashore and groups departed for the colony at between five and ten minute intervals.

Movement toward the trail was begun by one bird, usually one of the last to arrive from the sea. Passing through the group on the beach and perhaps trumpeting once, it was followed immediately by others, each falling in line single file and more or less the same distance apart. It was unusual for the entire group to join the procession.

The mile-long trail to the colony traversed grass-covered ground most of the way, first going directly inland along a valley, then circling upward over a hill of gradual incline and back to a knoll on Sparrow Point, 200 feet above the sea, less than a quarter of a mile from where the trail started.

The trail, even without the Gentoos on it, was clearly marked. From a distance its course up the gentle slope was bright green where the grass, nurtured to lushness by the birds' excrement, stood out against the uniformly-gray hillside. Close up, the trail was slightly sunken and, where it crisscrossed up a peat embankment, was deeply sunken and well worn. There was every evidence that the trail had been used for many years. Although the Gentoos move their colonies slightly each year, they keep them in the same vicinity and reach them by the same path most of the way.

We found that the birds on the trail were usually wary and never permitted us to come as close to them as when they were on the beach or in the colony. At the same time they showed a reluctance to leave the trail, running from us up or down it, depending on the direction of our approach. When we deliberately blocked their passage in both directions, the birds left the trail helter-skelter in all directions, running and tobogganing in complete disarray. As soon as we moved away, the birds came back directly to the trail before continuing up or down—in whichever direction they were headed in the first place. It seemed to us that the Gentoos "knew" only one way to reach the colony and return to the sea, and that was by the one trail. Off the trail they appeared bewildered and confused.

The Gentoos proceeded down the trail in groups just as they started up. Where the trail left the colony, a group gathered slowly and finally started to leave single file. No concern or hostile attitude was evident as one group of birds met and passed another on the trail which was wide enough to permit two birds to pass without touching.

Travel on the trail was featured by stops for rest at varying intervals, the birds standing quietly. If, while one group rested, another caught up, the arrival of the second group often started the first moving again. Rarely did one group overtake and pass another. Occasionally, when a group became

Figure 4 (*above*). Young Gentoo Penguins of the year undertaking one of their first adventures in the sea. Photographed in early March.

Figure 5 (*below*). Young Gentoo Penguins of the year at the edge of the sea.

alarmed—at us, a sheep, or most anything—and halted, one bird, trudging on behind and unaware of possible trouble, simply kept on walking past the motionless birds which promptly "came to life" and plodded after it.

The Gentoos did not travel on the trail by night, but all during the day groups paraded up and down at irregular intervals, except in the first hours of the morning when many groups went down and in the last two or three hours of the day when many groups went up. In the early morning or the late afternoon the groups followed one another so closely that the trail looked from afar like a black-and-white ribbon resting loosely on the gray-green moor.

Groups arriving on the beach from the trail usually went directly into the water. As a rule, on nearing the surf they began to run and, once in the water halfway to their flippers, plunged forward into the waves and disappeared, to start porpoising shortly thereafter in deeper water. Less commonly the birds walked in slowly—sometimes stopping to drink on the way—and settled on the water. When the birds were frightened and fled to the water, they often swam about on the surface like ducks but lower in the water with just their heads showing appreciably.

Groups of young Gentoos in the colony, once fully grown and having shed their down, found their own way to sea during mid-day by proceeding directly down the step-like ledge shelves to the uniformly rocky shore, only 300 to 400 feet from a colony. Here they splashed about in the tidal pools and waded into the surf but did not swim away. (See Figures 4 and 5.) In the late afternoon—the time when the majority of adults return from the sea to feed their young—they worked their way back to the colony to meet the adults coming up the trail. On successive days the young Gentoos repeated this performance, each day going farther into the surf and eventually swimming beyond it.

These first sea adventures were undertaken in groups of several dozen each. The birds in each group stayed close together, moving into the sea and returning to land in tight bunches. Rarely was one bird farther from his group than two feet. Generally we could approach the young birds on the rocky shore more closely than we could approach the adults on the sand beach. Once, while we were watching a group in the surf, a low-flying plane (a rare event in the Falklands!) caused panic among the young Gentoos which ran, fell, splashed, and otherwise stumbled ashore. Their instinctive reaction was to seek the shore, not the sea. This behavior has been noted in Gentoos under different circumstances by Murphy (1936) and others. The common explanation for resorting to land when alarmed is that the principal predators on adult penguins (e.g., sea lions, *Otaria byronia*) lurk in the sea.

We concluded from our observations that at least a large proportion of young Gentoos reached the sea by direct route—that is, by going down over the ledges—instead of following the trail used by their parents. We saw no young birds on the trail to the beach, but we are unable to say that none took it since we did not follow activities in the colony during the last days that young birds were present.

The location of the Gentoo colony at Sparrow Point, high on a knoll, is a good example of the Gentoo trait called "mountaineering" by Murphy (1936) who was impressed with the habit at South Georgia. The Adélie Penguin *(Pygoscelis adeliae)* is reported to have the same habit (e.g., see Levick, 1914). We found a more extreme instance, in the Falklands at New Island lying off West Falkland, of a colony numbering about 50 pairs on the summit of a 600-foot hill on the west side of the island, reached by the birds over a trail that began on the east side, wound up through a valley, and then up the final slope

Figure 6 (*above*). A pair of Rockhopper Penguins standing on the rim of a shag nest, Kidney Island.

Figure 7 (*below*). Rockhopper Penguins nesting on a talus slope—a small part of the colony of 20,000 pairs at New Island.

of the hill. The course taken by the trail seemed to be by way of the incline with the least gradient.

Why should Gentoos establish their colonies on such high ground when there are many available areas nearer the sea that would require much less effort to reach? Safety to their nests cannot be a selective factor because the only predator on their eggs and young is the Skua *(Catharacta skua)* which can attack them anywhere on land. The only answer so far put forward is by Murphy (1936) who speculated that the species clings to an inherent habit of climbing to the bare ridges between ice-filled valleys during the last period of glaciation.

The Rockhopper Penguins

Rockhopper Penguins (Figure 6) are not only smaller than Gentoos, standing about 15 inches high, but are livelier and more agile in all their actions. As their common name implies, they have, beside a forward-walking gait, a method of progression by jumps, with feet together, which are like those of a man in a sack race (Murphy, 1936). No doubt such locomotion, coupled with the sharp nails on their toes, is an adaptation for maneuvering over rocks and abrupt, rocky inclines. Certainly hopping on level ground is of no benefit. We have movies showing Rockhoppers hopping and walking side by side with no difference in forward speed. Flippers during locomotion were held out from the sides and down when walking, forward and down when hopping.

Our principal observations on Rockhoppers were made at New Island, where 20,000 pairs nested in a colony on the upper slopes of several rock-strewn bluffs, 200 to 300 feet above the sea. (See Figure 7.) Below the colony and between it and the sea were west-facing perpendicular cliffs, cutting off access from the sea except through two steep ravines.

Landing places for the Rockhoppers were several jagged ledges and gigantic slabs of rock that tipped sharply into the sea, like ramps, from the wide shelf at the base of the cliffs. No spot could be considered a beach or a shingle in any sense of the word. Below the high-tide mark were thick mats of stringy kelp. Against these landing places the sea, constantly whipped by the ever-prevalent westerly winds, often at gale force, surged and crashed, sending up great geysers of spray. At no time, however, were the swells mountainous enough to prohibit the Rockhoppers from coming ashore or departing.

Like the Gentoos, the Rockhoppers were consistently gregarious in all their actions and never more so than when coming to land. Offshore we would discover a tightly-knit group porpoising toward a favorite ramp, then suddenly vanish below surface to appear far offshore. Again they headed for the ramp, again they retreated. There were many such starts, especially if the sea was running high. What prompted the ultimate "decision" to come to land we could never determine, but it was made in due course. On the crest of a breaking wave, or in front of it, they began the dash to the ramp, shooting as high as four feet clear of the water, with flippers beating the air, and then plopped on the ledge or in the kelp, feetfirst if they were lucky but more often on their bellies. Recovering instantly, they started hopping like so many jumping beans to reach high ground before the next breaker. Almost invariably a few of the birds mismanaged their landing by getting entangled in the kelp, by failing to jump clear of the wave, or by not getting far enough up on the ramp, whereupon they were at the mercy of the next breaker and soon overwhelmed under an avalanche of white water and pulled by the undertow

Figure 8 (*above*). Rockhopper Penguins at New Island resting briefly on ledge above the surf after their return from the sea.

Figure 9 (*below*). Rockhopper Penguins at New Island starting to move onto the trail leading up to the nesting colony.

back into the sea. But no matter, they eventually emerged on the back side of the spent wave and renewed their struggle toward the ramp. Rockhoppers, we realized, are no more harmed by tempestuous surf than flying birds by raging winds.

The size of the groups coming ashore tended to be governed by the height and ferocity of the surf; thus, the greater the surf, the larger the group. With moderate surf, the groups ranged from two or three dozen to a hundred in size, but with surf lashed by stormy winds the groups numbered several hundred individuals. During the height of a gale I estimated as many as 1,500 individuals in one collective dash to a ramp. The larger group usually resulted when smaller groups, returning successively from the sea, caught up with one another offshore and joined together as they hesitated with repeated starts and retreats before committing themselves to the final land-bound rush.

The presence of sea lions—or just one—offshore from a landing ramp was sufficient to cause delay in coming ashore and the build-up of a large group of Rockhoppers from several smaller aggregations. Until the sea lion disappeared, the birds remained far out—porpoising about in circles, rarely if ever idling on the surface—waiting.

Once on the ledges above the surf (Figure 8) the Rockhoppers rested briefly, shaking water from their heads, flippers, and tails, and preening. Then the procession to and up the ravines began (Figure 9), most of the group participating. As the trails narrowed, they moved single file.

Both trails passed over hard, sedimentary ledges and loose rocks whose upper faces were often tilted at a near-perpendicular angle and had deep, vertical scars or grooves formed by the nails of the Rockhoppers, no doubt by the yearly passage of millions of them over many centuries (see Figures 10, 11, 12, and 13).

Watching the Rockhoppers climb these ledges, we noticed that they used their slightly-hooked beaks as well as their nails for holding on to the surface when it became excessively steep. We observed too that they could climb more effectively by hopping than walking, gaining as much as 10 to 12 inches per hop—provided that their nails were sunken firmly in grooves so as to prevent any slipping backward.

Where rocks on the trail were piled one upon the other in step-like recession, the Rockhoppers were able to hop from one up to the other, if the height of the step was no more than 12 inches.

The birds were not especially wary of us if we sat quietly or moved slowly. Almost at our feet they went by unconcernedly, intent on their business of climbing which required great effort. In the sheltered ravines any appreciable sunlight caused them to breathe audibly, even pant, and to sneeze frequently, clearing the rapidly-accumulating moisture in their throats. If we intentionally disturbed them, by coming quickly down on them from above, they panicked instantly, jumping, slipping, and tumbling down the trail in a general pile-up which soon blocked passage of birds coming from behind. As soon as we drew back up the trail or sat still, the procession began again as if nothing had happened.

Much of the activity on the trail was similar to that of the Gentoos. The birds stayed in groups and moved single file. Passage took place only in the day and it was sporadic except in the early morning when it was heavy going down and in the last two to three hours of the afternoon when it was heavy going up. Birds going down and up passed one another without incident.

Figure 10. A small nesting colony of Rockhopper Penguins (upper part of photograph) at Land's End, New Island. The trail to the colony leads from the landing ramps (lower right) up and across the face of the cliff.

Figure 11 (*above*). Rockhopper Penguins walking up a ledge on the trail to the nesting colony.

Figure 12 (*below*). Another view of Rockhopper Penguins on the same trail. In both views, the ledges have been scarred by the birds' nails.

Figure 13. Detail showing the scars on a ledge, made by the nails of Rockhopper Penguins.

The trip down the trail involved considerable jumping from step down to step. Where the birds had to climb by beak and nail when making their ascent, they frequently stood sidewise and slid down on their feet, one foot in advance of the other, while keeping the body upright all the while.

Once down the trail and on the landing rocks, the Rockhopper group chose to go into the sea by different ways, depending on the state of the surf. If the surf was running high, they walked out onto rocks or ledges that rose straight up above the surf, sometimes as high as 10 feet. From here they jumped either feetfirst or, less commonly, headfirst. The act of plunging was almost always preceded by long periods of hesitancy during which the birds went to the edge, looked down, stepped back, rested, looked down again, and so on. At long last, one bird dropped off and the others followed en masse. By contrast, if the surf was moderate, the Rockhoppers went to the landing ramps and ran down into surf, a feat they could not accomplish when the surf was mountainous since they would have difficulty entering the water before being swept back on the ramp.

Adélie Penguins enter the sea, usually from shelf ice, by diving headfirst (Sladen, 1958). Murphy (1936) asserts that Rockhoppers are unlike the Adélies in this respect, jumping feetfirst instead. However, as I have stated above (and shown on motion-picture film), Rockhoppers are apparently quite versatile, being accustomed to jump or dive as they choose.

The broad shelf below the cliffs proved to be a loitering area for many Rockhoppers. Some were obviously yearling birds, others may have been adults "unemployed" during the current nesting season. In any case, this was a site of much activity. Where there were depressions in the ledge shelf, fresh water collected after rains. In these pools the loiterers frequently bathed together, splashing water over themselves with their flippers, diving as deeply as the pool would permit, and now and then playfully chasing one another. Certain individuals repeatedly ran into a pool and swam across it, splashing all the way, and returned. We saw several birds take long drinks of fresh water, others pick up pebbles on the edges of the pools and swallow them.

Probably the most astonishing sight were Rockhoppers standing in turn under a tiny stream of water that spilled down from an overhanging face of a cliff. As the water fell on their backs they went through numerous preening and bathing movements, fanning their flippers, in an obvious state of physical satisfaction.

Adjacent to the Rockhopper colony at Kidney Island (Figure 14), which we studied for several periods during the nesting season, was a loitering area on a roof-like ledge, its slopes etched with numerous horizontal ridges on which the birds stood, slept, and preened—just passing time. Here, more than in any other situation, we noticed a preference among penguins for individual distance, each bird occupying a position just beyond the reach of its fellows. We called the area the "Rockhopper Club" as all available standing spots were usually occupied and membership seemed exclusive. Many a penguin on entering the club with the intention of loafing was soon rejected by jabs and whacks from unfriendly beaks and flippers—all for the simple reason that it could not find a spot with proper isolation.

Jackass Penguins

The Jackass Penguins (Figure 15), intermediate in size between the Gentoos and Rockhoppers, were no less distinctive in their locomotion on land. Like the Gentoos they walked with high, short steps but swayed only slightly side to side; at the same time they stooped forward (like a man with a bad case of lumbago) and kept their flippers either at the sides or a bit forward. They were more agile than Gentoos, less so than Rockhoppers. When tobogganing they proceeded speedily by running on the tips of their toes and flippers, bellies clear of the ground.

Besides their manner of locomotion, another distinctive action of Jackass Penguins, shared by all members of the genus *Spheniscus,* is that of swaying or weaving the head from side to side, peering first with one eye and then the other, at any object close to and directly in front. This, as Murphy (1936) has explained, is because the head is "wall-sided" and the eyes therefore cannot "point forward in bifocal vision."

Jackass Penguins were similar to Gentoos in coming and returning to the sea. They chose mainly beaches and seldom attempted to maneuver over rough terrain.

Unlike the Gentoos and Rockhoppers, Jackass Penguins were conspicuously gregarious only on the beaches or loitering grounds and in the sea. In nesting, they showed little tendency to colonize—that is, to nest close together and to participate in concerted activities. At New Island we noted some pairs occupying burrows, generally widely spaced, on the same hillsides (Figure 16) and others entirely by themselves. It was not unusual to find one pair with its own peat bank. At Kidney Island, one of the many small islands completely covered with tussock grass, pairs burrowed under the hummocks of tussock at widely-separated spots.

Jackass Penguins dug their burrows in slopes overlooking the sea and went to and from the water by the most direct route which, during the course of the nesting season, became a well worn path. Sometimes a pair had its own private path all the way to the beach but more often the paths of several pairs converged into one as they neared the beach.

Figure 14. Part of the colony of Rockhopper Penguins at Kidney Island. The photograph shows both nesting and loitering birds.

Figure 15 (*above*). Jackass Penguins off the beach at Kidney Island.

Figure 16 (*below*). Jackass Penguin at the entrance to one of two nesting burrows. Two other burrow entrances can be seen in the background.

Figure 17. An assemblage of adult Jackass Penguins on a beach at Kidney Island in December.

It is possible, if I may judge by accounts of this species and others of the genus *Spheniscus,* that the lack of colonialism in the Jackass Penguin may be a situation peculiar to the population in the Falklands. Murphy (1936) cites observations of this species on the Patagonian coast that suggest colonialism; and Kearton (1931) tells of the Jackass Penguin *(S. demersus)* on the coasts of South Africa that would appear from his description to nest colonially and to follow much-used trails, as the Gentoos do, over courses that are far from the easiest and most direct.

Trips over paths by Jackass Penguins in the Falklands were more often by individuals walking alone than by a group. There was no time of day when their movements were more evident although it may be surmised that they, like the Gentoos and Rockhoppers, went to and returned from the sea more commonly in the early morning and late afternoon.

Jackass Penguins were more wary of us when we came upon them away from the water and shore than the Gentoos and Rockhoppers. No matter how slowly we approached them, they almost always increased their walking speed, sometimes breaking into a run or tobogganing to move away from us. There were, however, exceptions such as when we stood in the path which they used for reaching the water. There was no deterring them—and I received bruises on my shin one day when I thought I could. Walking up to a Jackass Penguin proceeding down its path over a grassy slope to the sea, I found myself three feet from a bird, determined not to budge, not to step aside. For several moments it looked up at me with one eye and then the other as it swayed the head from side to side. Then in an instant, to my complete surprise, it grabbed the top of my boot with its sharply-hooked beak and proceeded to pummel my leg with the full force of both flippers. Kicked off, it attacked again and again. To make a long story short, it was I who ultimately—and gladly—stepped aside.

This experience gave both Mrs. Pettingill and me a special respect for the Jackass Penguins we met on the narrow paths through the thick tussock grass on Kidney Island. We never hesitated to step aside in the tussock to let them pass—which they proceeded to do with dignity and unconcern.

Aside from the peculiar intransigence of Jackass Penguins on their paths, our strongest recollection of them was their sporadic, well-attended gatherings on the beaches, usually those below the slope on which they nested. There was no accounting for the time of day or period in the breeding season when they gathered, nor the circumstances which brought them together, except possibly the weather, because in all instances noted it was mild and sunny. The size and duration of the assemblage, and the action and interplay that took place at the time, prompted our calling it a "party"—a beach party—for it bore every resemblance to a social occasion which it undoubtedly was.

One such party, typical of the few that we saw, was held under bright sunlight in December on a sheltered beach at Kidney Island (Figure 17). As many as fifty individuals, all adults, were involved. While some rested on their bellies or stood in a slumped position, others collected in groups of two, three, or more to click their bills together and to jostle one another, circling, playfully nibbling one another with their bills, and striking lightly with their flippers. Infrequently an individual attempted copulation, or threatened another with gaping and head-weaving. Now and then a bird trumpeted, giving one of its prolonged, doleful brays, and thereby setting off a "wave" of trumpeting through the congregation, one bird after another doing the same. Although sometimes ignored, the trumpeting more often than not attracted other birds close to the performer and set the stage for a bout of bill-clicking and jostling.

Certain aspects of these activities — notably bill-clicking, jostling, and trumpeting—are strongly reminiscent of certain group activities in the Common Puffin *(Fratercula arctica)* of the North Atlantic. Like Jackass Penguins, Common Puffins gather on a loafing ground in the vicinity of a nesting colony and indulge in bill-clicking (an almost identical performance), jostling, and gaping (Lockley, 1953; Pettingill, 1959). Their attitude toward one another is similarly more playful or amorous than bellicose.

Another feature of the beach party at Kidney Island was when several Jackass Penguins momentarily took leave, ran into the water, quickly submerged, and—as we could discern from an overlooking slope—torpedoed away from shore and back in a wide circle, emerging from the seat at the point where they started, and hustling up on the beach. Sometimes they repeated the whole act, sometimes not; but at no time did they chase each other and make any movements that simulated bathing. The action from start to finish can only be described as a group play in which there was every evidence of enjoyment.

On a sunny day in early March at the end of the nesting season we saw another larger party on a broad beach at Kidney Cove, East Falkland. The group was comprised of about 150 fully-grown young Jackass Penguins which had probably collected from burrows on the adjacent slope. Much of the time they stayed huddled together in a tight pack without regard to individual distance. At intervals, however, a few left the pack to enter the slight surf and be sent sprawling by a breaker. Some of them, after gaining confidence, proceeded to bathe by dipping forward and bringing water over their backs or by rolling over on their backs. All the while their flippers and feet kept the water splashing and boiling. Occasionally one of the birds deliberately drank or swam a short distance without submerging. At no time did we see bill-clicking or jostling; in fact, the birds paid little attention to one another. Compared to the participants in the party at Kidney Island, this group was decidedly docile and phlegmatic.

In Summary

The Gentoo, Rockhopper, and Jackass Penguins at the Falkland Islands showed certain distinctive differences in locomotion on land. In coming ashore, the Gentoo and Jackass Penguins chose mainly beaches and avoided rough terrain. Rockhoppers, on the other hand, preferred to land on rocks and ledges and confined themselves to cliffs and steep, rocky slopes. For locomotion in such places their habit of jumping was a special adaptation. The Gentoos and Rockhoppers were consistently gregarious at all times on land, the Jackass Penguins only on the beaches. The size of Rockhopper groups coming ashore was governed by the condition of the surf. Both Gentoos and Rockhoppers followed ancestral trails to the nesting colonies, in all cases conspicuously worn. Rocks on the Rockhopper trails were scarred by foot action. The Gentoo trails were peculiarly long and circuitous, leading to colonies that were in some cases on notably high ground. The behavior and action of Gentoos and Rockhoppers on their trails have many and varied features. Fully-grown young Gentoos tend to ignore the ancestral trails when going to sea for the first time, instead taking a more direct route. When returning to the sea, Rockhoppers may jump in feetfirst or headfirst. Pairs of Jackass Penguins often have their own paths between their nests and the sea. All three species of penguins have loitering areas close to the sea. While loitering the Rockhoppers may form "clubs" and the Jackass Penguins may gather occasionally in "parties" during which there is considerable action and interplay.

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THE RADAR VIEW OF BIRD MIGRATION

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Those who study bird migration have long searched for a way to view nocturnal migration. Of course there are spectacular migrations visible by day such as those reported from Hawk Mountain or Cape May. At the proper place and time one can count large numbers of migrants, but many of these are birds that have moved into the area during the *night*. Diurnal observations of most species are observations *preceding* or *following* a *nocturnal flight*. Even such an excellent project as Operation Recovery, a program of netting and banding during migration, records numbers of birds that have *already* made a flight of some duration (Baird et al., 1959). Data taken after the fact of migration do not reveal the source of the migrants, the route taken, or the orientational clues involved. Also, the weather at the time of arrival is not necessarily the same as during the time of departure (Swinebroad, 1960). To solve some of these problems, some field workers have tried to estimate the route and starting point of particular flights. This procedure can be extrapolated to the place where the estimates of routes and origin are made because they support an hypothesis designed to reveal routes and origins (Raynor, 1958).

Scientists have made many laboratory investigations of orienting responses, biological clock phenomena, and gross metabolic activity such as molt and fat deposition in birds. They have used nocturnal restlessness (zugunruhe) as a response correlated or equated to migratory activity. Most of these studies have indicated fruitful areas for further examinations. To relate these studies to actual migration we need precise information about the duration, direction, and timing of nocturnal flights.

A major problem recognized by many students is to determine the adequacy of the sample taken of migratory populations. We are not sure what the numbers of birds seen or netted represent as to the actual size of migration. Small numbers may mean either that there are few migrants or that only a few alighted in our study area. Large numbers may mean a big migration or a higher percentage of migrants alighting from a small flight. Laboratory and field studies, then, may be strengthened by better measurements of the size and nature of actual migration. One method has been to observe birds passing across the lunar disc (Newman, 1952). Now, we are using radar as a tool to provide additional measurements especially of nocturnal migration.

How successful has the use of radar been in studies of migration? How reliable are the results? To answer these questions we will consider a little of the history of bird watching by radar, review some of the current techniques, and then summarize some of the published results.

History of Bird Watching by Radar

Radar operators in Europe detected gull-sized birds on radar as early as 1940 (Lack and Varley, 1945). From the 1940's until 1955 little more was done with bird detection. In fact, many radar operators and physicists rejected the idea that the myriads of unidentified "angels" showing on the screen were returns from birds. They suggested these angels were caused by meteorological events such as clouds of ions. I have had a radar engineer suggest that the angels might be returns from the masts of fishing boats off the New Jersey coast. The various ideas were hard to support when observations showed that these "meteorological events" moved faster than the wind—and could even move against it, or that the "fishing boats" sailed right across New Jersey and Pennsylvania! With the development of more sophisticated radar, the occurrence of returns from birds became an operational hazard (Lack, 1958). The Royal Radar Establishment investigated this problem and found no correlation between the unidentified echoes or returns and meteorological factors. In England, W. G. Harper (1958) and, in this country, R. E. Richardson and colleagues (1959) reviewed the evidence and reiterated the fact that radar could and did detect migratory birds. From 1955 onward various British governmental and private agencies have made available their reports and records of bird observations, and have permitted ornithologists to view radar during times of migration. The result is a series of papers and reports by David Lack and his associates. William H. Drury, the first to conduct extensive radar studies of migration in North America, has with his colleagues presented their interpretations of the data (Drury and Keith, 1962). In 1962, Richard R. Graber and Sylvia Hassler discussed the use of small portable radar sets and presented some of the information thus obtained (Graber and Hassler, 1962). The New Jersey radar studies were started at Rutgers University through the efforts of Roscoe B. Kandle, Commissioner of the State Department of Health, and Oscar Sussmann, Chief, Bureau of Veterinary Public Health, and with the cooperation of the United States Air Force, Air Defense Command, New York Sector. These studies are continuing and, pending complete reports, I have taken the liberty of mentioning some of our preliminary findings in this discussion.

Current Techniques and the Procedure Used

To be able to interpret the value of radar studies of migration we must know some of the techniques. I will describe the general procedure used in the New England and New Jersey studies with the large coastal surveillance radar operating at a 23-centimeter wave length.

The radar operator sits in a darkened room viewing what appears to be a television console. The 21-inch screen has a faint blue or greenish glow. The screen may have what looks like a TV test pattern of concentric circles divided into pie-shaped sections by thin spokes radiating from the center. The circles and spokes glow with a white fluorescence. The circles show range at consecutive 10-mile intervals. The spokes are degree lines showing every 10 degrees of direction starting with zero degrees at true north. The location of every target can be ascertained using these range and angle marks.

A thin white line sweeps around the screen like a fine, rapidly-moving second-hand of a clock. This line correlates to the rotation of the radar antenna. As the antenna line moves around, small spots of fluorescence suddenly flare up behind it as if tiny fragments were torn from the line. These spots fade to a dull glow only to be re-alighted as the antenna line sweeps around again. Many of the spots may fade out and not appear again, others persist rotation after rotation. The spots vary in size, some are as large as the head of a tack while others look like dust on the screen. These spots may represent the echoes or returns from a moving target such as birds, planes, or clouds, or they may represent static—that is, "noise" such as clutter which is stray energy bouncing back from objects near the ground. See Figures 1, 2, and 3. Clouds usually appear as great luminescent masses and rain shows as an incredible vibrating jumble of dust-like dots. The center of the screen is obscured by clutter so that the innermost one or two rings are completely filled with a white fluorescence and individual targets within 10 or so miles of the antenna cannot be detected. A remarkable problem is created by the range of the larger radar installations. For bird detection the range may be set at a radius of 70 to 100 nautical miles, and the screen may represent a view of over 30,000 square miles. On this scale *no movement is apparent*. A bird

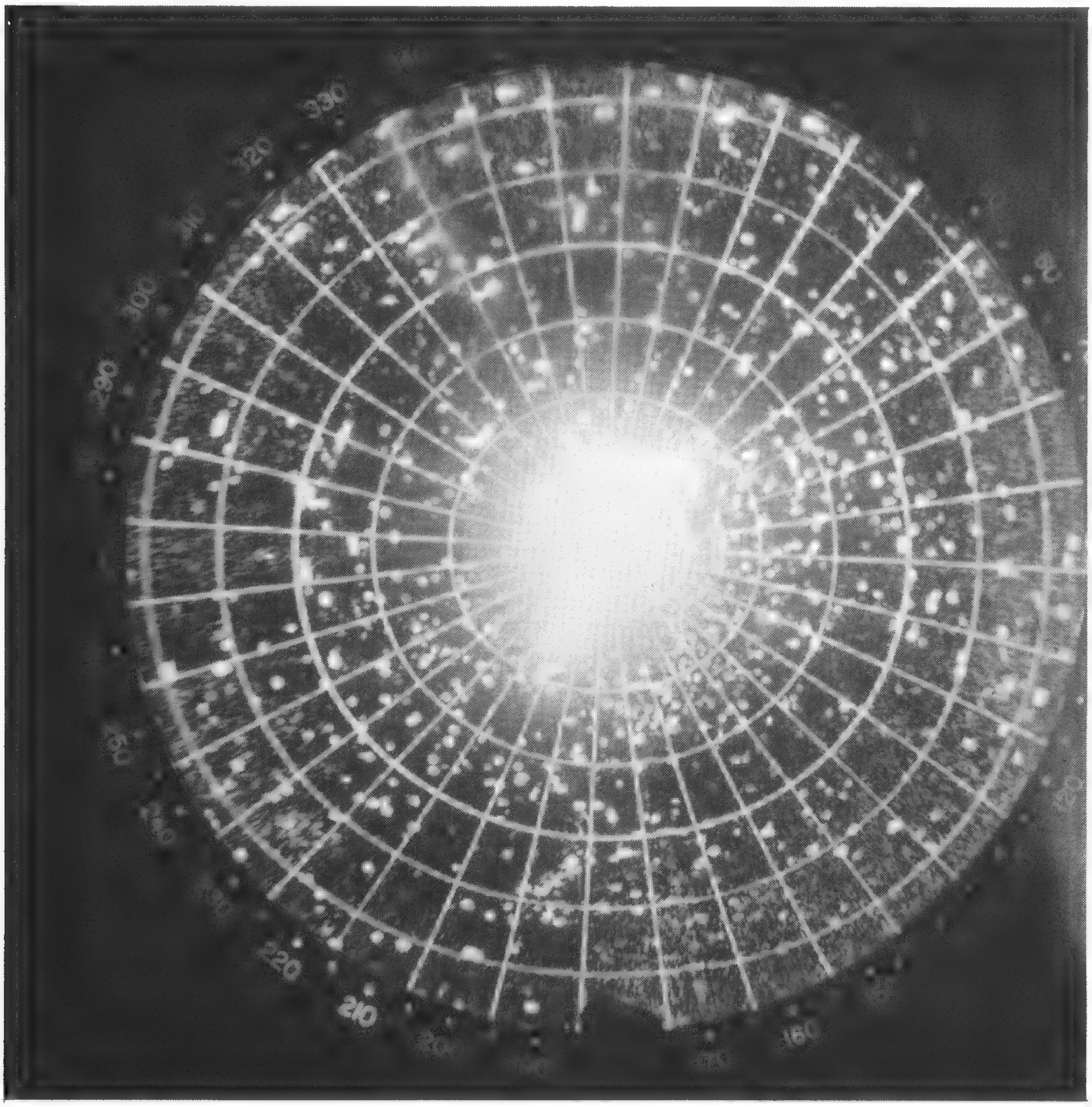

Figure 1. Photograph of a radar ("video") screen. Here the screen of the radar console shows a diameter of 120 miles. Aerial objects and static appear as many white dots scattered across the screen. Not many birds are shown. The photograph was taken at 6:00 PM, 21 September 1960, in New Jersey.

When a photograph of this sort is taken, the camera is held at arm's length from the radar screen by means of a sturdy steel frame. The camera and the light pathway from the radar screen are enclosed in a black hood.

flying at a ground speed of 30 knots would take three hours to move across the screen or about seven inches per hour! Our eyes cannot separate this very slow movement from the stationary dots caused by clutter and other noise also echoing on the screen. In fact, it is difficult to pick up aircraft movement. No wonder many operators reject the idea that some of the noise on their set is migrating birds and not static. Each time we use a different radar station in New Jersey we have to wage a new campaign to convince the radar crews that we really can "see" birds with their instrument. This leads to a considerable problem when using military or commercial radar. Unless each operator believes the effort is worthwhile, the technical level of information obtained will vary widely from time to time and make deciphering of the record an arduous task.

The usual display is a Plan Position Indicator (PPI) where targets are shown at the true (scale) location from the antenna, and track (direction of movement) and speed can be measured directly. The PPI does not show the true size of the target, but gives some relative information on it, and shows nothing of height. The latter can be measured by other kinds of radar. The

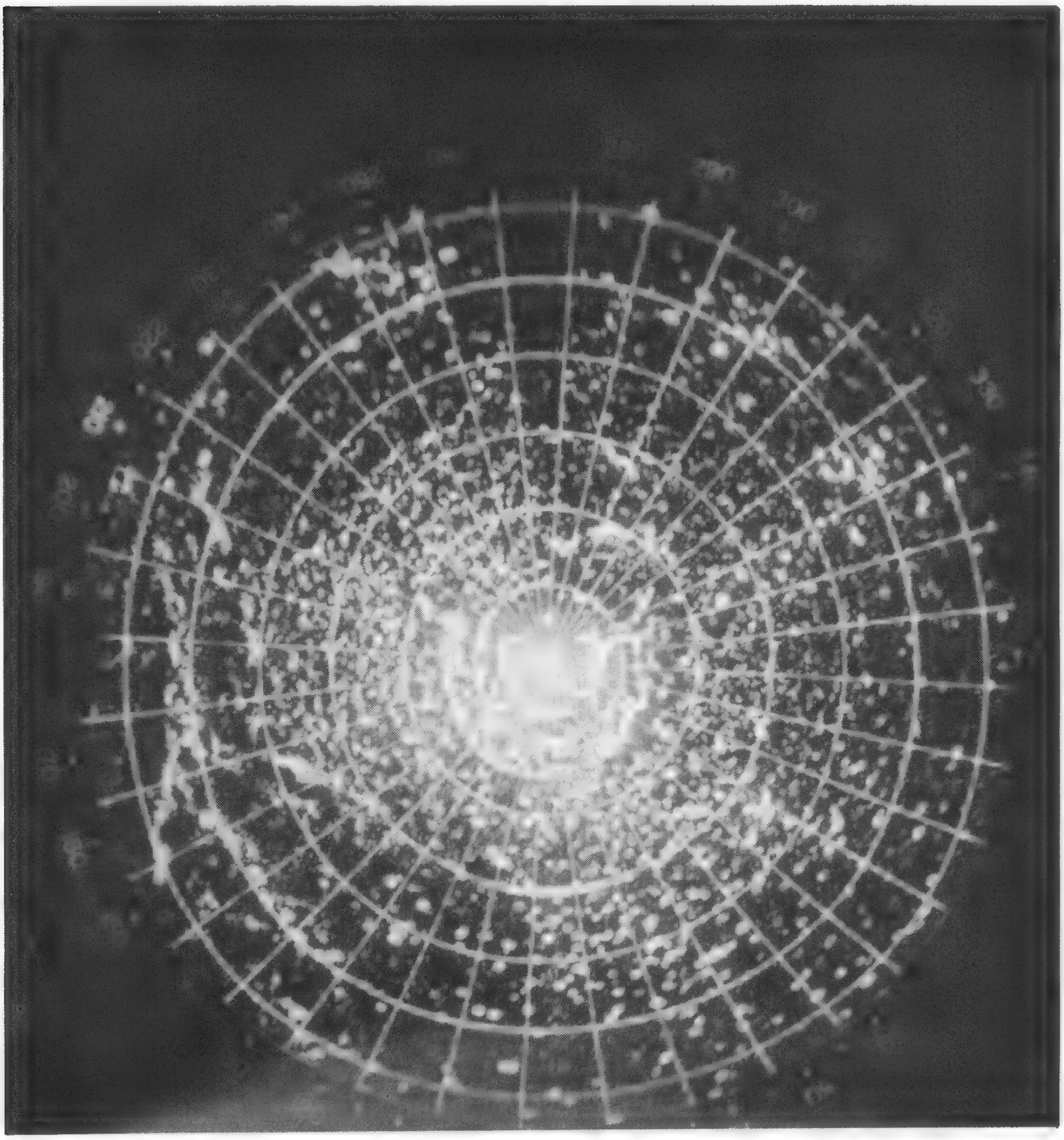

Figure 2. Photograph of the same radar screen as in Figure 1, four hours later (10:00 PM). More birds are in evidence.

PPI display may be of normal video, or of the Moving Target Indicator circuit (MTI). The use of MTI eliminates stationary objects and thus clears away the clutter at the center of the screen and eliminates much of the noise. Unfortunately MTI also removes many bird returns depending on their direction and speed, and makes difficult the tracking of individual targets. For various reasons, we use the normal video most of the time in New Jersey.

The returns or echoes that show on the screen as fluorescent dots represent an amplification of energy bouncing back from a target. Energy pulses are sent out from the radar antenna; depending on a host of factors, some of the energy may be returned to the antenna from targets of suitable size and within suitable range.

One of the difficulties involved in the use of radar is to calculate for any combination of factors just how many targets of what size, speed, and density will give a return.

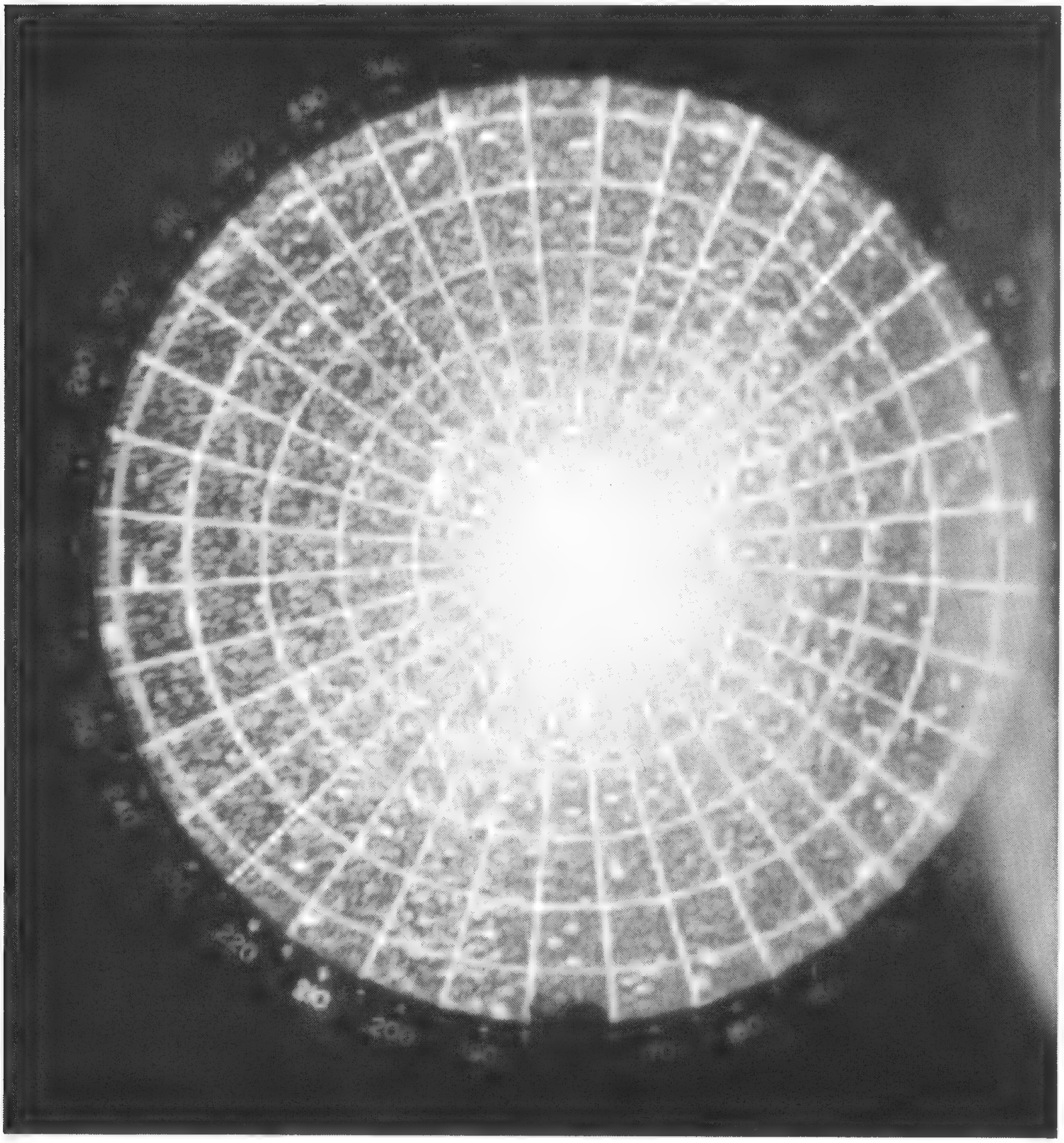

Figure 3. Photograph of the same radar screen as in Figure 1, six hours later (midnight). A moderate migration is obviously in progress.

To detect movement of returns and thus separate birds from noise we photograph the screen of the console, exposing one frame of film for each sweep of the antenna. These films are then processed and viewed with a film editor which shows them at normal motion picture speed. This results in a speed-up of movement some 300 times, and, like magic, myriads of the small dots begin to flow across the screen, while the static, though it may twinkle, stays in one place. The movement does not appear smooth and continuous because some returns scintillate or flicker; some fade out; some flick in and out; and—unless the operator has been careful—many get lost in the static scattered across the screen. If many birds are passing over, the returns blend into a mass of light and the area of clutter seems to grow from the center of the screen outward. In extreme cases the entire screen is lit up and individual targets can be separated, if at all, only at the extreme limits of the range.

There are other types of radar with a yellow fluorescence on the screen where moving targets leave a tail or afterglow. Some idea of migration may be obtained by merely looking at the screen. This technique has been used by Lack in England. The disadvantage here is that there is no film record of the migration which may be viewed repeatedly and re-evaluated as our understanding of the technique improves.

In a recent paper, I. C. N. Nisbet (1963) has attempted to determine the relation between the number of returns shown on the screen and the actual number of birds aloft. Even a casual reading of this paper will evidence the difficulties encountered in deciphering the radar picture. For example, consider the problem of accounting for the usual decrease in returns with an increase in range. This "thinning" is noticeable on all radar sets, and is due partly to the decreasing power of the radar beam with increasing distance. But, there can be other contributing factors. There could be a *real* difference in the number of birds with distance. It might be that at long range the birds are below the radar beam, or that they are flying at different directions at different distances, or that the flocks are of different size and shape, or that the individuals are of different sizes. Perhaps the thinning is due to the weather conditions or even a combination of all these things together! No wonder Nisbet (1963) concludes that, "Estimates of low migration density have a standard error of about 25%, but estimates of high migration density are less accurate, and very high migration densities cannot be measured at all, although they can be accurately identified as such." Although the foregoing strictly applies to the radar at South Truro on Cape Cod, it is a good general statement of what can be obtained with the long range radar currently in use. In other words, we can say that a migration is large or very large in contrast to small or no migration and yet not know just how many birds are involved. Of course, new radar eventually available to ornithologists may make more accurate measurements possible; nevertheless, to have even a gross idea of what is going on over thousands of square miles at night is a considerable step forward as we shall see presently.

A question often asked is: Does each return represent one bird or a flock of birds? And if a flock, how many birds are present? The answer depends on what type of radar is used and how it is operated. The smaller portable set can detect single thrush-sized birds (Graber and Hassler, 1963). The larger sets can pick up individual gulls, geese, and ducks, and may detect smaller individuals, but probably most of the returns are from flocks. Nisbet (1963) attempted to calculate the average flock size shown by the South Truro 23-centimeter radar. His very comprehensive analysis emphasizes the difficulty of casually looking at a radar picture and making pronouncements about details of migration. It is not very satisfactory to read Nisbet's paper and see how many correction factors must be applied to the raw data before they can be used. For example, how convincing is it to learn that on one occasion seeing *three* birds is presumably equivalent to seeing *six hundred?* No matter how logical the mathematics, this kind of extrapolation which leaves the original observation far behind is a weakness of many ornithological studies including those using radar. The Illinois studies (see Hassler et al., 1963) recognize this problem, for they report only on the number of targets shown without any attempt to equate this to numbers of birds.

Does this mean that at present the use of radar is waste of time and money? Not at all! First we can get a *gross picture* of migration over large areas, as I have mentioned. We can tell whether or not the migration is relatively *large* or *small* without the level of ambiguity found in netting data or visual observations. We can see *direction* of flight over a considerable distance. We can get information on the *height* of movement. We can tell the *time* of movement. We can follow the *movement* of individual flocks as they fly over certain topographical features such as rivers and coast lines. We can observe the *distribution* of flocks before or after frontal cloud masses (which show up well). These records of migration can be obtained in the day or — what is most important — at night, and, to some degree, regardless of the weather. Anyone who has used the moon-watching technique will appreciate how welcome any of the foregoing information is. The radar information can be compared to that from ground observers, netting programs, and moon watchers. *Used with care,* the radar data may aid immeasurably in any comprehensive study of migratory behavior.

Some Results from Bird Watching by Radar

The papers now published illustrate what has been learned by using radar even though the technical problems are considerable.

First, many persons using radar have been impressed by the volume of nocturnal migration. Regardless of how many birds are detected it is most impressive to see a film of one night in which hour by hour, thousands of targets pour across the screen. Compared to what we see by daylight, even on a big day in the spring, we must be looking at only a tiny fraction of the nocturnal movement. The data from New England indicate that there is good correlation in early spring between arrivals noted by ground observers and movements shown on the radar screen. Later on in the spring and in the fall, the ground observer's reports of a general exodus of birds also apparently agree fairly well with the radar data, and both techniques seem to coincide in reporting local movement (Drury and Keith, 1962).

Apparently there is less agreement between radar data and ground observer reports for much of the fall migration in New England, though this is difficult to tell from the published reports. In New Jersey the studies to date show some disparity between the radar records and those of ground observers or of coastal netting programs. On some nights the radar shows considerable activity but the netting catch and observers' reports indicate little movement, whereas on several occasions when large numbers are seen or netted the radar picture of the previous night shows little migration. Neither the New England nor New Jersey studies have yet published a detailed report with appropriate statistics, though Drury and Keith (1962) have discussed some qualitative material. Still these investigations seem to agree with Lack's comments (1959) that "Radar confirms that the migration visible by day may not be merely incomplete but also unrepresentative of what is passing overhead."

Anyone who has read papers about weather and bird migration is aware of the complexity of the problem and the consequent different theories advanced. Radar has not solved these problems but rather has indicated the degree of complexity in the problems to be investigated.

In Illinois the radar shows that wind shifts from north to south probably correlate with large flights in the fall. Passage of a cold front seems less significant. Overcast skies may negate the immediate effect of the wind shift (Hassler et al., 1963). In England, Lack (1963) also considers that radar shows wind direction to be important and that cold fronts are only incidentally involved. In New England, Drury reports that southward migration of passerines evidently follows cold fronts (Drury and Keith, 1962). The New Jersey data so far show no good correlation between nocturnal fall migration and either cold fronts or wind direction. Some of these contradictions may be due to the different regions and species being studied. Some are due to subjective evaluations of the different investigators. For example, how soon after a frontal passage does a flight have to occur to be considered as correlated with the front—two hours, two days, four days? Various investigators may differ on this. Even so, the inability of radar to separate species is probably the cause of much of the problem. Different species responding in different ways still may present a total average picture not true of any contributing group. Because radar cannot separate species we should not say species act alike because we see no difference between them—and therefore rest comfortably with the assumption that we do not need to distinguish species anyway. Circular reasoning is not eliminated by the use of sophisticated machinery!

Perhaps the most spectacular findings yet reported from radar have to do with the direction of migration. Radar has shown directions of migration not previously known and has caused some revision of ideas about known flight directions. Lack (1963), for example, comments on what he observed on September migration in England: "Hence of the six main passerine movements, two were previously unsuspected, two others in part were wrongly interpreted, and the largest was thought to occur in a different direction from that actually taken."

Observations by radar in midwestern United States show an eastward direction to both spring and fall migration. Bellrose and Graber (1963) suggest that many birds migrate along elliptical clockwise routes from wintering to breeding grounds.

Radar records from coastal North America show some rather startling directions of migration. The South Truro radar has tracked migrants heading southward over the Atlantic. Drury and associates interpret these as flocks of passerines, particularly the Blackpoll Warbler *(Dendroica striata),* flying over the Atlantic directly from New England to the Antilles and South America (Nisbet et al., 1963). The New Jersey radar has shown targets which pass over the state from the northwest and proceed southeast out of sight 70 miles off shore! These targets vary in characteristics but include passerine-type and shorebird-type among others.

Both New England and New Jersey radar have shown "reverse" migration of considerable magnitude, whereas the seasonally wrong-way movement has not been seen in Illinois. Neither of the east-coast sites has obtained any evidence so far of re-orientation after wind drift.

Some measurements of the height of migration have been made at different places. In this country Nisbet (1963) finds the concentration of targets usually to be between 1,500 and 2,500 feet above sea level. Bellrose and Graber (1963) present graphs which indicate a concentration of migrants between 2,000 and 5,000 feet. Their data show a slightly higher average for fall than spring.

Considering all of the above, radar must be of some value. Certainly, it is not the ultimate tool for studies of migration. Radar records must be interpreted together with ground-observer records, keeping in mind the technical problems of radar. We must take into account some of the published reports as a basis for programs of investigations rather than conclusions. New types of radar will mean the resolution of some of the present problems, but will not be a substitute for the wealth of information still to come from ground observers, netting programs, and moon watching.

We need a coordinated program using the new types of radar, correlated with extensive netting programs and ground-observer reports. Such programs are starting at several places in the country including, we hope, New Jersey. These programs need financial aid, for radar is an expensive tool, but perhaps we can learn enough from it to be able to discard it eventually.

We should not view radar as a miracle tool, nor should we dismiss it as valueless. We do not expect an immediate practical value from the radar studies of migration, though there may be many uses of such information outside the realm of pure science. The use of radar in migration studies will certainly enable us to know more than we do now and will help us to formulate meaningful questions. It has already caused us to re-examine some of our present ideas and concepts, which is, after all, the best justification for any new technique.

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BREEDING BEHAVIOR OF THE AMERICAN KESTREL (SPARROW HAWK)

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The purpose of this paper is to describe the breeding behavior of the American Kestrel or Sparrow Hawk *(Falco sparverius)* and to present some experiments on the role of environmental factors which influence reproduction in this species. Since the American Kestrel is the most familiar and abundant member of the family Falconidae in North America, one of the easiest raptors to observe, and adjusts easily to caged conditions, it provides a convenient starting point for comparative studies of falconiform behavior.

A primary objective has been to throw light on the mechanisms of "pair integration" in a predatory species. By pair integration we mean the establishment of a bond of social cooperation and physiological synchronization between a male and female to form a functional reproductive unit. Our initial hypothesis was that pair integration may well involve special problems for predatory birds, because they are frequently solitary and pugnacious towards each other during much of the year and because they possess beaks and feet especially adapted for killing other animals—including, in the case of falcons and some other forms, birds their own size and larger. Quite possibly a predatory bird represents a potential hazard to its mate and young. If so, then important social processes must be brought into play to modify the aggressive tendencies of predatory birds during the breeding season.

Methods

Most of our observations were made on captive birds which were kept at Syracuse University in six unheated flight rooms measuring 6 feet wide by 8 feet high by 12 feet long. Each room was illuminated solely from inside by a 150-watt incandescent lamp, controlled by a clock-timer switch, and by a continuously burning 7.5-watt bulb which allowed the birds to gain a perch at night. The lights were located at the front of the room on the ceiling. A nest-box 11 inches to a side with a 3-inch diameter hole near the top was present at the rear of each room near the ceiling, and perches were provided near the back, middle, and front of the rooms 4 to 7 feet above the floor (see Figure 1). Observations were made through an 11.5-inch-square "one-way glass," or half-silvered mirror window at the front of each room.

The birds were fed mainly raw beef heart sprinkled with a commercial vitamin-mineral preparation (Theralin, Lambert-Kay Inc., Los Angeles) and bone meal. After several months, paprika was added to help prevent loss of color in feet and cere. Dead mice were occasionally provided also. Food was

Figure 1. A pair of captive American Kestrels, Male 53 and Female 56, showing the type of nesting box used in the experiments.

placed on a board about 10 inches square on the cage floor. Drinking water was available at all times, but the birds seldom drank or bathed.

Most of the captive birds were trapped near Gainesville, Florida, in early February 1962. We are indebted to Dr. Daniel A. Belkin for help in catching these birds. Three males were also obtained near Syracuse, New York. Birds were kept in pairs, male and female, starting from early in February 1962 and continued to mid-July 1963 when the last captives were released. Table 1 lists the birds used, dates and places of acquisition, body weights, and the individuals with which each was mated.

During periods of breeding activity, the captive pairs were observed daily or every other day for two to five hours at feeding time, usually between 8:00 AM and 1:00 PM, and frequently at other times of day also. In addition to studies on these birds, some initial observations were made by the junior author in 1954, 1960, and 1962 on three other captive pairs which were kept under conditions similar to those described above.

Field studies of wild Kestrels were conducted in the vicinity of Syracuse, New York. Most observations were made in 1962 on five nesting pairs and on four other pairs whose nests were not found.

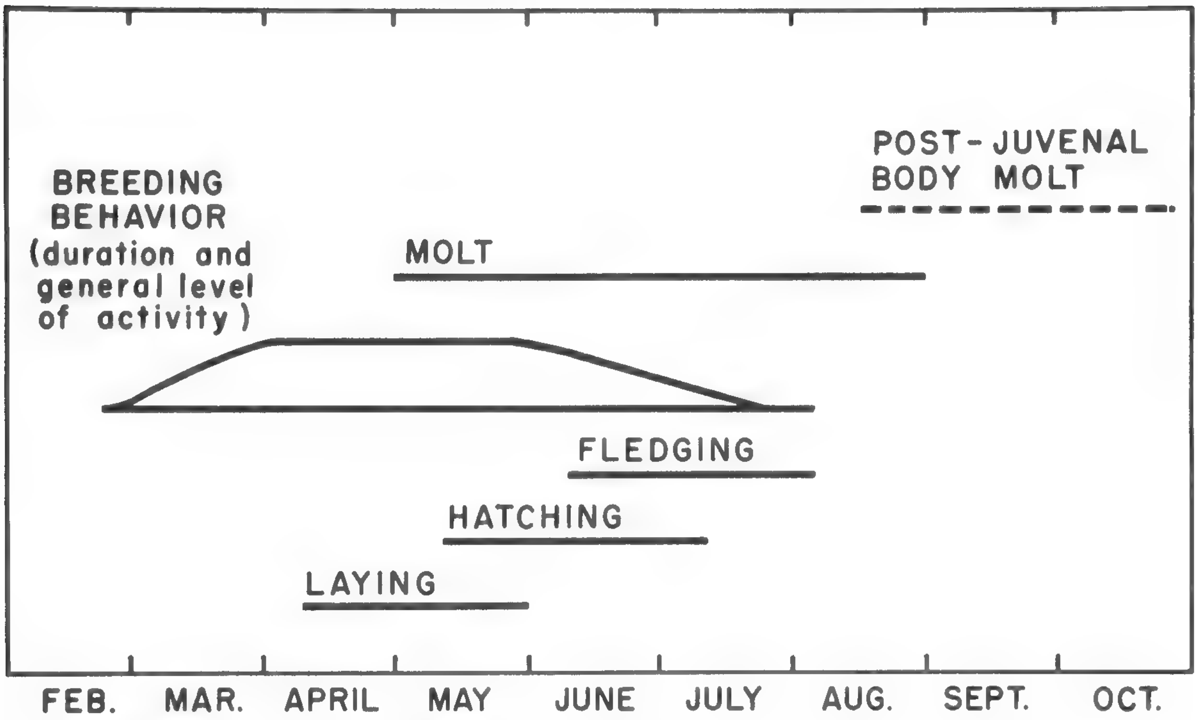

Figure 2. General timing of events in the annual cycle of the American Kestrel in New York State. Laying, hatching, and fledging periods are based on information obtained by us and on extrapolations from egg dates given by Bent (1938). The period of post-juvenal molt is based on data given by Parkes (1955) and by Roest (1957).

Annual Cycle

The timing of the major events in the breeding cycle of Kestrels in New York is summarized in Figure 2. The first signs of sexual behavior—birds associating in pairs, whining vocalizations—appear about the last week of February. The level of pre-incubation activities—vocalizations, copulation, courtship feeding, nest-site inspection—reaches a peak in the first week of April. The first eggs are usually laid early in April, but laying continues through May for some pairs. Captive females laid eggs at intervals of two or three days.

Clutch size is ordinarily 4 or 5, occasionally 3, and rarely 6 or 7 (Bent, 1938). Twelve completed clutches laid by captive females averaged 3.66 eggs with a range from 3 to 4.

Eggs hatch after about 30 days of incubation. Sherman (1913) observed incubation periods of 29 and 30 days in a clutch at National, Iowa, and Roest (1957) noted an incubation period of 30 to 31 days in the vicinity of Bend, Oregon. The time from last laying to last hatching in 5 clutches of eggs of captive Kestrels at Syracuse University averaged 28.4 days with extremes of 27 and 33 days. According to Roest (1957), young Kestrels leave the nest 30 or 31 days after hatching.

Although the female generally does most of the incubating, the male occasionally does part of it. Roest (1957) observed an instance in which the male of a pair apparently spent the night on the nest, and D. A. Belkin and T. J. Cade watched a pair which nested in a building on the campus of the University of California, Los Angeles, in which the male invariably spent the night on the eggs. Our captive males, on the other hand, were seldom seen covering the eggs.

Very little is known about the migration of the American Kestrel. Roest (1957) summarized some meager banding returns which indicate that Kestrels from New England and the central Atlantic coast winter in the Carolinas and

Georgia. We trapped wintering birds of the race *sparverius* in the vicinity of Gainesville, Florida, in late January and early February 1962. Around Syracuse the wintering population is very sparse, roughly one-fourth or less of the summer population, and seems to consist mostly of males in a ratio of about 6 to 1. Roest (1957) mentioned a similar situation occurring near Bend, Oregon, where the few Kestrels noted in winter were all males. In southern California, however, there is a preponderance of females in the wintering populations. Out of 728 Kestrels which were identified as to sex, during roadside censuses conducted by the junior author between Los Angeles and Sacramento in January 1954 and 1956, only 277 were males, giving a ratio of 1 male to 1.62 females. Too little is known about the movements of the American Kestrel to understand the significance of this variation in sex ratios in wintering populations. At any rate, most of the Kestrels which winter around Syracuse leave the area in late winter and are replaced by the breeding population which arrives in March and departs by the end of October.

Reproductive Behavior

Cycle of Events

Cade (1955) has previously outlined the annual behavioral cycle for Kestrels in southern California. He found that mating behavior of most Kestrels there begins in January, although some pairs may be seen copulating in December before Christmas. Until April or May when a nesting-site is occupied, paired birds in California engage in an association characterized by aerial displays, hunting together, courtship feeding, and frequent copulations. Such a prolonged pre-nesting association is not evident around Syracuse, New York, where in some cases mates appear to pair up on the breeding area and in other cases, to arrive already paired. Within a month after their arrival, the breeding birds occupy nesting sites.

During the pre-nesting, courting period Kestrels tend to be rather sociable and are sometimes seen in groups of three or more in the same area, even hunting togther. Captive mates showed this sociable tendency by perching close together, even touching sides, and sometimes uttering soft chitters. This tendency to perch close together appeared before copulation and fully-developed courtship feeding and was the first manifestation of pairing.

Figure 3 summarizes the sequence of conspicuous behavioral changes associated with breeding in captive Kestrels. The same relative time scale also applies to wild birds, but wild birds do not necessarily have the same absolute timing as shown. The significant aspects of breeding behavior can be divided into five main categories—whining and chittering vocalizations, courtship feeding, copulation, nest-site inspection, and aerial display.

Whining and chittering vocalizations, associated with social interactions, appear quite early in the pre-nesting phase, rise gradually to a peak of occurrence well before the eggs are laid, and gradually decrease through the incubation and nestling periods. Copulation by wild birds around Syracuse also appears early, in the last part of March, or even in February in the case of wintering birds, and in some cases before the occurrence of courtship feeding. The frequency of copulation reaches a peak just prior to laying and drops to a low level quickly after the last egg is laid and incubation begins. Feeding of the female by the male begins about the same time as copulation or a little later, reaches a peak by the time the first egg is laid, and continues at a high level through the incubation and early nestling periods, diminishing

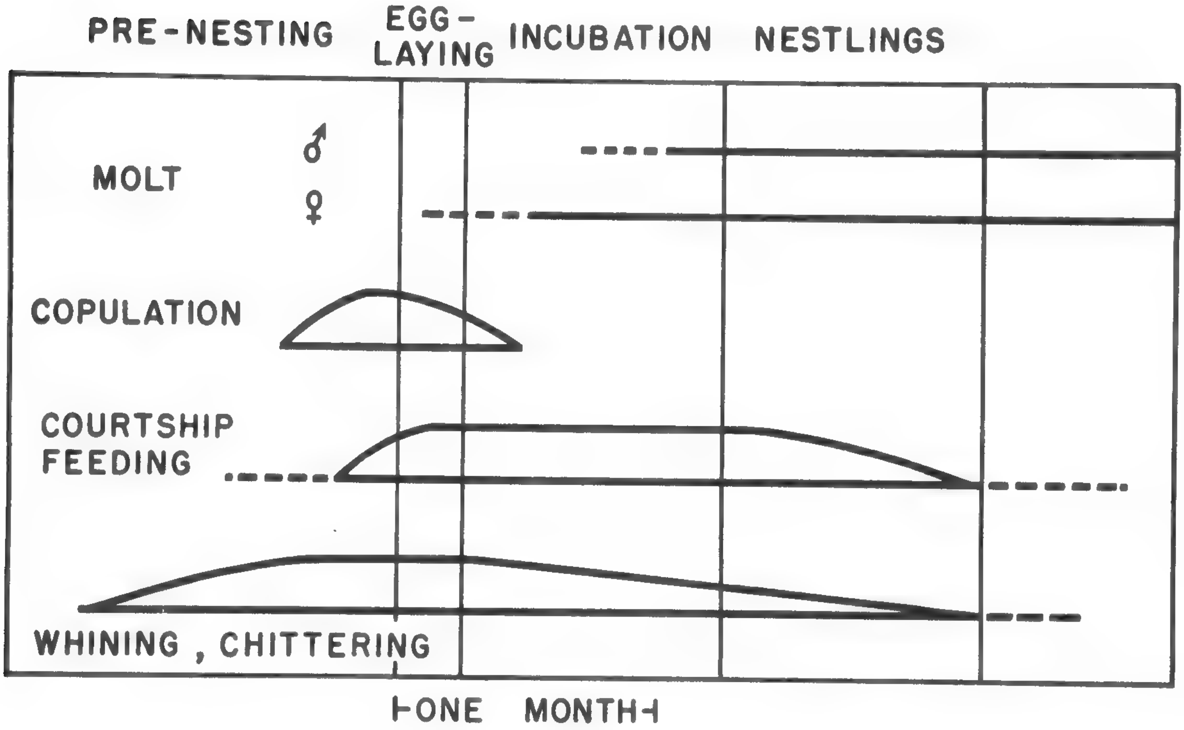

Figure 3. Timing of breeding behavior in captive American Kestrels at Syracuse University, with duration and peaks of the conspicuous behavioral components diagrammed. Broken lines indicate periods of partial or sporadic occurrence.

to a low level by the time of fledging. In some cases it continues to occur sporadically for a few weeks longer or builds back up to a high frequency in those southern pairs which nest a second time.

Vocalizations

The repertoire of basically distinct calls utilized by adult Kestrels is limited to three, which we designate as the Klee (the familiar "killy" of most bird books), the Whine, and the Chitter.

(1) *Klee*—This call is the most common and characteristic vocalization of the American Kestrel. It is uttered by both sexes, usually as an expression of generalized excitement, any time of the year. Figure 4 shows sound spectrograms of this call from three captive Kestrels. The call is given in a rapid series of three to six notes and is customarily represented as *killy,* but a closer rendition to our ears is *klee.* There is much variation in tonal quality (harshness) and pitch among individuals, as well as in the frequency with which the notes are given in a series. As a rule, females have lower pitched, harsher voices than males; and bigger birds have lower pitched voices than smaller ones regardless of sex. Some of the circumstances which elicit this call include: (a) Approach of a human observer close to the nest, (b) foiled attempt at catching prey, and (c) interspecific or intraspecific aggressive encounters.

(2) *Whine*—There are two variations of this call which we have named the Simple Whine and the Treble Whine. The Treble Whine seems to be a higher intensity expression of the same basic tendency which underlies the Simple Whine. Spectrogram D of Figure 5 represents a Simple Whine. Usually, but not always, this note is given a rising intonation. The Treble Whine (Figure 5, E) is essentially the same note, without the rising intonation, broken into three distinct segments with a stop before each. Between these two extremes occur calls which form a transition from the simple type to a tremu-

lous whine to the distinct treble type, representing various intensities of expression.

These whines are primarily associated with food and feeding, secondarily with copulation. The fledgling gives the Treble Whine when begging for food from its parents, and the adult female gives this whine when begging for food from her mate. The adult male seldom utters the Treble Whine. The Simple Whine is given by both sexes in connection with courtship feeding and copulation.

(3) *Chitter*—This is the most frequently used call in interactions between male and female. Spectrogram F (Figure 5) illustrates a typical chitter. The most characteristic feature is that the sound is pulsed at a rate of about 20 per second. This call is doubtlessly the one referred to previously by Cade (1955)

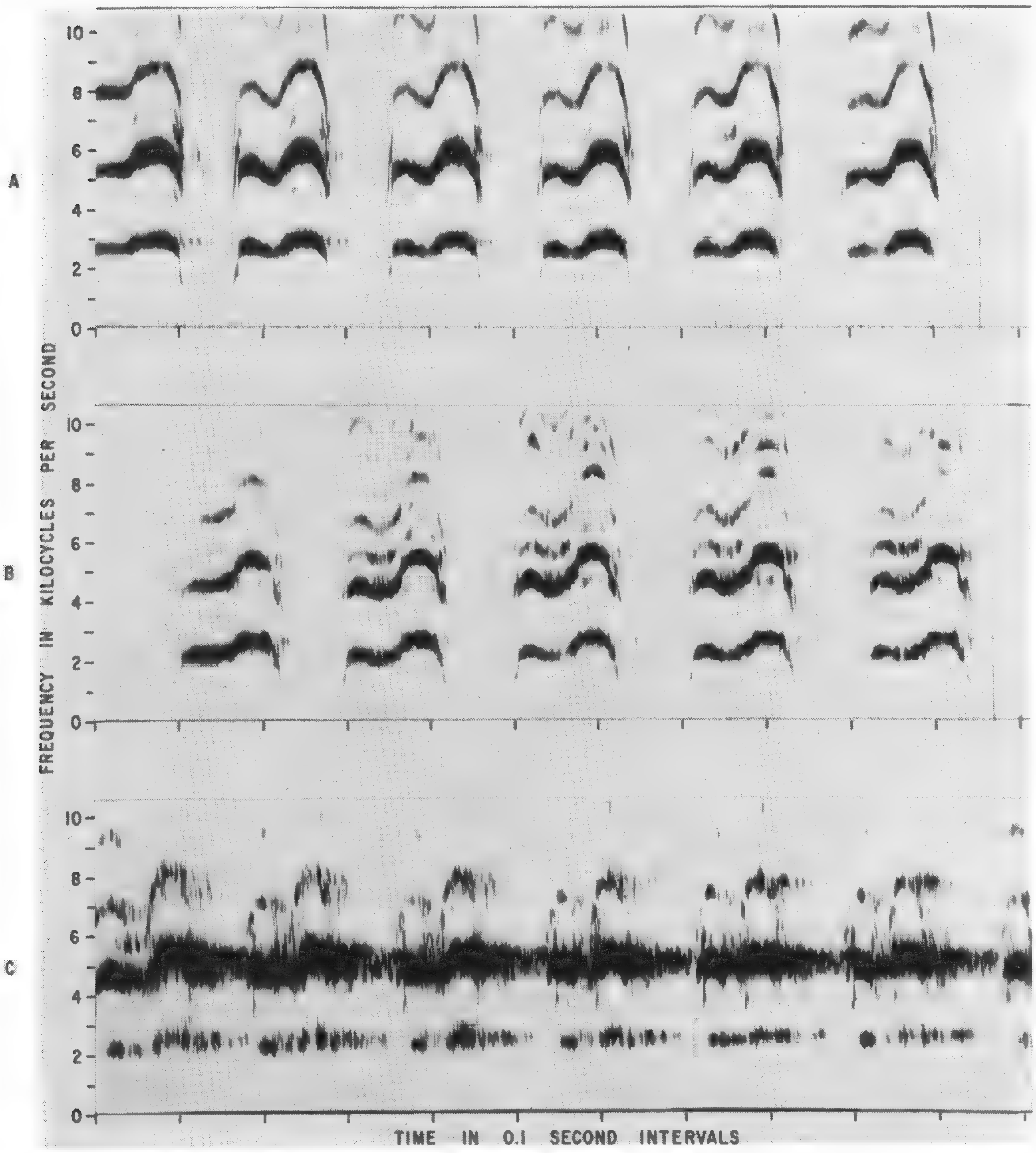

Figure 4. Sound spectrograms of the Klee note of three captive American Kestrels. Salient features are the presence of regular harmonics and a quick upward slur in the middle of the note. A, from Male 62; B, from Female 61; C, from Female 56. Recordings were made on a Nagra IIIb portable recorder (Kudelski, Lausanne, Switzerland) using an AKG model D200K microphone with a tape speed of 15 inches per second. Spectrograms were made on a Kay Electric Company sound spectrograph.

as chittering and is the homologue of the chitter uttered by the male Peregrine Falcon *(Falco peregrinus)* during courtship feeding and copulation (Cade, 1960).

The chitter varies in loudness and duration depending on the intensity of expression and the behavioral context. Both sexes utter this vocalization, and it is associated with "friendly" approach and bodily contact. Chittering occurs during courtship feeding, copulation, nest-site inspection, and the feeding of nestlings. Chitters are frequently uttered by one or both mates as one approaches the other, and the sound evidently signifies sociable, non-aggressive tendencies. A bird may give chitters before it starts to approach another as a signal of intention to do so.

(4) *Whine-Chitter*—A vocal pattern we call the Whine-Chitter, ordinarily given only by the male, consists of the Simple Whine and Chitter combined in a short phrase. The whines, two or more usually, are followed immediately by a chitter. This combination is often given by a male flying toward his mate or toward a customary feeding perch with food intended for her. The whine is

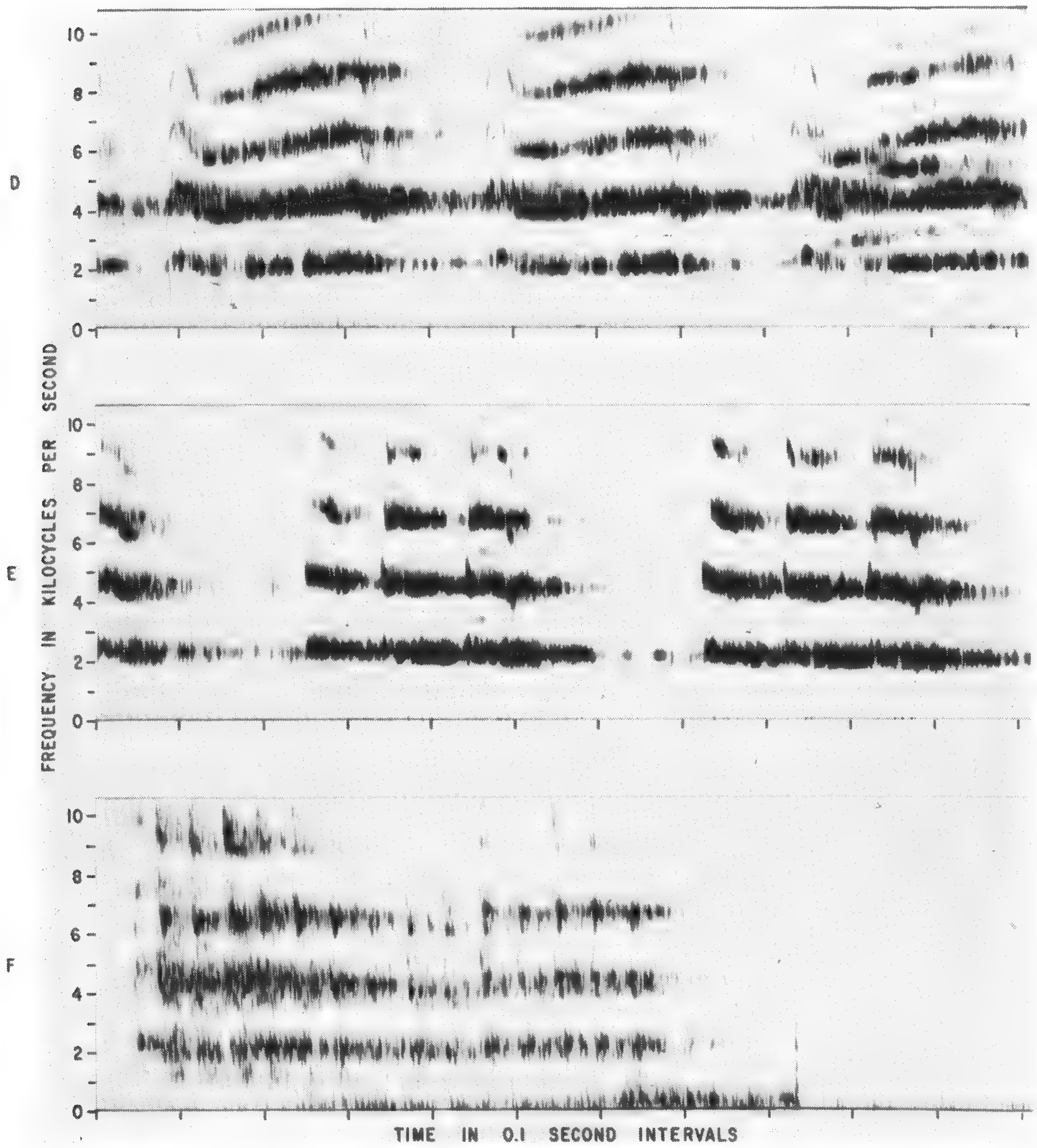

Figure 5. Sound spectrograms of American Kestrel vocalizations. D, Simple Whine from Male 64. E, Treble Whine from Female 65. F, Chitter from Male 58.

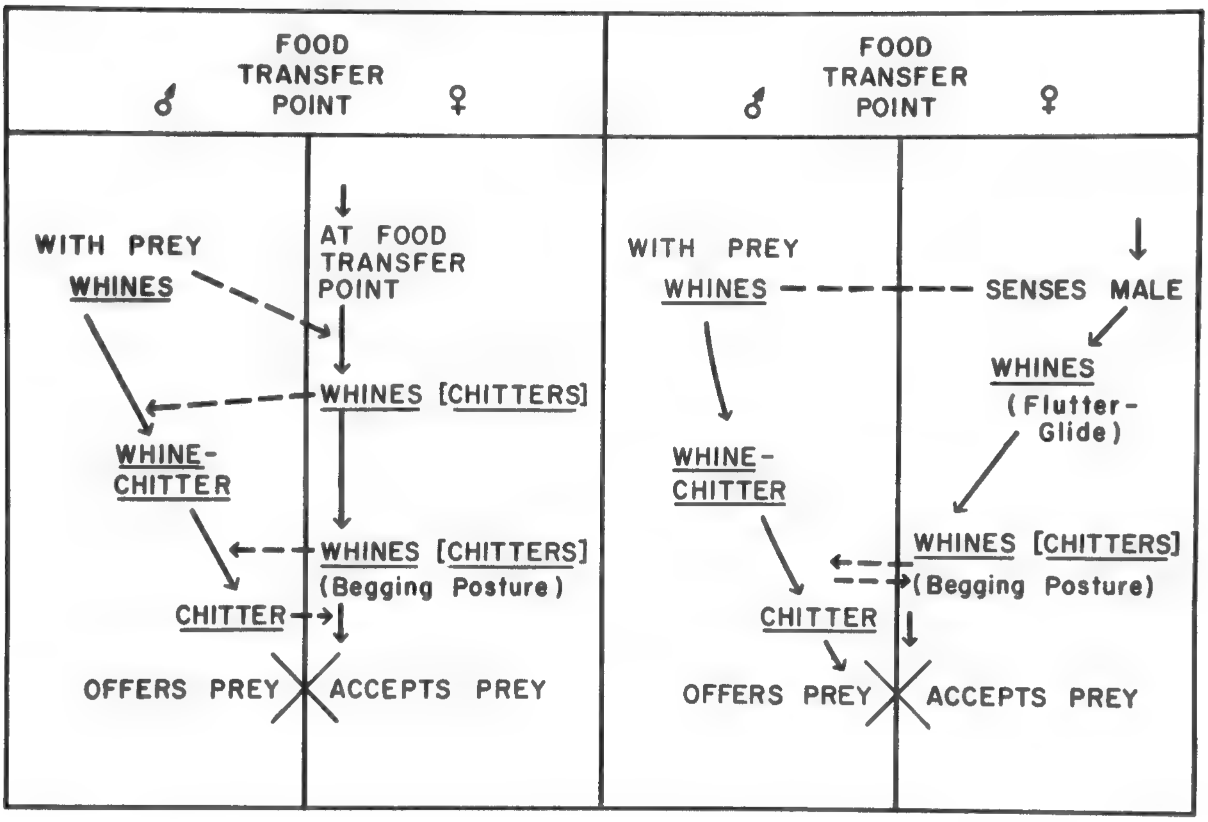

Figure 6. Diagrams of behavioral sequence and interaction between mates in two common variations of courtship feeding of the American Kestrel. Horizontal axis denotes relative distance from the central food transfer point (vertical line), while the vertical axis represents time progression from top to bottom. The solid arrows indicate time-distance progression for the individual; the dashed arrows, reciprocal interactions pointing to the individual responding to the action of the other. The large X at the food-transfer point denotes transfer of food from one to the other. Parentheses show actions occurring at higher levels of motivation; brackets indicate alternative actions. Vocalizations are underlined.

probably associated with the food and courtship-feeding tendency, while the chitter is connected with his friendly approach toward the female.

One of the striking features about the adult Kestrel is its limited repertoire of distinct calls. These three basic vocalizations serve as signals for all interspecific and intraspecific interactions which we have observed, each functioning in its special social contexts. By comparison, the domestic fowl has six classes of adult auditory signals (Collias, 1960), the Canada Goose *(Branta canadensis)* has eight (Collias and Jahn, 1959), and a number of passerines have upward of a dozen or more different calls (Thorpe, 1961, Table 1; Collias, 1963).

Courtship Feeding

In the American Kestrel, as in many other avian species which maintain a strong pair bond, courtship feeding occurs prominently in social interactions between the mates. Usually only the male feeds the female. Courtship feeding appears to serve two major functions: (1) To maintain the pair bond and (2) to act as a mechanism to secure food for the female and young. Regarding the latter function, the male continues to hunt food for the female while she is incubating and later for the small nestlings and her. In this way the female is able to spend more uninterrupted time incubating the eggs and caring for the young, an obvious advantage for a predatory species which often must hunt a long time without success. This division of labor is common in birds of prey (Tinbergen, 1953).

Fully developed courtship feeding involves active participation by both mates, the male bringing prey to the female and she begging for it and taking it from him. There is much variation in the pattern of interaction, depending on the level of motivation of each sex and on environmental circumstances. Figure 6 illustrates two common variations in the normal sequence of courtship feeding, and Figure 7 shows sequences of behavior when one of the mates is highly motivated to courtship feed and the other is not. The diagrams in Figure 7 are less generalizable than those in Figure 6 because the behavior of the birds in these situations is extremely variable as a result of individual peculiarities and the lack of mutually appropriate stimulation to direct the tendencies of the birds into the normal sequences of courtship feeding. Florence Bailey beautifully describes the behavior of such a maladjusted pair (see Bent, 1938:121).

The Whines and Whine-Chitters of the male apparently serve to alert the female to his approach with intent to feed her and to evoke her begging responses when she is receptive. Sometimes the female approaches the male, begging when he does not have food, and he may then go off to obtain prey and bring it to her.

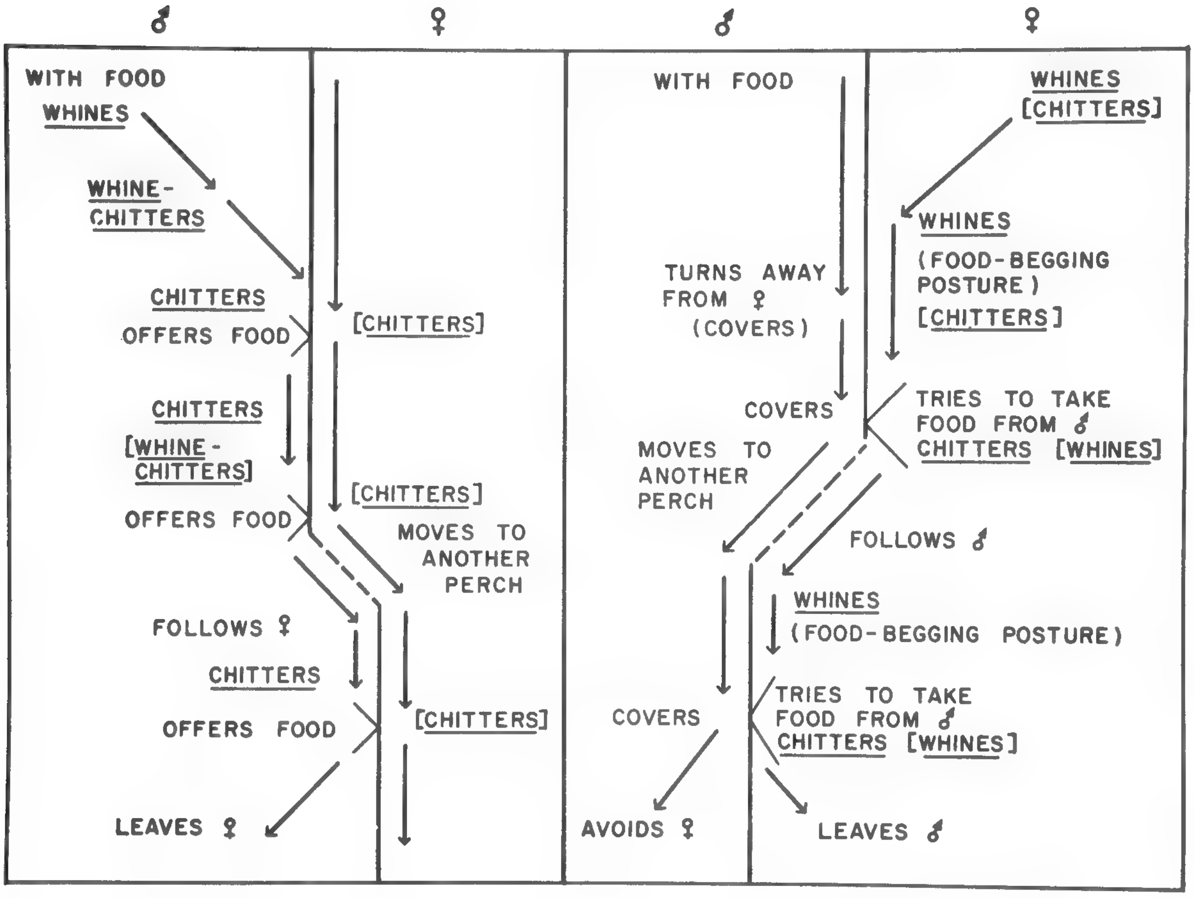

Figure 7. Diagrams of behavioral sequence and interaction between mates of American Kestrel when one is highly motivated to courtship-feed and the other is not. Left, the male is highly motivated; right, the female is highly motivated. Symbolism as in Figure 6. The large darts at the vertical line indicate unsuccessful attempts by one bird to transfer the food.

The active part played by each sex in courtship feeding is most clearly seen during the early development of the behavior patterns which lead to courtship feeding in captives. In the captive male, the first indication of a tendency to engage in courtship feeding is his utterance of Simple Whines at the sight of food. In a few days Whine-Chitters and then Chitters are added as he picks up some food and takes it to a perch to eat. After picking up a piece of meat, he may look up at the female while holding the food in his beak and chittering. Finally the full pattern develops: the male whines at the sight of food, whine-chitters when he picks up a piece of food, chitters as he flies toward the female, and holds the food up to her beak still chittering (see Figure 8). At this point a highly-motivated male may repeatedly try to stuff the meat into his mate's beak if she does not take it from him when he offers it.

In the captive female, the first sign of a tendency to engage in courtship feeding is her willingness to wait and watch the male get his food and eat it instead of going immediately to obtain the food herself. In a few days she starts whining and chittering, and she may follow after the male and try gently to take his food from him if he is unresponsive. When the female is highly motivated and the male is unresponsive, she may forcibly take his food even when plenty is available on the feeding board; or she may try to give food to him if he does not have any. A female which is highly motivated to be fed by the male will sometimes go for a long time without eating when the male is unresponsive to her begging.

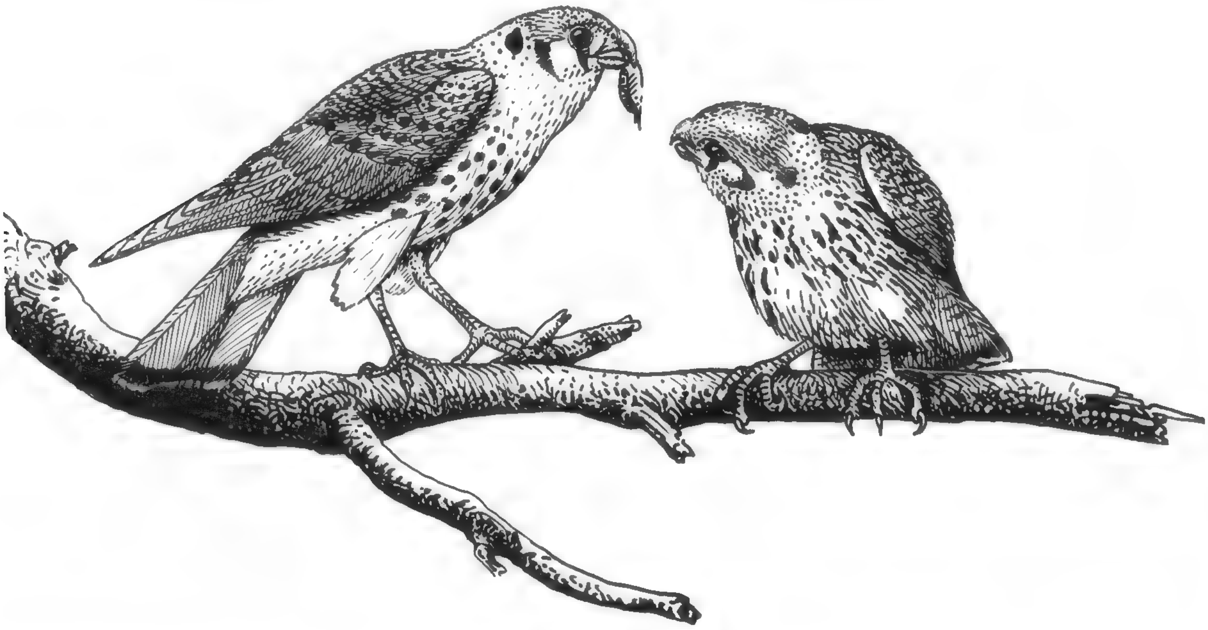

Figure 8. A male American Kestrel presenting food to his mate.

The term "Flutter-glide" refers to a special movement of the wings used by the begging female falcon in flight and by the male occasionally in connection with courtship feeding and copulation (Cade, 1960). It consists of shallow, quick wing-beats executed with the wings fully spread but arched below the horizontal axis of the body. The bird flies slowly but buoyantly while using this wing action. Our captives had limited opportunity to perform such behavior, but we saw it frequently around the nesting sites of wild Kestrels.

Copulation

Copulation as we use the term refers to the mounting of the female by the male and to the subsequent copulatory movements of the mates, whether insemination occurs or not. Copulation is remarkable for its early appearance in the pre-nesting period of the American Kestrel and for its occurrence in many instances before courtship feeding. In the spring of 1962, we saw copulation by a wild pair on 17 March and noted it frequently in various pairs after that time, but we first saw courtship feeding on 27 March by a wild pair which had been seen copulating several times since 20 March. In three of the five pairs which bred in captivity that spring, copulation was observed 2 days, 13 days, and 17 days, respectively, before courtship feeding. In the other two pairs courtship feeding was seen nine days before copulation. Because of the interrupted nature of our observations, we cannot say definitely when courtship feeding and copulation actually began in any given case, but the relative frequency of the two kinds of behavior in the early part of courtship certainly varies among different pairs. The early occurrence of copulation has also been noted by Hartman (1959), who observed a pair of captive Kestrels which started copulating frequently in the latter part of March although the first egg was not laid until 6 May, and by Childs and Mossman (1952) who did not observe eggs in the nest of one pair until six weeks after the first copulation was seen.

Copulations occur rather frequently until the last egg is laid and diminish quickly after the female starts incubation. During the early part of the pre-nesting period, when sociability of the Kestrel is high, copulation is sometimes promiscuous. Although we have not seen any definite instances in New York, it has been reported by Cade (1955) who observed promiscuous matings between members of two pairs in Los Angeles, California, by Childs and Mossman (1952) who observed a group of Kestrels at Berkeley, California, in which two males copulated twice with the same female, and by Fast and Barnes (1950) who described an instance in which one male apparently copulated with two females in succession at Washington, D. C.

The high frequency of copulation by mated Kestrels has been commented on by several authors. Bishop (1925) saw a pair copulate 5 times at 5-minute intervals on 14 April, and 3 times in 15 minutes on 15 April. Cade (1955) counted as many as 6 copulations in half an hour, and Hartman (1959) had a captive pair which copulated 14 times in the space of 36 minutes. Our captive pairs varied considerably in the frequency of copulation: In one case a pair copulated 6 times in 27 minutes, but another pair which produced fertile eggs was never observed in copulation.

The act is accomplished by Kestrels in the following way. The female bows deeply with her legs extended beneath her so that her back slopes head down at an angle of 30 to 50 degrees to the horizontal and with her tail held in a line with her body or angled up slightly and compressed. The male squats on her back on his tarsi with his toes balled into fists, balances with his wings raised over his back and flapping, and brings his tail down vertically to one side of the female's so that the cloacae come in contact (see Figure 9). During copulation the male utters repeated loud Chitters; the female repeatedly gives either Chitters or Simple Whines. Copulation lasts 2 to 10 seconds, and repeated cloacal contacts are made during the longer episodes. The male mounts the female either by stepping up onto her back from the perch beside her or by alighting on her back from the air. Often a flight by the male ends directly on the female's back with copulation following at once. In such instances the female seems to anticipate the male's approach by standing in the copulatory position before he reaches her. Sometimes a female prevents an intended mounting by raising her wings or by hopping off the perch as the male is attempting to settle onto her back.

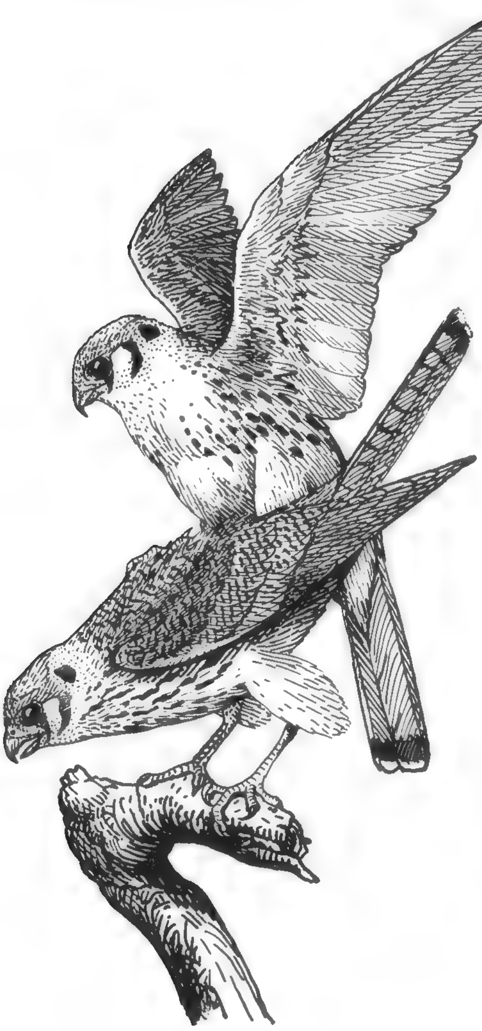

Figure 9. A pair of mating American Kestrels in the characteristic posture.

Activities Directed Toward the Nest Hole

During the period when the nesting site is chosen, wild Kestrels were sometimes seen inspecting old woodpecker holes and other cavities, clinging to the entrance of the hole and looking inside. We do not have enough observations to hazard a generalization on the role of the sexes in this activity, except to say that both sexes actively explore for holes. Several times we saw our captive pairs engaged in activity consisting of either mate going repeatedly in and out of the nesting box and chittering. Perhaps this sort of behavior by the mates—direction of attention and activity toward the nest-site—is important in establishing attachment of the mates to a mutually-acceptable nest and in stimulating the birds sexually.

Flight Displays

Besides the Flutter-glide, Kestrels perform a flight display which we call the Dive Display. It is performed primarily by the male in the nesting or prospective nesting territory during the pre-nesting, incubation, and nestling periods, but probably most frequently during the early phases of courtship. The display consists of a series of climbs and dives with continuous, powerful wing-beats and with a series of three to five Klee notes uttered near the peak of each ascent. The vertical depth of the dives is around 30 to 60 feet. The displaying bird usually starts by banking vertically and dropping at a steep angle of about 50 degrees to the horizon with powerful wing-beats which achieve great speed. At the low point the bird climbs steeply with wings still beating deeply. At the high point the Klee notes are given just as the bird banks and starts down again. Two to six such dives may be performed in succession, and a strong wind seems to stimulate this kind of activity. Sometimes the male swoops over the perched female at the bottom of his dive. The function of the Dive Display is probably analogous, at least in part, to that of the aerial displays of other open-country breeding birds—namely, territorial advertisement, attraction of a mate, and repulsion of rivals (Armstrong, 1947).

Difference in Size Between the Sexes

The well-known difference in size between the male and female of most predatory birds has led to speculation on the biological function and the evolution of this kind of sexual dimorphism. Amadon (1959), Cade (1960), and Selander and Giller (1963) have reviewed theories on the function of sexual-size dimorphism. Cade (1960:244) concluded that for large falcons like *F. peregrinus* and *F. rusticolus* "a reproductively successful pair bond can result only when the female falcon is clearly dominant to the male and when the

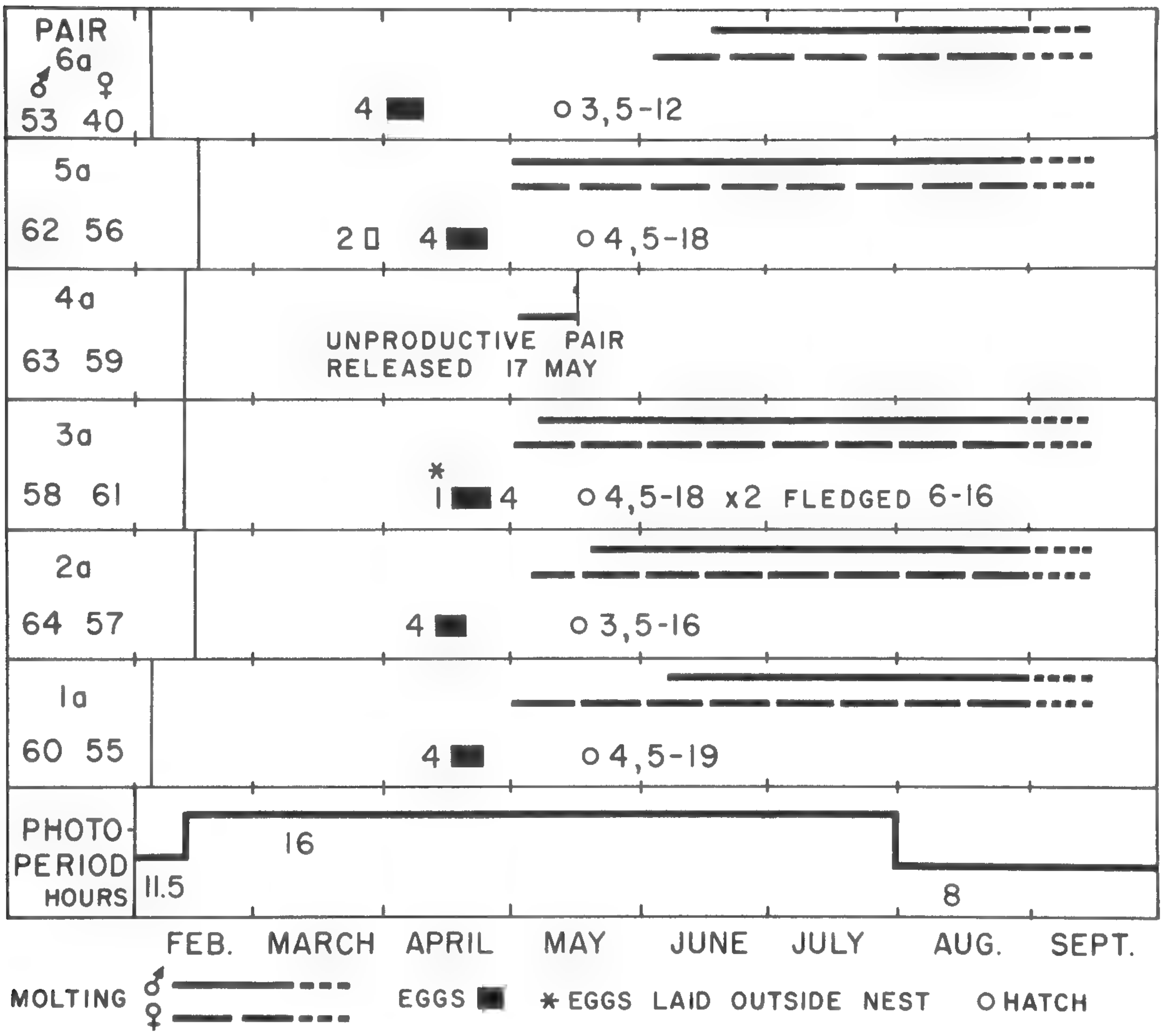

Figure 10. Summary of the breeding performance of captive American Kestrels at Syracuse University in the winter and spring of 1962. Solid black bars for eggs indicate the period of laying; size of the clutch is indicated by a numeral. The open bar for Pair 5a indicates the laying of a damaged and infertile egg which was removed before the final clutch was laid. Dates and number of eggs hatching are indicated for each pair. Dotted lines for molt indicate periods during which molt ceased, but the exact times were not determined.

male makes a biologically adequate adjustment to his subordinate role in the pairing situation." Since large falcons are stronger and more dominant in intraspecific relations, selection could have favored the existence of a difference in size between males and females. These considerations led us to attempt to test the possible social function of the female's larger size with our captive Kestrels.

The female American Kestrel averages slightly larger and heavier than the male, but size dimorphism is not as marked in this species as in many larger falcons (Cade, 1960). There is, however, a good deal of geographic variation in

TABLE 1

History of American Kestrels Used in Experiments

Bird	*Origin, Date*	*Weight in grams*		*Mates*
		Trapped	*Captive*	
Males				
53	Florida, 3 February 1962	112	158	a. 40 b. 56
54	Florida, 3 February 1962	69	69	died 11 February 1962
58	Florida, 3 February 1962	—	111	a. 61 b. 55
60	Florida, 3 February 1962	80	94	a. 55 b. 57
62	New York, 2 December 1961	—	151	a. 56 b. 61
63	New York, 2 December 1962	—	114	a. 59 released 17 May 1962
64	New York, 13 February 1962	—	165	a. 57 b. Young
66	Florida, 26 November 1962	95	114	b. 65
Females				
40	Florida, 3 February 1962	—	100	a. 53 died 30 October 1962
55	Florida, 3 February 1962	120	166	a. 60 b. 58
56	Florida, 3 February 1962	85	116	a. 62 b. 53
57	Florida, 3 February 1962	101	136	a. 64 b. 60
59	Florida, 3 February 1962	116	116	a. 63 released 17 May 1962
61	Florida, 3 February 1962	118	158	a. 58 b. 62
65	Florida, 26 November 1962	83	110	b. 66
Young	Captive-bred, hatched 18 May 1962	—	109	b. 64

size, and by trapping individuals of the small Florida race, *F. s. paulus,* and of the large northern race, *F. s. sparverius,* we were able to obtain males which weighed only half as much as the largest females and females which were one-third smaller than the largest males (see Table 1).

We assumed that if the female must be dominant in the pair for successful mating and if her dominance depends on larger size, then a pair in which the male is larger than the female might show aberrations in behavior and breeding performance. The captive birds were mated in the three possible combinations with respect to size. In the first breeding cycle of the captives there were three pairs in which the male was bigger than the female, two in which the female was bigger than the male, and one in which both were the same weight. In the second breeding period there were two pairs of each combination. Figure 11 shows the breeding performance of the ~~six~~ pairs in the spring of 1962. All but one pair laid eggs and hatched them. The female of the pair which did not breed was sexually unresponsive, did not beg to be fed by the male, and was peculiar in having many broken remiges in her left wing, making flying within the cage difficult. She was the same size as her mate.

The other pairs of this group showed no basic differences in performance. Obviously the various size combinations did not interfere with production of

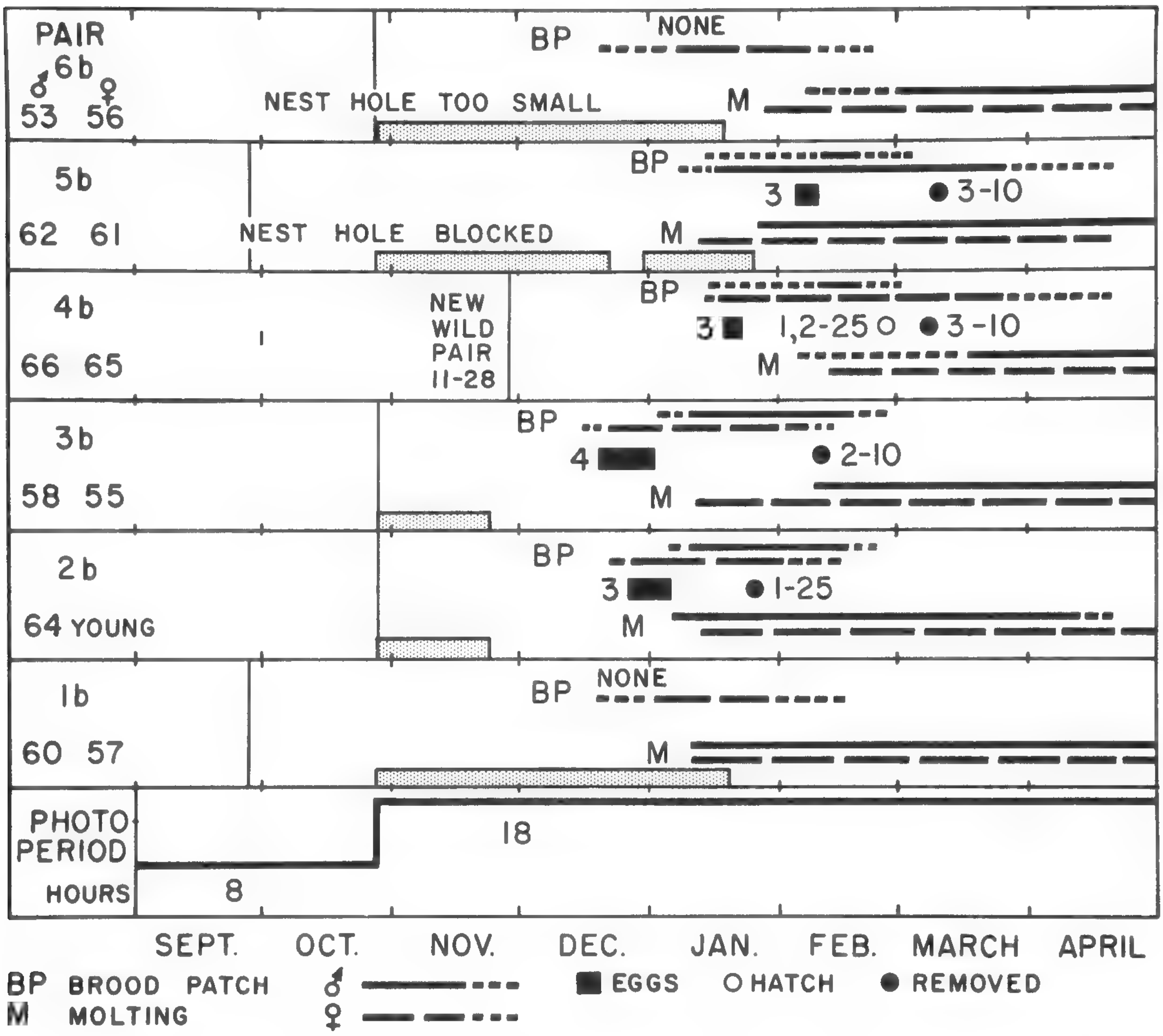

Figure 11. Summary of the breeding performance of captive American Kestrels in the fall and winter of 1962-63. Gray bars indicate periods when nest holes were obstructed. Black bars indicate laying periods. Dotted lines for brood patches show periods when bare areas were less than maximum, during formation and regression.

fertile eggs, even though in one case a small female had difficulty supporting a heavy male during copulation. Moreover, we saw no consistent or marked indication of dominance-subordination relationships between the mates. Only one of these pairs, however, was successful in fledging young. Pair 3a, consisting of a small *paulus* male and a very large *sparverius* female, fledged two of four chicks. A total of 18 chicks were hatched, but all save these two were eaten by the parents within a week after hatching. We do not know whether these chicks were killed by the adults or died from some other cause and were then eaten.

We can only conclude that, so far as these experiments indicate, size difference between the mates has no marked effect on social or sexual behavior in captivity. This result may be specifically associated with the small size of the American Kestrel, its lesser degree of sexual dimorphism in size, and its sexually dimorphic plumage, as compared to its larger congeners. See Cade (1960) for pertinent discussion.

Environmental Factors Influencing Breeding

Photoperiodicity

Farner (1959) reviewed photoperiodic control of gonadal cycles in birds and compiled a list of 27 species in 12 families in which photoperiodic stimulation of gonadal devlopment has been experimentally demonstrated. At the time of this writing no species in the Falconiformes had been investigated. In order to bring our captive Kestrels into reproductive condition to study their behavior, we manipulated the photoperiod, and while our conditions were not designed to provide a rigorous test of photostimulation with an adequate control group, our results are worth considering within the framework of photoperiodic theory.

Our manipulations of light were based on the assumptions that a long (summer) day length would be stimulatory for Kestrels and that a short day length would be non-stimulatory. The following photoperiodic regimen was followed during our study of the captives: 12 February to 31 July 1962, 16 hours of light and 8 hours of darkness; 31 July to 27 October, 8 hours of light and 16 hours of darkness; 27 October to 6 May 1963, 18 hours of light and 6 hours of darkness. A few days prior to 12 February 1962 the birds were held on a day length of 11.5 hours.

In the first group (Figure 10) there was a close synchrony of egg-laying by the five pairs which bred, the average time between initiation of the 16-hour day and the first egg being 54.6 days with extremes of 43 and 63 days. Temperature in the cages closely approximated that outdoors. A naturally-mated pair of *F. s. paulus* kept under comparable but not identical conditions at the same time produced the first egg in 38 days. These results are not conclusive because the time of laying was approximately on the same schedule as in wild birds around Syracuse, but they provide a useful comparison with the results of the second breeding cycle which is summarized in Figure 11.

Pairs 2b, 3b, and 4b of Figure 11 are considered equivalent since they were subjected to an artificially lengthened photoperiod in fall and winter, as well as to other comparable conditions. The average time between start of the 18-hour day and first laying was 54.8 days with a range from 51 to 60 days, a period of time which is strikingly similar to that obtained in the first breeding cycle. The other pairs in the second breeding cycle received different treatment involving their nest-sites and are discussed in the next section. In

1959-60 a male and female of the *sparverius* race were kept on a 14-hour day beginning 16 December; the first egg was laid 91 days later on 17 March.

The eggs of Pairs 3b and 4b were fertile, but only one egg hatched. The eggs of Pair 2b appeared on examination after the incubation period to be infertile; at least no development had occurred. These eggs were laid in December and January when temperatures in the cages were frequently below freezing. The average "daytime" temperature in the cages for the month of January 1963 was 45°F. The fact that laying occurred in December and January when temperatures were declining, whereas wild Kestrels around Syracuse lay in April and May, is a strong indication that the photoperiod was the important stimulating factor.

Influence of Nest-Site

The fact that Kestrels are active in and around the nest-site prior to egg-laying suggests that the nest-site may play a role as an important stimulant for production of fertile eggs. Brockway (1962) found that the nest-box is necessary for full ovarian development of the Budgerygar *(Melopsittacus undulatus)* in captivity. An experiment was done to compare the behavior and reproductive performance of mated Kestrels having nest-boxes with standard 3-inch holes with that of other pairs having nest-boxes with obstructed holes. Figure 11 summarizes the conditions and results.

In Pair 1b the nest-hole was blocked from the onset of the long photoperiod until 19 January. Pairs 2b and 3b had nest-holes blocked only until 23 November and, with Pair 4b, constitute the control group with nest-holes. Pair 5b had its nest-hole blocked until 25 January, except for a week between 22 and 30 December; and Pair 6b was provided with a nest-hole only 1.5 inches in diameter — just big enough to admit the head of a Kestrel — until 18 January, when the hole was enlarged to a diameter of 2 inches. On 25 January, this hole was further enlarged to the standard 3-inch diameter. In the last instance, the regular hole was covered by a pasteboard front with the smaller hole in it to see whether or not the birds would try to enlarge the hole to permit their use of the nest-box. Pair 6b showed no interest in the small hole and is, therefore, placed in the group without nest-holes.

Absence of a nest-hole prevented or delayed egg-laying. The female of Pair 5b laid three eggs beginning nine days after the nest-hole was unblocked the second time and 18 days after the last egg of Pair 4b had been laid.

There were obvious disturbances in courtship feeding in the pairs without nest-holes. In Pairs 2b, 3b, and 4b, which had normal nest-holes, courtship feeding developed fully. Courtship feeding was not observed in Pairs 1b and 6b, but the females showed some tendency to do so—interest in the male's food and occasionally begging to be fed—but with little or no cooperation from the males. The male of Pair 6b did not progress past the whining stage, the male of Pair 1b consistently avoided his mate's approach when he had food, and the male of Pair 5b was not seen to engage in courtship feeding until 17 days after the nest-hole was opened the second time.

The female of Pair 5b may have laid eggs as soon as nine days after the nest-hole was opened on 25 January because the nest-hole had been open for a prior time between 22 and 30 December and thus may have served to stimulate the birds. Both mates spent a considerable amount of time inside the nest-box during that week in December, but even so the eggs showed no signs of fertility.

TABLE 2

*Data on Brood Patches for Two Pairs of Captive American Kestrels

Date	*Pair 4b*		*Pair 5b*	
	Male	*Female*	*Male*	*Female*
22 December	none	none	none	none
27 December			none	none
5 January		none		
9 January			none	
10 January	none	R 4x1.5 L 3x1 +		
16 January	none	R 3.5x1.5 L 3.5x2	R 1.5x1 L 2.5x1.5 +	R 3.0x1.5 L 3.5x2 ++
25 January			R 2.0x1.0 L 1.5x1.5 +	R 3.0x2.0 L 3.5x2.0 ++
4 February	R 2.3x1.0 L 3.0x1.5			
10 February	R 2.2x1.5 L 2.6x1.5	R 3.2x2.0 L 3.5x2.3 +++		
12 February			R 2.0x1.1 L 2.0x1.4 ++	R 3.8x2.0 L 3.7x2.1 +++
17 February	R 2.5x1.5 L 2.5x1.5			
23 February			R 1.5x1.2 L 2.0x1.5 ++—	R 4.0x2.2 L 4.2x2.4 +++
5 March	R 2.0x1.3 L 3.2x1.8 +++	R 3.0x2.0 L 3.0x2.0 +++—		
10 March	R 2.2x1.3 L 2.5x1.8 ++	R 3.0x1.7 L area patchy +++—	none	R 4.0x2.2 L 4.0x2.5
19 March	R 2.2x1.2 L 3.0x1.5 +++	feathers growing in patches	none	R 3.0x1.8 L 3.2x2.0 +++—
8 April	R 2.5x1.4 L 3.5x1.4 ++—	none	none	R 3.4x1.7 L 3.0x1.5 —
20 April	R 1.9x1.6 L 2.0x1.6 ++	none	none	R 2.8x1.5 L 3.0x1.5 — (scattered bare spots)

*Measurements in cm; R indicates right hand patch, L the left; + means patch forming with down falling out, ++ indicates vascularization, +++ indicates vascularization and edema, and — means regression with new feathers growing out of bare areas.

Brood Patches

The development of brood patches in these birds helps in understanding the effects of this experiment. Although Bailey (1952) grouped the Falconiformes among those orders in which birds develop a single median patch and in which only the females have patches, we found that both sexes of the American Kestrel developed bare, oval incubation patches on each side of the breast in the apteria between the axillar and sternal regions of the ventral feather tracts. Male and female Peregrines in the Arctic have brood patches in the same areas (Cade, unpubl. data). In falcons the sternal and abdominal regions of the ventral tract lie close to the mid-line, and there is little space in the median ventral apterium for the development of a brood patch, but in buteonine forms the sternal and abdominal regions are in lateral positions with a very wide ventral apterium (see Compton, 1938). In our captive Kestrels the brood patches measured approximately 3 to 4 by 2 to 3 cm with the long axis extending antero-posteriorly. The skin in these areas in both sexes became highly vascularized and edematous, with the edema occurring for a shorter period than the vascularization.

Table 2 presents data on the brood patches of Pairs 4b and 5b, and Figure 12 includes data on brood patches for all pairs in relation to laying and molt. All females developed brood patches at very nearly the same time, except in Pair 4b, regardless of what was done to their nest-holes. Males developed brood patches except in pairs in which the female laid no eggs. Females developed maximum bare areas during or just before laying, while males developed theirs just after completion of the clutches.

It thus appears that a nest-site is not necessary to stimulate the female Kestrel to the stage of brood patch formation and that development of the patch progresses just as fast in females without nests as in those with nests. On the other hand, ovulation is inhibited by the absence of a suitable nesting place.

Conclusions and Summary

A study of the breeding biology of *Falco sparverius* was undertaken with the purpose of describing breeding behavior and determining behavioral and environmental factors involved in integrating the pair. Observations were made on nine pairs of wild birds around Syracuse, New York, and experiments were carried out on 20 captive Kestrels held in large flight rooms.

The American Kestrel has a well-defined spring and summer breeding season. Although usually solitary and hostile to others of the species during the fall and winter, Kestrels become sociable at the beginning of the breeding season and form pairs which function as well-integrated breeding units. Breeding behavior is characterized by copulation, courtship feeding, nest-site inspection, and aerial display, all of which have pair-integrating functions. Vocal signals are conspicuous features of these behavioral patterns. The Klee is an expression of excitement in aggressive contexts; the Whine, of which there are two types called the Simple Whine and the Treble Whine, is primarily a food call; and the Chitter is associated with sociable approach and bodily contact.

The early and frequent occurrence of copulation in the pre-nesting stage of the breeding cycle suggests that copulation may have some function in pair integration other than fertilization. Possibly the act serves as a ceremony to bring potential mates together and to hold them together early in the season, especially since our observations indicate that copulation often appears before courtship feeding develops. In this case, courtship feeding may gradually be substituted for copulation as a pair-binding process later on when the birds are occupied with incubation and care of nestlings and have little opportunity to engage in mating activities.

Copulation may also serve in sex recognition. Although there is marked sexual dimorphism in the plumage of the American Kestrel, it cannot be assumed without experimental evidence that these sexually-dimorphic characters function in sex recognition. Many falcons lack sexually-dimorphic plumage patterns. Rather, it seems plausible to suggest that the sexes are drawn together initially by the occurrence of a generalized social tendency early in the breeding season and that they subsequently pair off male with female through the influence of complementary behavioral roles in copulation and feeding ceremonies. In this connection, it is interesting to note that Cade (unpubl. data) failed to alter the normal relations between the mates of two pairs in southern California by dyeing the males a uniformly black color which obscured all pattern.

No clear-cut social dominance by the female appeared under our experimental conditions, possibly because social dominance in falcons is concerned mainly with conflicts over food and our captives were always well fed and, in fact, considerably fatter than when first trapped (see Table 1). When Kestrels are reduced in weight, dominance-subordination patterns soon develop (Cade, unpubl. data). Nonetheless, the female was sexually dominant in our captive pairs (see Noble, 1939, for the distinction between social dominance and sexual dominance). This sexual dominance of the female takes the form of controlling the time of copulation and nesting, and she often initiates episodes of sexual activity.

Our experiments indicate that the nest-box somehow served as a sexual stimulant for the captive Kestrels. Absence of the nest-hole appeared to inhibit full sexual behavior in males and prevented ovulation in females, but the specific characteristics of the nest-site which evoke sexual responses are not yet known.

As in many north-temperate-zone birds, photoperiodic stimulation is the most important environmental factor governing the seasonal timing of the breeding cycle in North American populations of the American Kestrel. In mid-winter and despite cold temperatures, captive Kestrels responded to a long photoperiod by coming into breeding condition and producing fertile eggs approximately three months ahead of the natural schedule at Syracuse, New York.

We hope the ease with which both the male and female Kestrel can be brought to full reproductive performance in captivity will attract the interest of photo-experimentalists who are accustomed to working with the generally less responsive passerines. Breeding populations of *Falco sparverius* range from near the northern limits of the boreal forest in Alaska and Canada, approximately 65°N. Lat., south through much of the tropical and equatorial regions of Central and South America all the way to Tierra del Fuego, approximately 55° S. Lat. (Peters, 1931). With such a latitudinal distribution, the American Kestrel provides an unparalleled opportunity to study the relative importance of environmental factors such as photoperiod, temperature, rainfall, and food supply on the reproductive biology of closely related populations which live in a diversity of environments.

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THE SONGS OF THE APAPANE

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Photographs by the author

The Apapane *(Himatione sanguinea)* is surely the best known of the 22-odd genera in the famous family of Hawaiian honeycreepers (Drepaniidae). Visitors and residents in Hawaii see this scarlet bird readily at such popular places as the Volcano House in Hawaii Volcanoes National Park (Island of Hawaii), the Kalalau Overlook at Kokee State Park (Kauai), Hosmer Grove in Haleakala National Park (Maui), and on many of the forest trails in the mountainous regions of the six major islands where the ohia tree *(Metrosideros polymorpha),* a myrtle, grows and flowers.

The honeycreepers are among the best-known examples in the world of adaptive radiation in birds. We presume that, several million years ago, one or two species of birds somehow arrived in Hawaii, probably from America. Finding no competition they multiplied rapidly and then competed heavily with each other, thereupon exploding into several different forms: some with long bills for sipping nectar and eating insects; others with short, finch-like and even parrot-like bills for eating fruit and cracking seeds. These birds eventually became highly specialized, so much so that when the white man came to loose cattle in the forests—thereby thinning them—and change the pattern of the lowlands with sugarcane and pineapple fields and cities and towns, several species could not adjust and became extinct. The Apapane survived largely because its original habitat, the ohia forest, remained intact to a considerable extent. Old stories report that the Oo (*Moho* sp.) and Mamo *(Drepanis pacifica)* simply flew away whenever a cow or person walked through their territory. The Oo and Mamo are gone now; the Apapane tolerates visitors.

We must remember that the Hawaiian Islands are farther removed from a land mass than any other archipelago in the world. Such isolation plus a complexity of habitats, providing many potential niches, together with the fragmentation of the range into semi-isolated units (neighboring islands) which allowed colonization and recolonization provided the opportunity for specialization and for more genera in proportion to species than occurs in other places.

Recent Observations on the Apapane

Captain Cook who discovered the Hawaiian Islands in 1778 mentions the Apapane in his journals (see Cook and King, 1785) as "about the size of a canary-bird, of a deep crimson colour" and described the feather cloaks and caps made by the ancient Hawaiians of the red and yellow feathers from the Apapane and other birds. Today the Bishop Museum in Honolulu has a world-famous collection of feather clothing as well as study skins of present and extinct drepanids.

Since Cook's time, Henry C. Palmer, collector for the 1890-93 Rothschild Expedition, Scott B. Wilson, George C. Munro, Robert C. L. Perkins, Henry Wetherbee Henshaw, Dean Amadon, Paul H. Baldwin, William W. Dunmire, and Roger Tory Peterson have described the Apapane more fully. A few of these men were relatively short-time visitors. Munro, who died in 1963 at the age of 97, was the great exception; he came to Hawaii in 1890, assisted Palmer, and stayed on to write the "Birds of Hawaii" and become unofficial dean of Hawaiian ornithologists. I have known the Apapane since 1948; Mrs. Ward has known it all her life.

Previous writers have mentioned little regarding the great variety of songs and calls of the Apapane. Perhaps they were not in Hawaii long enough; possibly they did not travel widely enough to notice that these birds called and sang differently in different areas; certainly they lacked the modern tools for recording the vocalizations of birds. Wilson and Evans (1890-99) wrote: "The note of the Apapane is a feeble though clear *tweet* twice repeated, but it also has a pretty simple song, generally heard soon after sunrise or towards sunset." In 1902 Henshaw wrote: "The akakani's [local name around Hilo, Hawaii] song is sweet to the ear but is monotonous, and is delivered at all seasons of the year and at all times of the day. In fact this species and the Iiwi rank as the most persistent songsters the writer has ever heard. The akakani has a delightful habit of gathering together in loose companies in the tops of the leafy ohia trees about midday, when hunger is appeased and most of the other forest songsters are silent, when the males join in a subdued lullaby and literally sing themselves and their mates to sleep." George Munro (1960), whose 73 years of field work here equals in time that of all the other dedicated and competent ornithologists by several multipliers, said: "It has several calls and a sprightly song not particularly musical but cheerful; however, in continuous repetition by one bird it becomes monotonous. When large numbers are calling and singing together with other birds the effect is pleasing."

William W. Dunmire, formerly Park Naturalist in Hawaii Volcanoes National Park, wrote in 1961: "You will hear a constant chorus of short songs and notes from the highest ohia tops whenever Apapanes are about. The quality varies from sweet whistled notes to harsh chips and buzzes, usually intermixed. Probably the most varied songster in the park." Munro (1960) remarked: "It is a strong flier, vibrating its wings loudly in flight." Perkins (1901) observed: "The song of the 'Apapane' is short, monotonous, and often repeated, but not unpleasing. It has a singularly plaintive call-note." Baldwin (1953) stated: "Birds of this species sing at all times of the year. The variations heard in song from place to place and time to time are countless, in spite of several recognizable, basic patterns."

On our honeymoon in 1950 Mrs. Ward and I recorded just below the Volcano House an Apapane song that we had never heard anywhere else. Later, on Kauai, we listened to still different songs and calls. Since that time we have been back to these same places and heard, over a decade later, these same songs and no others. At first we thought that the population of Apapanes on each island had its own individual song; later we found great differences among the songs of the birds on the same island.

Figure 1 (*above*). Apapane habitat in ohia and fern forest near Volcano House, Hawain Volcanoes National Park, Island of Hawaii.

Figure 2 (*below*). Recording Apapane calls at Lua Manu Crater, Chain of Craters Road, Hawaii Volcanoes National Park, Island of Hawaii. Note the packboard for carrying the parabola.

While we were recording the bird songs requested by Dr. Peter Paul Kellogg for Peterson's "A Field Guide to Western Bird Songs," we made more Apapane tapes in more places and in comparing them began to realize how many different songs the Apapanes must have. A study of spectrograms, made for us by Dr. Robert C. Stein, showed that the differences among the songs were rather spectacular. When we compared some of the more complicated Apapane songs with spectrograms of other complex songs such as that of the Hermit Thrush *(Hylocichla guttata)* in Lanyon and Tavolga (1960), we decided that the musicianship of the Apapane appears to be unsurpassed. In this article, spectrograms of six calls and ten songs, made at eight locations on three islands, illustrate these variations. There probably are so many others unrecorded that we wonder if the songs of the Apapane might possibly compete with the "twenty basic themes in forty-seven songs" of the European Mistle Thrush *(Turdus viscivorus)*, described in the work edited by Bell (1959).

Description

Apapanes average about 5.25 inches in length and are dark crimson above and below, brightest in the head and shading off to white on the abdomen. (See Plate I).The under tail coverts are white, the wings and tail black. It has a slightly-curved black bill and black legs. Although some of the earlier observers considered the female a bit lighter than the male, the sexes are quite similar. Immature birds are grayish brown above and buff below. Amadon (1950) gives detailed measurements and anatomical details.

The only bird that might be confused with the Apapane is the Iiwi *(Vestiaria coccinea)* which associates with it, yet is rarer. The Iiwi averages 5.75 inches in length and is vermilion with black wings. A longer and quite deeply-curved rose-colored bill and yellow legs distinguish the Iiwi from the Apapane.

Activities

Apapanes nest over a rather lengthy period, and we see immatures many months of the year. However, the heaviest nesting is from February through May. Nests are usually in high ohia trees, but, around Volcano House particularly, are sometimes in short, scraggly trees. The nest, open and cup-shaped, is 5 inches in outside diameter, 2 inches in the bowl, 2 inches deep, and loosely constructed of twigs, fibers, rootlets, and grasses. The only written descriptions of nesting behavior come from Seale (1900), who writes of a male spreading its wings and strutting on a branch like a turkey cock, and from Baldwin (1953), who tells of males driving other males from nesting trees. According to Bryan (1905) the egg is .75 x .55 inches with lilac spots or blotches on a white background. Munro (1960) states that the eggs are "three in a clutch .69 x .5 inch, white with streaky reddish brown spots thicker in a band round the large end."

Apapanes are not given to elaborate displays. Usually they are busy feeding, often in small flocks, combing through flowering blossoms in search of nectar and insects, or sometimes working over a branch for insects. At such times they call often while on the wing. When the male sings, he perches quietly and gives forth his song at intervals of from 10 to 30 seconds. No other Apapanes sing close to him, but one can hear other birds singing the

Plate I. Apapane in a flowering ohia tree. Painting by Robert Verity Clem.

same songs in the distance. We believe this is territorial identification. We have never heard Apapanes singing on the wing but this does not imply that they do not.

Apapanes are difficult to observe for they frequent the forest ceiling at a level high above the ground (see Figure 1). I well recall a morning with Guy Emerson when I tried to show him some Apapanes a good 75 feet above us in a forest canopy in Kipuka Puaulu, popularly known as "Bird Park," in Hawaii Volcanoes National Park. Even with binoculars we had difficulty keeping track of the movements and activities of the birds through intervening branches and leaves. Just as we were beginning to get an idea of what one group was doing, it flashed away so quickly that we did not know where it went.

A common sight is a small flock of from six to a dozen making a quick, undulating flight from one part of the forest to another. I have been close enough to flying birds to hear and record the buzz of their wings.

Perhaps the best place to look for Apapanes is from the edge of a volcanic crater where one is on a level with the crowns of the ohia trees growing up from the bottom. If such a tree is flowering, it is worthwhile to sit quietly for a few hours and try to get better acquainted with the species. We made several recordings this way. (See Figure 2.) I should add that trade winds blowing almost continually make recording of bird songs difficult in Hawaii. Baldwin (1944) wrote of irruptions of Apapanes—of thousands of birds attracted to some huge flowering ohias—in July 1937 and May 1942 at and near Kipuka Puaulu.

Ecology

The "lehua," the name of the brilliant red blossoms of the ohia tree, are pompom clusters (see Plate I) of hair-like stamens. A drop of nectar at the base of each hair attracts the Apapanes and other honey-eating drepanids. Cocking their tails wren-fashion at times the Apapanes flash in and out of the blossoms, searching for the nectar. Although they appear to rely on this bit of sweet, they also eat insects found in the forest. Baldwin (1953) gives a very complete account of the species of insects and plants used by these birds.

The truth is that Apapanes actually obtain their living in the habitat of flowering trees, primarily the ohias which are sometimes 100 feet tall. Ohias make up a major portion of the forest from sea level to 9,000 feet with the heaviest concentration from 3,000 to 6,000 feet. The birds also find nectar in the blossoms of a few other trees—for example, the mamani *(Edwardsia chrysophylla)* with bright yellow, pea-shaped blossoms. All ohia trees do not bloom at the same time. Almost always there is a tree in full bloom here or there. The birds have to migrate around a little, sometimes vertically, to find a tree in bloom but never have to travel far.

The House Finch *(Carpodacus mexicanus),* introduced before 1870, has invaded several Apapane habitats, particularly around Volcano House where it is picked up in the sound recordings, as has the Red-billed Leiothrix or Japanese Hill Robin *(Leiothrix lutea)* introduced in 1918. Fortunately the food habits of these two are not the same as those of the Apapane.

According to Perkins (1901) the Apapanes occurred at sea level in Captain Cook's time. Captain James King (see Cook and King, 1785), who continued Captain Cook's journals after his untimely death in 1779 at the hands of the Hawaiians, wrote of birds that appear to have been Apapanes feeding on nectar from coconut blossoms. Several old accounts describe storms that blew large numbers of Apapanes and Iiwis down to the lowlands where, unable to find their way back, they perished from lack of food. There are also old records of Apapanes being blown from the Island of Kauai across an 18-mile channel to Niihau where they died of starvation. We are unaware of any recent records of these birds being blown to the lowlands in any great numbers. Two Iiwis were found dead at 3,500 feet elevation on 5,500-foot Kohala Mountain on the Island of Hawaii in May 1938 and one Iiwi was found dead at sea level near Ewa on Oahu in 1963. This single bird must have come from the Waianae Mountains, elevation 4,000 feet. Aside from this, Apapanes and Iiwis no longer occur in the lowlands and city dwellers never see them.

Perkins wrote in 1901 and Amadon repeated in 1950 (but Baldwin in 1953 did not) that Apapanes sometimes get from island to island by accident during a storm. Amadon added that they get lost in fogs and fly to other islands.

The Apapane is a stronger flyer than the other honeycreepers; also it looks the same on all islands. Some have considered these facts as circumstantial evidence that interchanges among Apapane populations are possible, thereby preventing true isolation.

With the economic growth of the Hawaiian Islands, the reduced populations of Apapanes will keep more and more to their remote mountain habitats. The fogs in these mountains are local, never at sea level and never at great heights. Air trips among the islands show that fogs almost never, even in general storms, extend continuously from island top to island top. The United States Weather Bureau advises that occasionally, during southerly storms, a band of clouds may extend from one island to another. Birds flying in such a cloud could, by increasing or decreasing altitude, escape from it. I have the impression now, as have my associates in these studies, that the Apapanes travel very little between islands. Even if a storm blew a few to another island, they would still have the problem of finding their way up to the ohias again. The number of apparently "local dialects" that we have recorded strengthens these impressions. We are now presuming that the birds which may survive being blown to another island are too few to change the local dialects any more than several Englishmen moving to Honolulu would affect the pidgin spoken here.

Sound Recordings of Calls and Songs

This brings us to an analysis of the songs we have recorded. Just as the language of the Indians of North America helps trace their migration routes and tribal pattern; so the multiple calls and songs of the Apapane may give us clues to their movements, local populations, possible isolating mechanisms, and/or continuing adaptive radiation.

Our map (see Figure 3) pinpoints the recording locations and indicates the habitat of the Apapane which is about the same as the extent of the ohia forest except that the birds frequent the wet areas more than the dry and occur, for the most part, above 2,000 feet.

We use Tapesonic, Nagra, and Magnemite recorders at 15 inches per second, and an Altec 661-B microphone in a 40-inch parabola; we recorded all the songs and calls of the Apapanes on the Magnemite or the Nagra. Dr. Stein made the spectrograms which are reproduced in this paper. Frequency in kilocycles is indicated at the left of each spectrogram; time in seconds, below. The descriptions of the sample calls and songs of the Apapane that follow combine Stein's technical comments with my field notes.

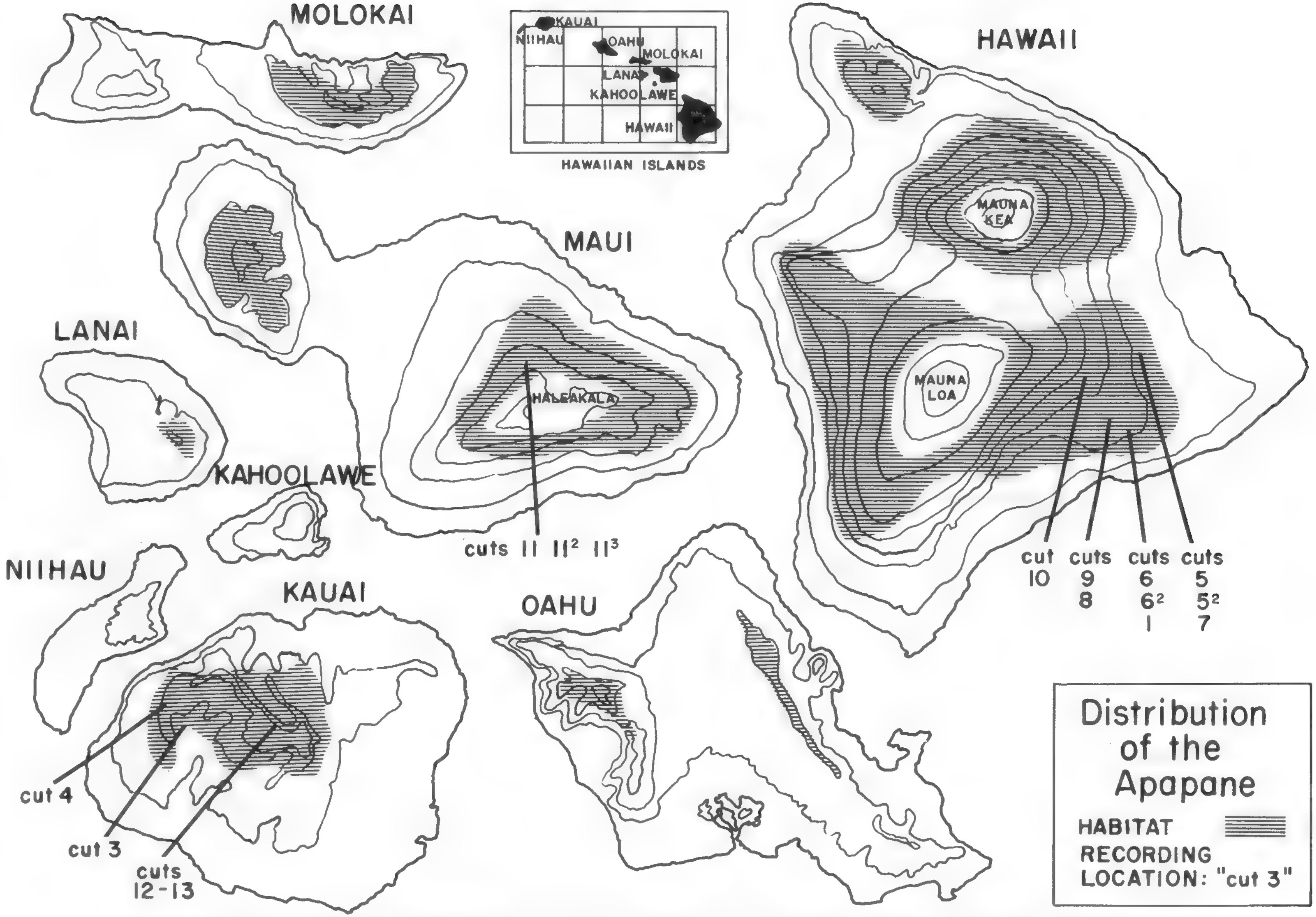

Figure 3. Approximate distribution of the Apapane in the Hawaiian Islands. Locations where recordings of the calls and songs of the Apapane were made are indicated by cut numbers.

Calls of the Apapane

A. Cut 6[1] (Figure 4). Lua Manu Crater, Chain of Craters Road, Hawaii Volcanoes National Park, Island of Hawaii, 30 May 1960. Elevation 3,650 feet. Rainfall 100 inches. Type of forest: thin, small ohia, tree fern, and various ground ferns.

A two-note whistle of relatively pure tones and no harmonics with a weak *chuck* between the first and last syllables. The chuck is seen as a faint mark at about the 5-kilocycle level. The graph (Figure 5) with the narrow (40 cps) filter pinpoints the frequency more closely.

B. Cut 6[2] (Figure 6). Made at same location and approximate time as A.

A short, rolling call repeated twice. The spectrogram shows that the bird was resonating on two frequencies at the same time: one at about 4 kilocycles and another about 2.75 kilocycles. There is a small amount of background noise at the 3-kilocycle and lower levels.

Figure 2 shows the actual recording of these two calls. The birds were flitting about in the tops of ohias growing up from the bottom of the crater, and apparently feeding on insects and nectar from a few lehua blossoms.

Although Mrs. Ward and I have been visiting this locality for twelve years, we have heard only calls, no songs.

C. Cut 10 (Figure 7). Keauhou Ranch above middle northern boundary of Hawaii Volcanoes National Park, 24 June 1961. Elevation 5,000 feet. Rainfall 50 inches. Type of forest: ohia and koa, some mamani, tree fern, and ground ferns.

A 3-note whistle with accent on the last and longer syllable. The recording, made between gusts of wind on a rainy day, is clean with no background noise. The notes are quite pure and change only in pitch and amplitude.

William Dunmire and I were only eight miles northwest of where the two previous recordings were made and were trying to record a rare Akaipolaau *(Hemignathus wilsoni),* which refused to vocalize, when an Apapane gave this call. Other Apapanes in the vicinity were giving the same call. We wonder whether the birds giving these two different calls are of two different populations which do not mingle due to some isolating mechanisms or if Apapanes simply react differently in different environments. Banding would be helpful in solving this problem. However, we must first devise a method of trapping the Apapanes since, according to Baldwin (1953), they ignore nectar-baited traps. The birds in these two areas had no special display patterns; the calls appeared to be merely conversational.

D. Cut 11[3] (Figure 8). Hosmer Grove, Haleakala National Park, Maui, 24 February 1962, 2:30 PM. Elevation 6,500 feet. Rainfall 80 inches. Type of forest: exotic pines, firs, cedars, eucalypti, together with endemic ohia, koa, mamani, and others. No tree ferns.

A 3-note whistle with a brief, faint *chuck* at the end probably indicated by the two vertical bars. It has some of the complexities of the songs which follow and is often used to lead into the song described below in Cut 11[2] (Sample K). The first syllable is a pure tone. The second diminishes in amplitude and a second frequency band comes on here giving an aural impression of a third syllable. Birds producing these calls were flitting up and down a ravine, calling to each other as they travelled. We heard no other calls at the

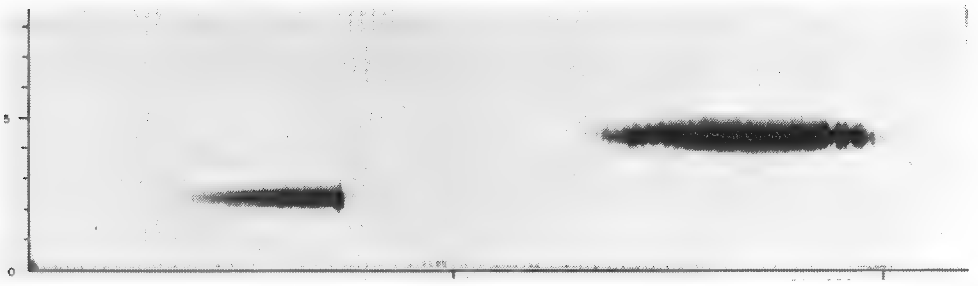

Figure 4. Sample A. Cut 6¹. Lua Manu Crater, Island of Hawaii. Filter: 400 cps.

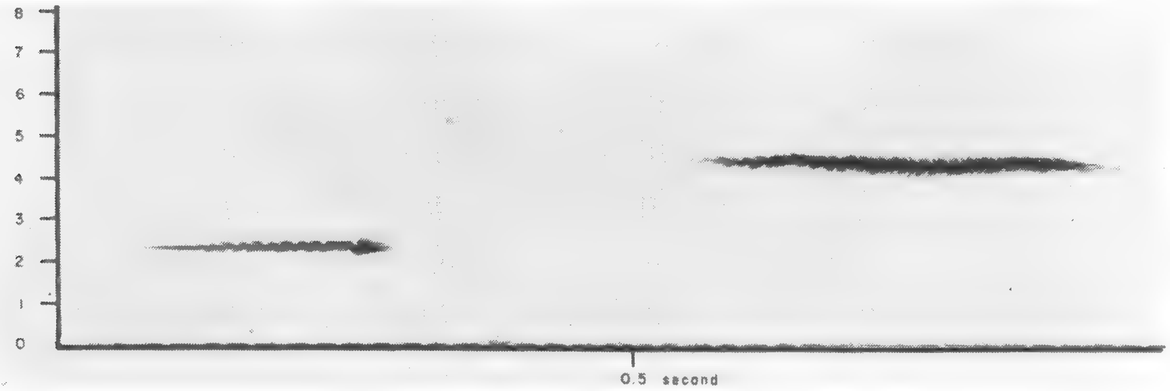

Figure 5. Detail at 40 cps of call shown in Figure 4. Filter: 40 cps.

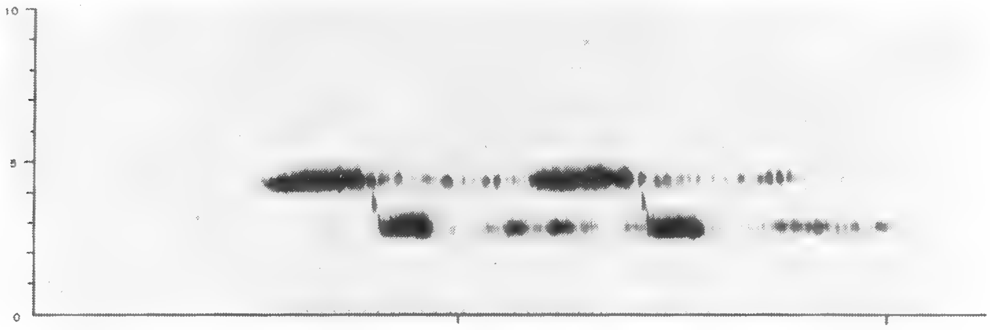

Figure 6. Sample B. Cut 6². Lua Manu Crater, Island of Hawaii. Filter: 400 Cps.

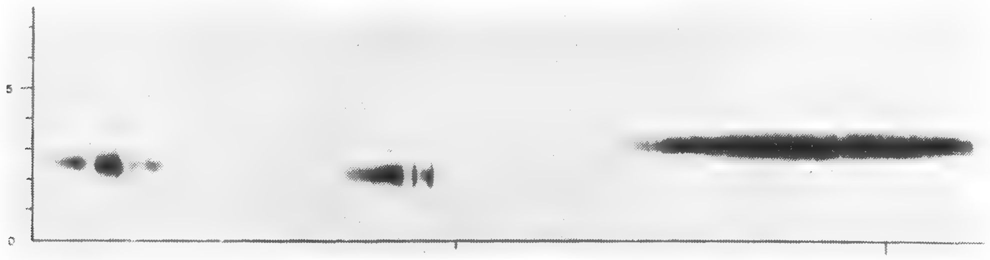

Figure 7. Sample C. Cut 10. Keauhou Ranch, Island of Hawaii. Filter: 400 cps.

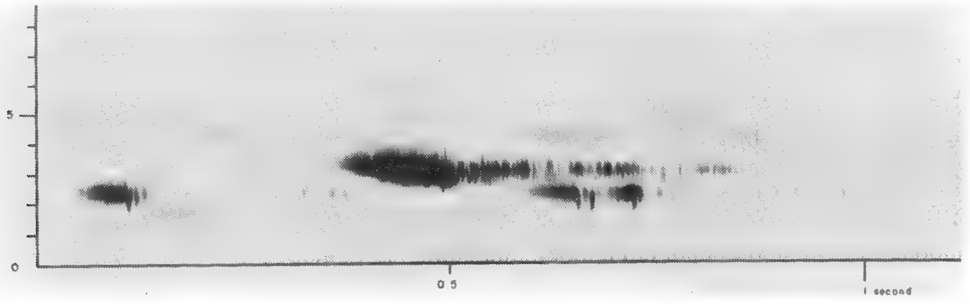

Figure 8. Sample D. Cut 11³. Hosmer Grove, Haleakela National Park, Maui. Filter: 400 cps.

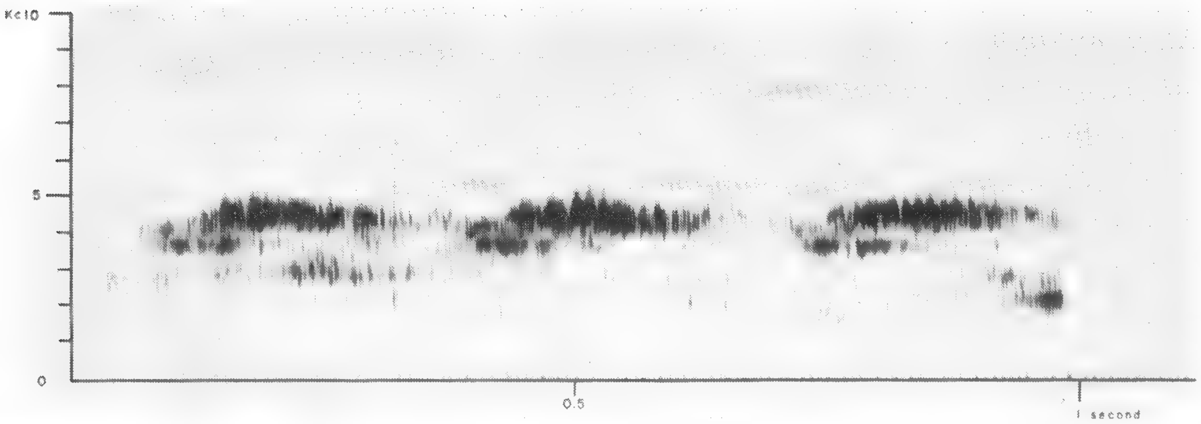

Figure 9. Sample E. Cut 13. Alakai Swamp, Kauai. Filter: 400 cps.

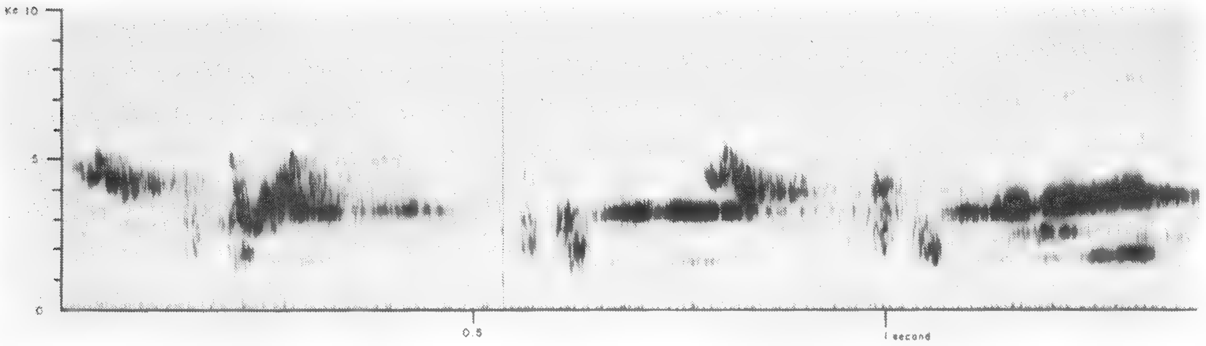

Figure 10. Sample E. Cut 9. Halemaumau Trail, Hawaii Volcanoes National Park, Island of Hawaii. Filter: 400 cps.

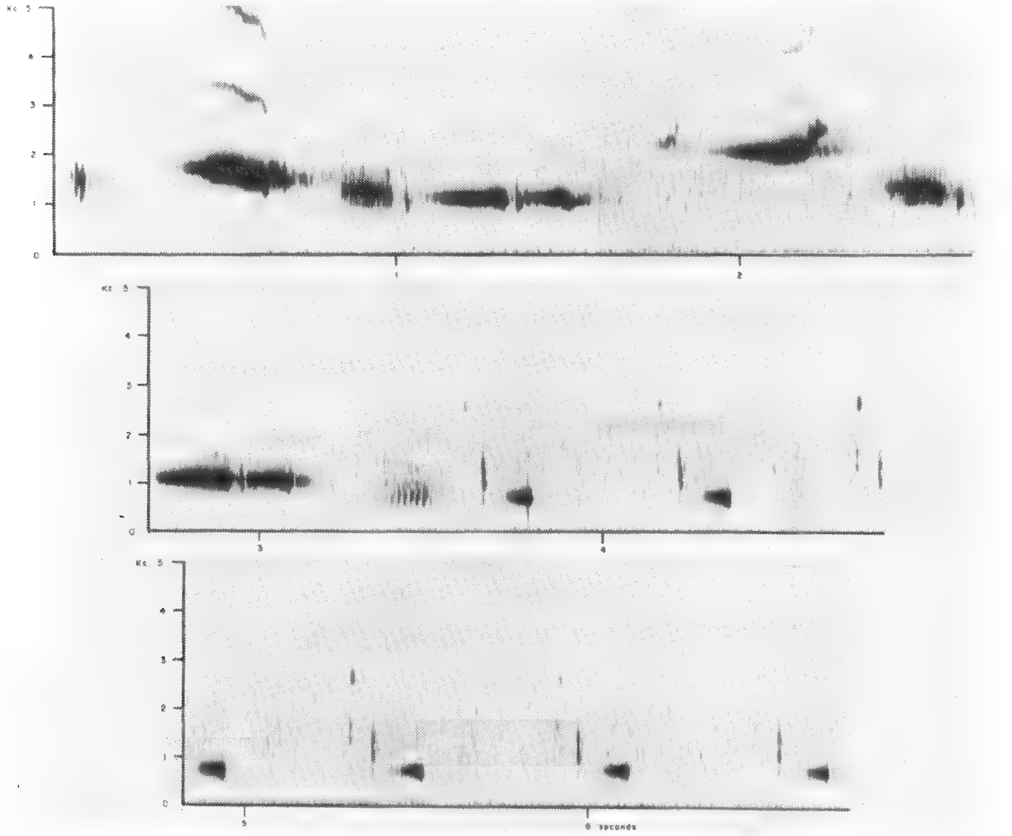

Figure 11. Sample G. Cut 3. Halemanu Valley, Kokee, Kauai. Filter: 400 cps.

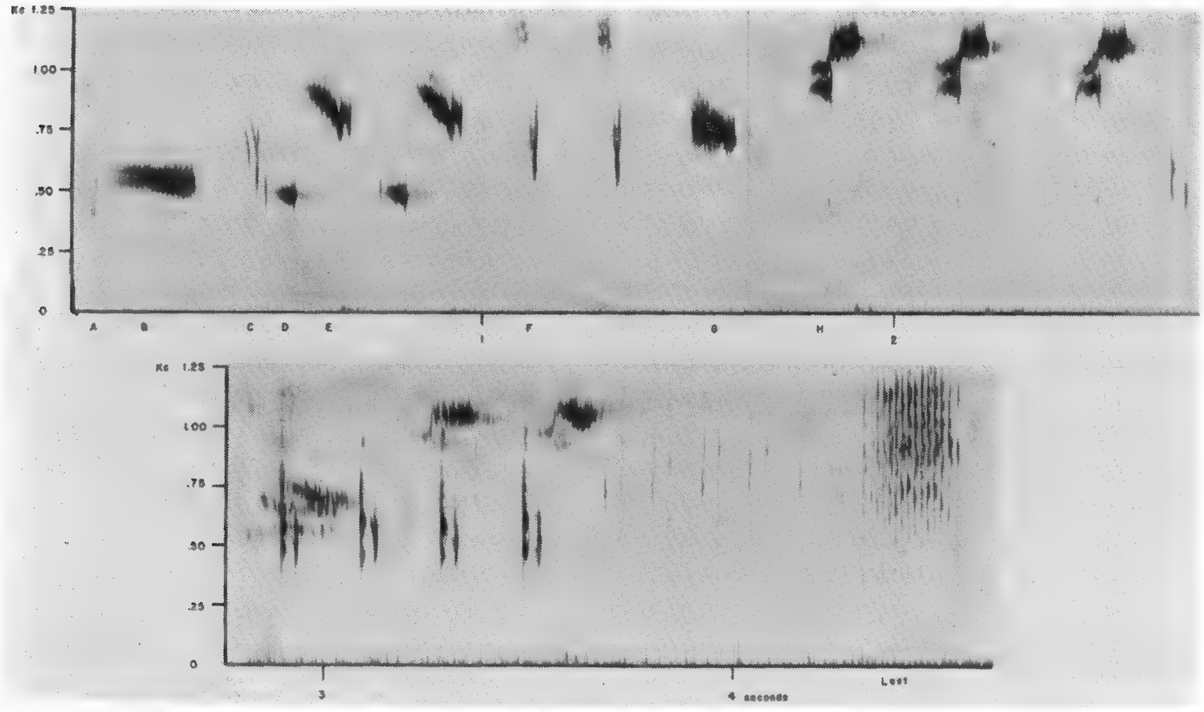

Figure 12. Sample H. Cut 12. Alakai Swamp, Kauai. Filter: 200 cps.

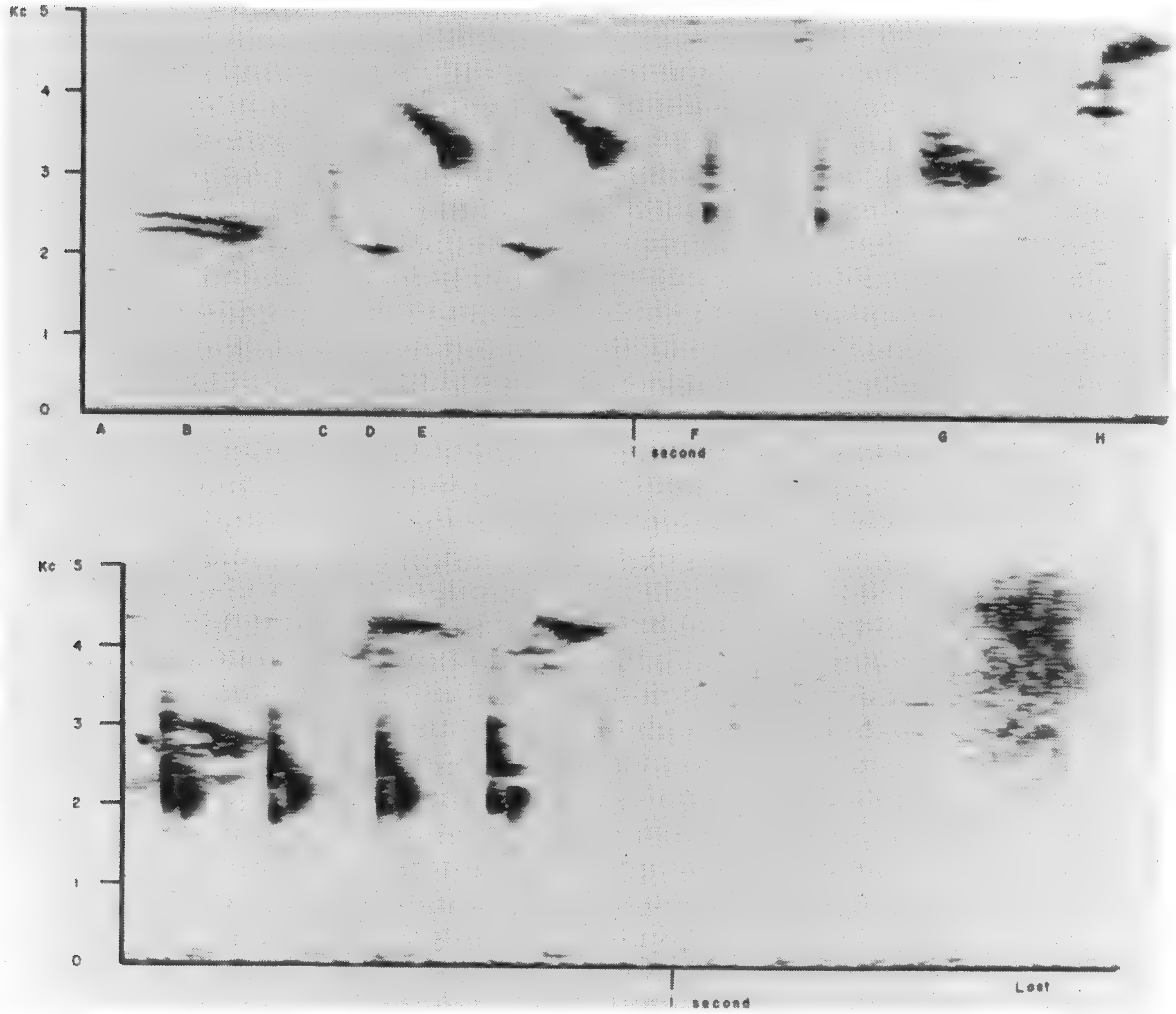

Figure 13. Sample H. Cut 12. Detail at 20 cps of song shown in Figure 12.

time. Subsequently we recorded two songs (Cuts 11 and 11², Sample K) in the same area. The birds were perched while singing.

E. Cut 13 (Figure 9). Geology Cabin, Koaie Stream, Alakai Swamp, Kauai, 21 April 1962, 4:00 PM. Temperature 68°F. Elevation 3,500 feet. Rainfall 200 inches. Type of forest: scrubby ohia, koa, fern, and bog plants.

A rolling call of 3 notes. The graph indicates that each syllable starts off on two separate frequencies, and that there is great change in amplitude in each syllable. The end of each syllable is broken into vertical lines, which suggest a mixing of the two frequencies. It must be noted that Kauai is more isolated than any of the other main islands.

F. Cut 9 (Figure 10). Halemaumau Trail below Volcano House on edge of Kilauea Crater, Hawaii Volcanoes National Park, Hawaii, 17 June 1961, 6:30 AM. Elevation 3,800 feet. Rainfall 120 inches. Type of forest: ohia, koa, tree fern, and ground ferns. The live volcano in the crater has little effect on birds except during eruptions which are confined to small areas.

A short *squawk,* then an ascending scale. The graph is most complex and shows many characteristics of the songs described later. Background noise of trade winds confuses interpretation. The weak horizontal-frequency bars beneath the dark heavy bars show that the loudest frequency is not the fundamental but the second harmonic.

We made this recording about two miles north of and within a few minutes flying time from the Lua Manu Crater where we taped Sample Calls A and B, yet it is different. During our many visits over a period of 12 years the birds here have always used different vocalizations than those at the Lua Manu Crater.

Songs of the Apapane

G. Cut 3 (Figure 11). Halemanu Valley, Kokee, Kauai, 16 April 1960. Elevation 3,350 feet. Rainfall 50 inches. Type of forest: koa, ohia, lobelia, and many exotics such as pines, firs, silk oak, redwoods, and cedars.

A short song with 8 chucks on the end (only 6 of which are graphed). The second syllable, very loud, has at least two harmonics which are visible above it and are down-slurred. Remaining syllables are up-slurs of fundamentals, whistles, clicks or modulation-like sounds similar to Syllable 3.

H. Cut 12 (Figure 12). Alakai Swamp, Kauai, 21 April 1962, 9:30 AM. Temperature 60°F. Elevation 4,600 feet. Rainfall 200 inches. Type of forest: ohia, koa, fern, and bog plants.

A rolling call, followed by 3 whistles, 5 chucks, a drawn-out note, and a faint squawk at the end. The spectrogram shows it to have greater variation in sound structure than our other Apapane recordings, and to rank with other very complicated bird songs.

Syllable B is a mixture of two different fundamentals given simultaneously; and is best shown by the narrow-band (20 cps) filtered spectrogram (Figure 13). The quarter-speed spectrogram with 800 cps filter (Figure 14) shows this syllable as a series of dark blobs representing an interference pattern of interaction between the two fundamentals. Syllable C might be a series of slurs. Syllable D is probably a pure tone which increases in amplitude and is then reduced. Syllable E may be an irregular down-slur, but Stein thinks

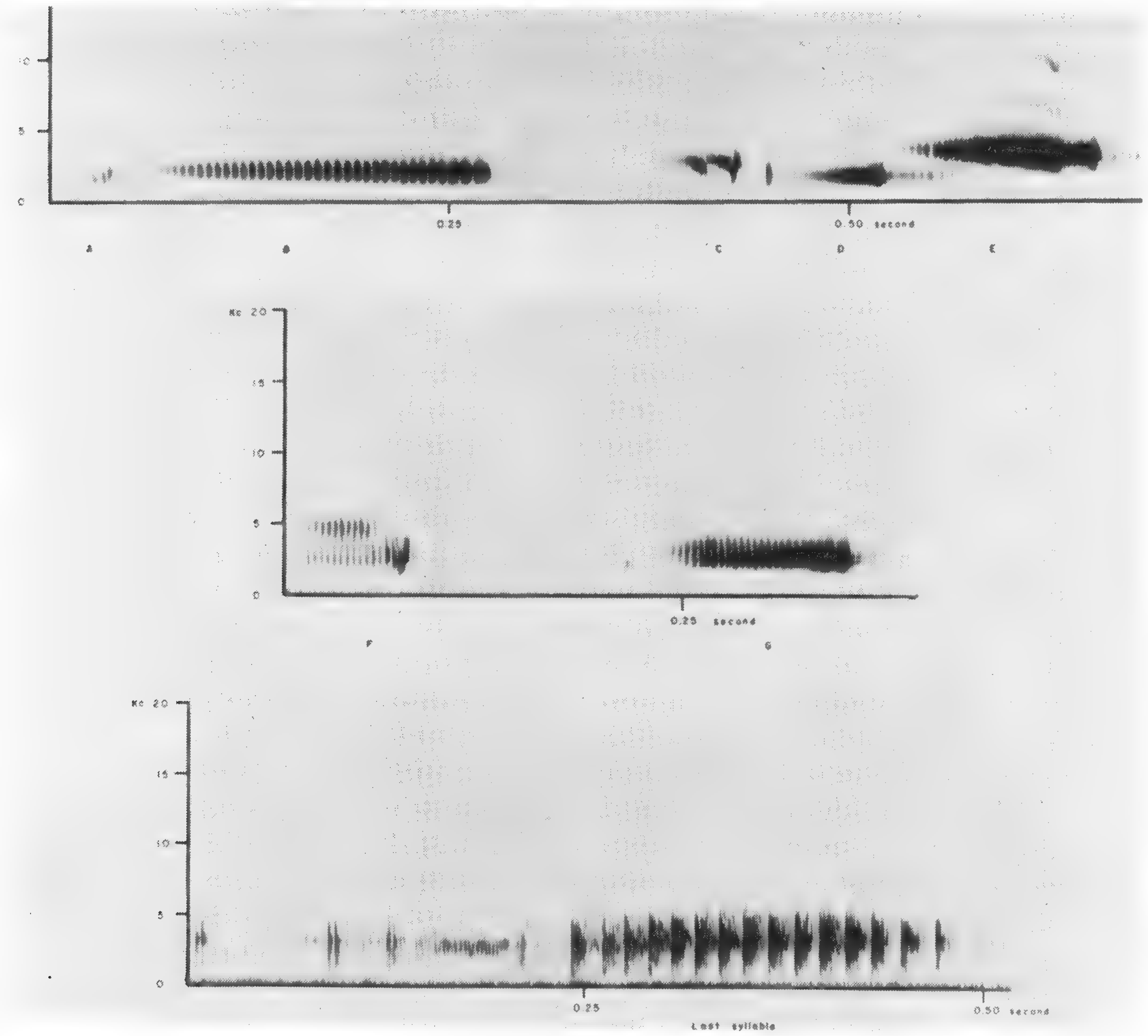

Figure 14. Sample H. Cut 12. Detail at 800 cps of song shown in Figure 12.

it is more complex. (Syllables D and E are repeated.) Syllables F and G may be modulated signals. Stein did not comment on the rest of the syllables until he came to the final one which he thought might be produced by starting and stopping the vocal air stream. He says it is a form of sound production which the Laboratory is still investigating and on which he has few ideas as yet, adding that this phrase alone could be the basis of a separate paper.

We made this particular recording in Alakai Swamp (see Figures 15 and 16), a plateau on top of the island of Kauai, not far from Mt. Waialeale where over 465 inches of rain falls annually. Alakai Swamp is one of the remaining wilderness areas and is different from others in Hawaii in that there is almost no exotic vegetation. It is probably the one wilderness area that looks today as it did in Captain Cook's time and this may account for the fact that it has more endemic birds than any other locale. Frank Richardson rediscovered the Kauai Oo here in 1960.

We hiked in the Alakai Swamp for three days, back-packing recording equipment and hoping to tape the Oo but failed. The Apapane in this recording sat quietly over our heads in a scraggly ohia tree, uttering this song at frequent intervals with some modifications each time. We had never heard the song elsewhere. Other Apapanes in the vicinity were singing the same song with slight modifications.

Notice the great difference between this song and Sample G, Cut 3 (Figure 11), made at Halemanu Valley, Kokee, about six miles west of Alakai Swamp; and notice also that Cut 4, Sample G (Figure 17), made at Kokee within a mile of Cut 3, is also different.

Figure 15 (*above*). Recording the song of the Apapane in Alakai Swamp, Kauai.

Figure 16 (*below*). Looking into the tableland of Alakai Swamp and Mt. Waialeale, Kauai, where 465 inches of rain fall annually. It is one of the few areas of endemic vegetation left in Hawaii; consequently it is the home of endemic birds including the Apapane. Because of the faint trails and no guideposts, several people have become permanently lost in the area of the picture.

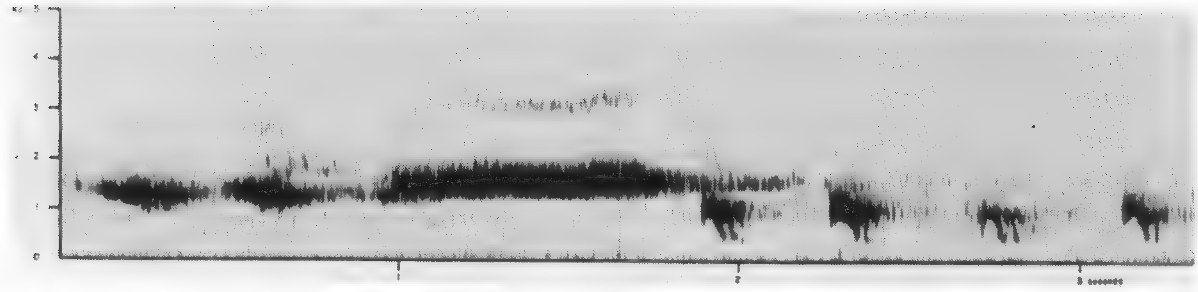

Figure 17. Sample G. Cut 4. Kokee Meadows, Kauai, 17 April 1960. Filter: 400 cps.

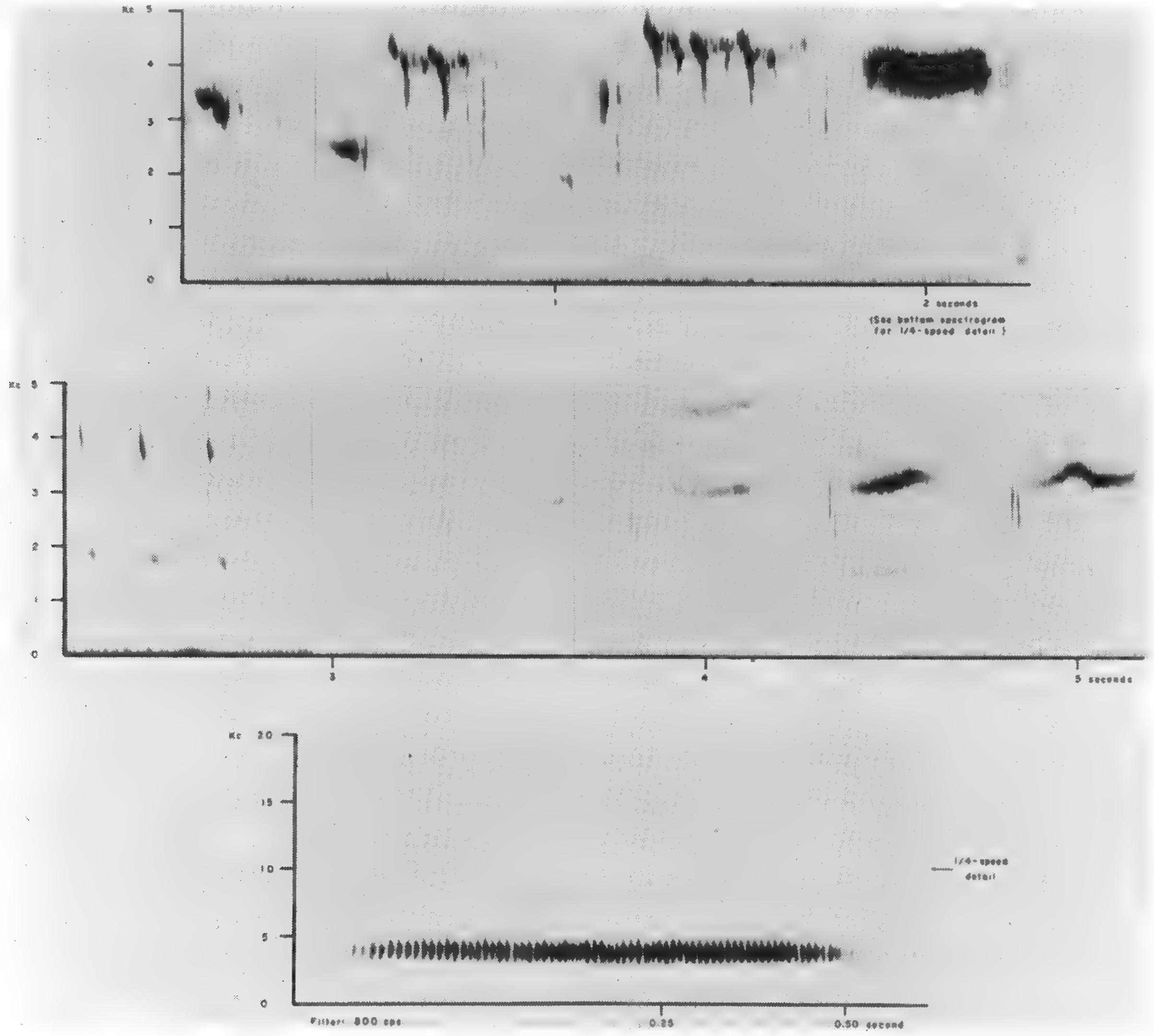

Figure 18. Sample I. Cut 5. Wright Road Clearings, Hawaii Volcanoes National Park, Island of Hawaii. Bottom spectrogram at 800 cps shows one-quarter-speed detail of the long, dark syllable at the end of the top spectrogram (400 cps).

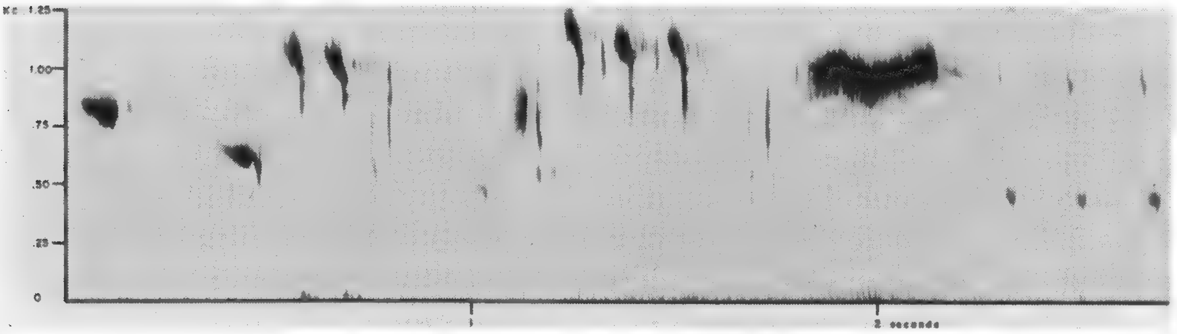

Figure 19. Sample I. Cut 5^2. Wright Road Clearings, Hawaii Volcanoes National Park, Island of Hawaii. Filter: 200 cps.

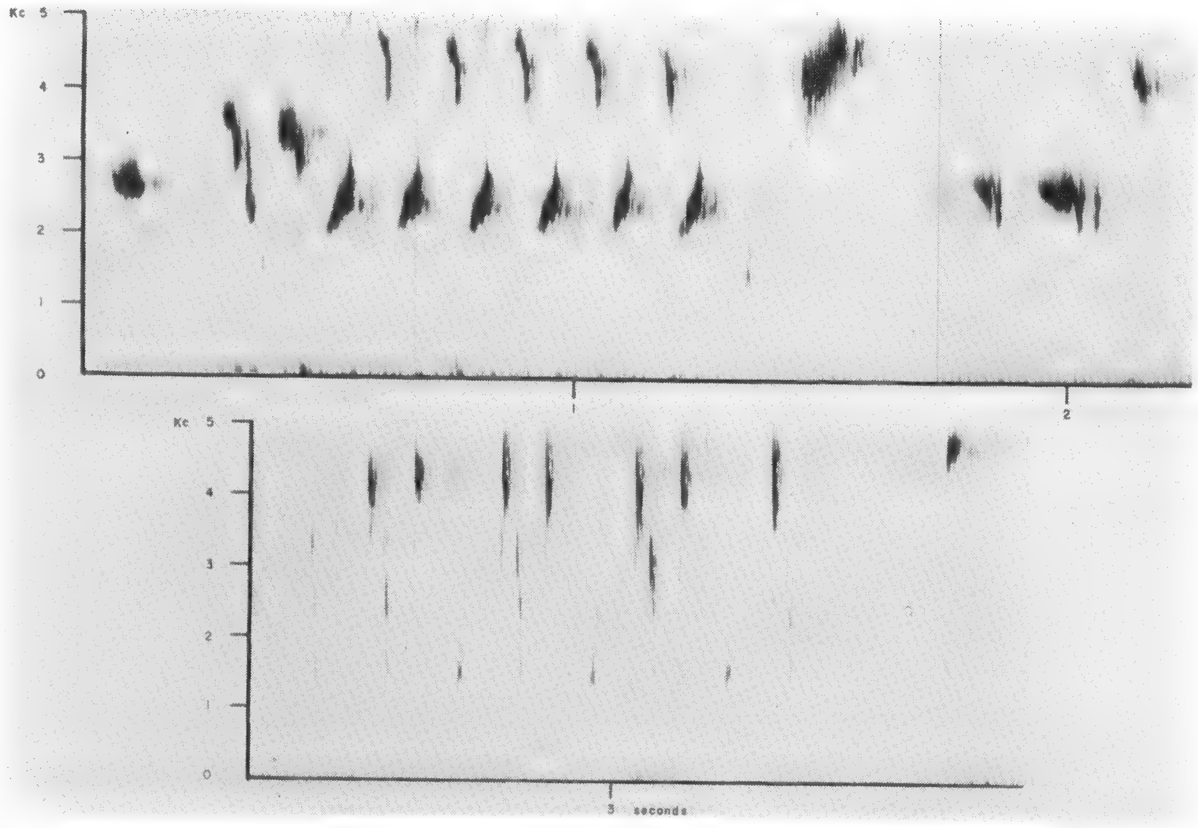

Figure 20. Sample J. Cut 7. Wright Road Clearings, Hawaii Volcanoes National Park, Island of Hawaii. Filter: 400 cps.

Thus we have three recordings, made within six miles of each other and each different from the other two. There is also great variance between the songs recorded in the Alakai Swamp and those in the forest at Kokee. Alakai has much more rain than Kokee. Alakai, an endemic area rarely has human visitors; Kokee, not an endemic area, is a state park and visitor center. If we rely on the recordings, there is apparently little exchange of Apapane populations between the two places. Bird-banding would help to clear this up.

I. Cut 5, Cut 5^2 (Figures 18 and 19). Wright Road Clearings (Hilo side) below Hawaii Volcanoes National Park, Hawaii, 29 May 1960. Elevation 3,500 feet. Rainfall 150 inches. Type of forest: ohia, koa, tree ferns, ground ferns, and exotic eucalyptus.

We have heard more varieties of songs in Wright Road Clearings than at any other recording locale.

These two cuts of two different birds were made about the same time and are similar. In Cut 5 (Figure 18), the last 4 syllables increase in amplitude. The fundamental is shown faintly under the next to last syllable with the second harmonic carrying the energy. The long, dark syllable at the end of the first section is also graphed separately at .25 speed. Stein thinks it is either a mixture of several sounds or a modulated signal, and quite possibly is a form of amplitude modulation which is relatively pure. Cut 5^2 (Figure 19) is similar to Cut 5 at its beginning.

J. Cut 7 (Figure 20). Wright Road Clearings a day later.

The syllables of this song are short and their construction strangely enough is somewhat similar to Cut 12 (Sample G) made in Alakai Swamp, Kauai. This is confusing because the two places are 300 miles apart on the two "end" islands of the chain. However, the song pattern of the graphs and the aural impressions are quite different.

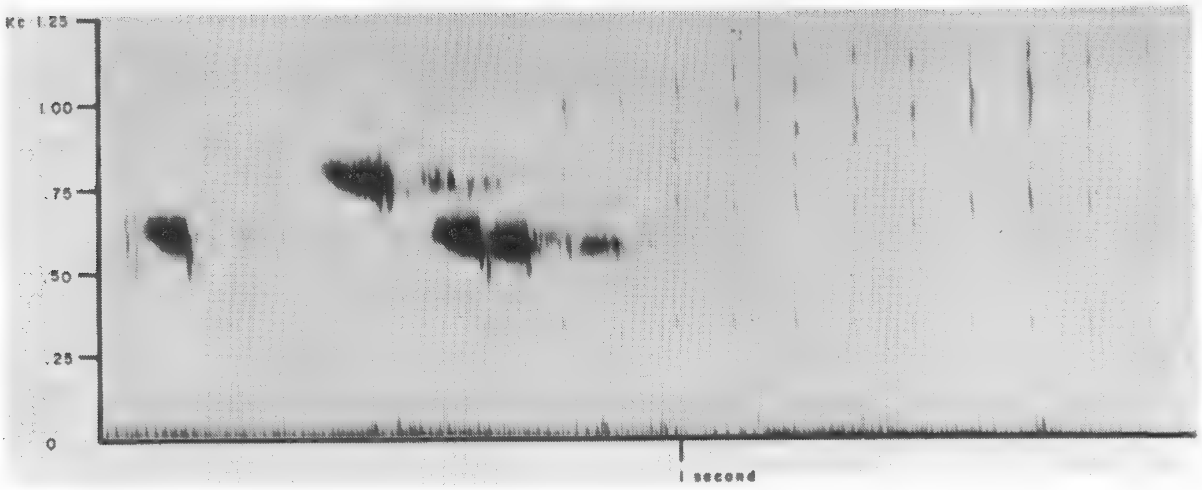

Figure 21. Sample K. Cut 11. Hosmer Grove, Haleakela National Park, Maui. Filter: 200 cps.

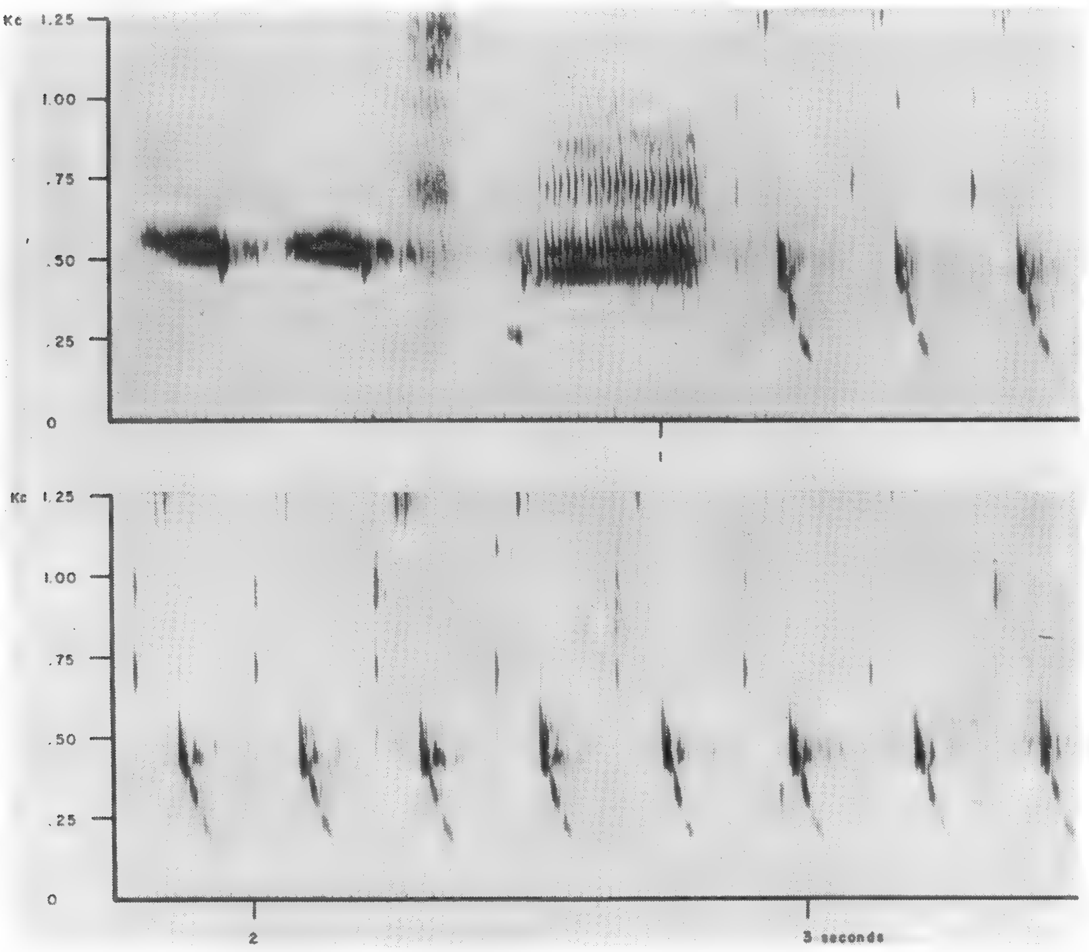

Figure 22. Sample K. Cut 11². Hosmer Grove, Haleakela National Park, Maui. Filter: 200 cps.

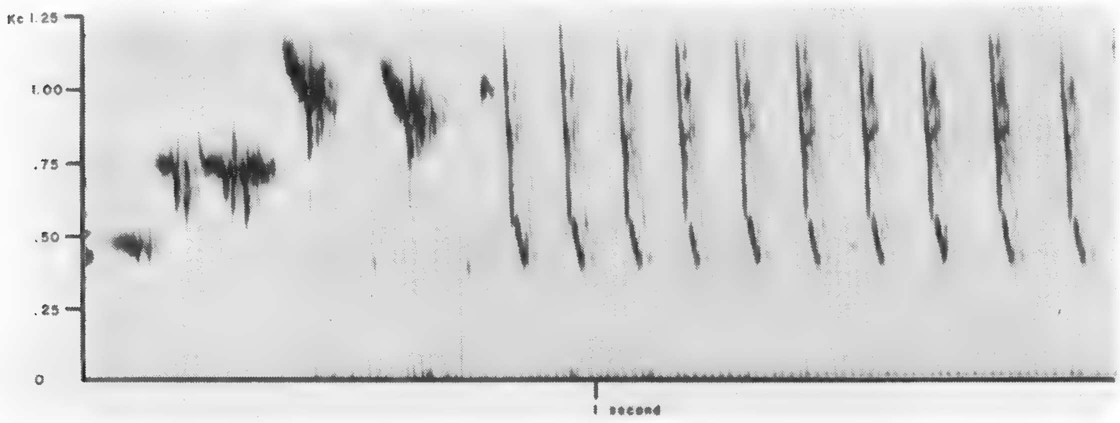

Figure 23. Sample L. Cut 8. Halemaumau Trail, Hawaii Volcanoes National Park, Island of Hawaii. Filter: 200 cps.

K. Cut 11 (Figure 21). Hosmer Grove, Haleakala National Park, Maui, 24 February 1962, 2:30 PM. Temperature 62°F. Elevation 6,500 feet. Rainfall 80 inches. Type of forest: many exotic pines, cedars, firs, redwoods, eucalypti together with native ohia, koa, mamani, and others. No tree ferns.

This song reveals no new sound structure, but the sound pattern and aural impression are again different. Stein believes the vertical lines may be resonated bill clicks. The song sounds like three short notes followed by 12 chucks.

Cut 11^2 (Figure 22). We made this the next day at the same place, about the same time, and under similar conditions. It gives us a complex phrase utilizing many sound-producing methods. It sounds like 3 notes, a buzz, followed by 11 chucks which according to the graph are a bit more complicated than the chucks in Cut 11.

L. Cut 8 (Figure 23). Halemaumau Trail below Volcano House on edge of Kilauea Crater, Hawaii Volcanoes National Park, Hawaii, 17 June 1961, 6:30 AM. Elevation 3,800 feet. Rainfall 120 inches. Type of forest: ohia, koa, tree fern, and ground ferns.

This delightful little lilting melody, repeated over and over as the bird perched, is presumed to be an identification of territory. We have heard this song only in this vicinity, and have heard it here for over 12 years, recording it first in 1950.

Stein believes that, in gross organization, this song bears a marked resemblance to Cut 11^2 (Sample K) made at Hosmer Grove in Haleakala National Park on Maui over 100 miles away. Both birds were perched while singing and appeared to be identifying territory. In each locality other birds were singing the same types of songs and behaving in the same way.

All of the above cuts, run at normal, one-half, and one-quarter speeds, and the songs and calls from which context the spectrogram cuts were made, are on file at the Laboratory of Ornithology, Cornell University.

Conclusions

In order to comprehend more fully the life of the Apapane and what it might teach us eventually about continuing speciation, we have a good many variables to keep in mind and to coordinate with the results of the careful studies made by previous ornithologists.

First, we must consider the position of Hawaii as the most isolated group of islands in any sea and the effect of this isolation, among other things, on the formation of genera and species and proportions thereof. Second, we must recall the extreme specialization of the members of the honeycreeper family and how some of them, like the outmoded craftsmen in the industrial world, could not adapt to changes in their habitats. They could not adapt as, for example, the birds of the eastern hardwood forests of the United States have adapted to the restricted conditions in Sapsucker Woods or in the urban environment of Ithaca, New York.

Dunmire and I agree, as does Baldwin, that the Apapane is a bird of many songs and calls. The question is whether certain groups singing certain songs in certain localities are separate populations or whether all Apapanes are able to sing many songs and by singing one song in one place are simply expressing their reaction to different environments.

Perhaps the reason the Apapane is alive today is its ability to adapt itself to cattle and people in the ohia forests. Is its ability to vocalize widely also indicative of other adaptabilities? We know nothing of the vocalizations of the Mamo and Oo. Did they too have a variety of songs? We shall never know. They disappeared before tape recorders; and early ornithologists, whose chief interest was morphology, made no comment.

This presentation, illustrated with 16 recordings made at eight locations on three islands, is only a beginning. We need several hundred recordings made throughout the year in scores of other locations on all six islands, plus an intensive program of banding, before we can form definite conclusions. Since the practical problem of bringing all this about right away is unsurmountable, we take note only of the direction in which our present data points.

The recorded songs and calls add knowledge to the work of Munro, Palmer, Perkins, Henshaw, Amadon, Baldwin, and others. Spectrograms prove Baldwin's comment that the bird is one of many songs, and adds the fact that many of the songs are very complex. Until we have further evidence, we are inclined to believe that Apapanes do not move around very much, even on a single island. My present conjecture is that small flocks keep pretty much to their own flyways on each island, following the flowering trees. Storms, and even volcanism, may interrupt somewhat and may even change the course of the flight patterns.

A further study of the Apapane's syrinx and related sound tubes would add to the available anatomical studies made years ago, which neglected the sound mechanisms. Also, we should know which calls and songs are learned and which are inherited, the length of the learning period, and the possibility of the birds learning other songs. At present I do not have adequate data to separate the local variations from the learned variations of a basic song pattern. Although the spectrograms seem to indicate completely different patterns, it would be premature to draw conclusions now.

Possibly we will find that Hawaii is a very special laboratory in which to study behaviorism — not only of honeycreepers, but also of the introduced birds, some of which have been here a century. Ordinary observation indicates differences in the behavior of Mockingbirds *(Mimus polyglottos)* and House Sparrows *(Passer domesticus)* in Hawaii; the same is true of certain insects and plants.

Song differences of Apapanes may, as Thorpe (1961) tentatively concluded with his Chaffinch studies, "on occasion play an important part in initiating as well as maintaining evolutionary divergences." He added that the play-back experiments of William C. Dilger and Stein indicated that song differences are important in keeping populations apart. Stein (1963) has since gone on to show that the difference between the "fee-bee-o" and "fitz-bew" songs of flycatchers are isolating mechanisms keeping populations apart. These experiments have a bearing on the variations of Apapane songs and point a direction for future studies. We should take advantage of our opportunities for, as Warner (1961) emphasized at the Tenth Pacific Science Congress, Hawaii has the distinction of "having perhaps the most extraordinary bird fauna of any island group in the world," and the drepanids "may be called a living museum of evolutionary processes" which of course are still going on.

Acknowledgments

In the preparation of this paper I am indebted particularly to the following persons: Dr. Peter Paul Kellogg, for encouraging and assisting me in the early phases of this study; Dr.

Robert C. Stein, for preparing the spectrograms and commenting on them; Dr. Paul H. Baldwin, for reviewing the manuscript and giving me helpful criticisms; and Mr. Robert Verity Clem, for painting the handsome portrait of the Apapane that embellishes this paper.

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2027 UALAKAA STREET, HONOLULU, HAWAII

TO A SKYLARK

Ethereal Minstrel! Pilgrim of the sky!
Dost thou despise the earth where cares abound?
Or, while the wings aspire, are heart and eye
Both with thy nest upon the dewy ground?
Thy nest which thou canst drop into at will,
Those quivering wings composed, that music still!

To the last point of vision, and beyond,
Mount, daring Warbler! that love-prompted strain,
('Twixt thee and thine a never-failing bond)
Thrills not the less the bosom of the plain:
Yet might'st thou seem, proud privilege! to sing
All independent of the leafy spring.

Leave to the Nightingale her shady wood;
A privacy of glorious light is thine;
Whence thou dost pour upon the world a flood
Of harmony, with instinct more divine;
Type of the wise who soar, but never roam;
True to the kindred points of Heaven and Home!

— WILLIAM WORDSWORTH

BIRDS IN ENGLISH POETRY

Thomas P. Harrison

Wood engravings by Thomas Bewick from "History of British Birds" (1797-1804)

By reason of their uniqueness in the world of nature birds have always peculiarly stirred imagination. The marvel of flight, the mystery of their sudden appearance in spring followed by their later equally sudden disappearance, and above all the infinite beauty of song unite to set birds apart from all other life. Accordingly, from its very beginning English poetry abundantly reflects this interest. It is only recently, however, that scientific study of birds has made it possible to identify the various species and to recognize the individual character of each. As knowledge has increased from age to age, poetry about birds has kept pace; earlier poets have led the way to a fuller understanding, hence to what is now considered more appealing verse, and finally to bird poetry as almost a separate kind. Wordsworth and Clare, for example, blazed a trail for Tennyson and Browning, as they did for Thomas and Hopkins. The present purpose is to illustrate something of this pageant by first touching briefly upon the early background, then, after a tentative definition of bird poetry, quoting from a handful of fairly recent poets who have written about migration, song, nesting, and flight.

"The Seafarer"

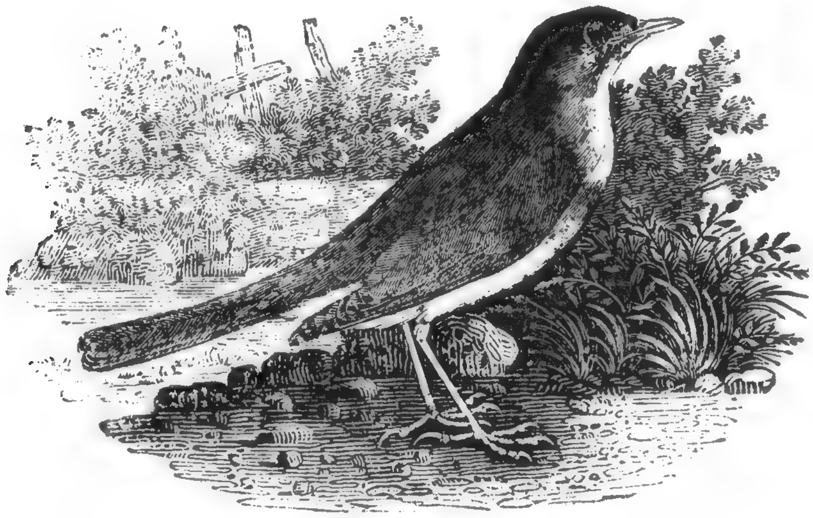
The earliest poem in which birds play an important role is the famous Anglo-Saxon, "The Seafarer," of the eighth century. Here an old salt, who is the singer, describes the hard life aboard ship. He hates the bitter cold murk of the North Sea, icicles clinging to the beard, the wild cries of sea birds in his ears; but as he remembers the soft life of the landlubber he would not desert the sea, the swan-road, the gannet's bath. In the course of his singing he names six birds, not for sweetness of song or beauty of plumage, but because their cries are a part of the wild, forbidding scene which he hates and loves (translation by C. W. Kennedy):

> In place of the mead-hall and laughter of men
> My only singing the sea-mew's call
> The scream of the gannet, the shriek of the gull.

Just as a gale would increase the difficulty of identifying sea birds, so the Seafarer's bird names have been variously translated. Whooper Swan, Sea Eagle, and Gannet are more certain than kittiwake, tern, and gull (Goldsmith, 1954). Whatever the original meaning of the Anglo-Saxon words, the fine spirit of the poem is vastly enhanced by the addition of this group of sea birds wheeling with white flashes amid the breakers, their cries mocking the loneliness of the seafarer:

> Yet still, even now, my spirit within me
> Drives me seaward to sail the deep.

Never again in English poetry were sea birds to appear so prominently and vividly. Unlike the passerines, pelagic birds or even shore birds do not readily lend themselves to poetic treatment. Their restless movements permit little familiarity, nor, except for the modern specialist, are their comings and goings observed to coincide with season change; no song of theirs announces the spring. "The Seafarer" stands alone.



Nightingale

Middle Ages and Renaissance

Over the centuries human imagination has conceived of birds as symbols of divinity, heavenly messengers, or as restless souls of the dead wandering forever. In the Middle Ages they became emblems of good or of evil, a mirror divinely provided as a guide to humanity. Long-necked birds — cormorants, herons, gulls — stood for Gluttony, doves for Chastity or, by reason of their "groaning," a reminder of our sad earthly lot. Often the same bird assumed many roles. The Nightingale sang the passion of Christ, or "she" became Philomel, the ravished Athenian maiden, religion thus yielding to pagan myth. Finally, when Sir Philip Sidney versified his heartsickness he contrasts his own grief with that of the Nightingale, whose side was imagined to be pierced with a thorn.

> Thy thorn without, my thorn my heart invadeth.

(Like many other birds, the Nightingale nests among thorns.)

Paradoxically, the literate man possessed no curiosity about the actual habits of birds, for did not books explain their meaning? Thus for centuries the only truly knowledgeable people with field experience were illiterate hunters, birdcatchers, fowlers, falconers. The most important bird book since Aristotle was the "De Arte Venandi cum Avibus" written by the Emperor Frederick II in the thirteenth century; yet, like the lore of hunter and trapper, this mass of acute observation on migration, speciation, and related subjects was felt to be unimportant beside the revered tradition which regarded all animal life as a moral guide. Poets, like everybody else, delighted in the freshness of a spring day with its choral accompaniment, but otherwise expressed little or no interest in birds. In his long epic-like "Polyolbion" (1612) Michael Drayton chronicles the natural wealth of England, county by county, but his bird lists are included chiefly for their gastronomic importance. Shakespeare, mistakenly believed by some to have been an acute observer of nature, knew more about plants than about birds. Often striking in his allusions to birds, he usually adhered to traditional beliefs. The Hedge Sparrow has its head bitten off by the fledgling Cuckoo it feeds, the Wren heroically defends its nest against the owl, the young pelican drinks the parent's blood. Accordingly, Shakespeare's allusions to birds hardly invite scientific scrutiny, for the time had not yet come for accuracy. Occasionally keen observation is encountered, as in "Macbeth" when, confronted by Banquo's ghost, Macbeth exclaims (3, 4, 71-73):

> If charnel-houses and our graves must send
> Those that we bury back, our monuments
> Shall be the maws of kites.

Shakespeare knew not only the Kite's thieving habits in nesting time but its owl-like disgorging of indigestible food. There are other examples, of course. From this same play everybody remembers the lines in which Banquo finely describes the nesting of the temple-haunting martlet, or House Martin.

The Modern Spirit

Two centuries after Shakespeare poets began to awaken to the wealth of nature when studied directly, and for this awareness the new scientific advance was responsible. Emphasis upon exact observation dissipated the old moral approach and turned the eyes of poets as never before to realities in the physical world. The growing attention to natural history gained much impetus through the example of Gilbert White, the unassuming parson of Selborne. Praising "the graceful simplicity of its style, the elevating tone of its spirit and the sympathetic chords it strikes," Alfred Newton (1893-96) states that "The Natural History of Selborne" (1789) "may be safely said to have done more to promote the love of Ornithology in this country than any other work that has been written." In his quiet chronicle, in which birds are a major theme, White gave expression to a spirit which had been growing during the century. Soon new histories of British birds were compiled, local societies devoted to natural history with their publications were organized, and later ornithological journals appeared.

Poets had always been bird watchers of sorts; now as the distinction between lay watcher and scientist became less finely drawn, it is not surprising to find Wordsworth and Coleridge eagerly reading "The Travels" of William Bartram and Tennyson acquiring binoculars and rejoicing over a set of Morris's "History of British Birds." Referring to his youthful poem, "An Evening Walk," Wordsworth declared, "There is not an image in it which I have not observed." The long passage devoted to nesting swans, he continues, "was taken from daily opportunities I had of observing their habits, not as confined to a gentleman's park, but in the state of nature." Writing of cygnets which "alternately" mount the parent's back, he added, "This is a fact of which I have been an eye-witness." Although this youthful enthusiasm was to diminish and his poetic theory to be modified, Wordsworth's later verse is filled with keen observations.

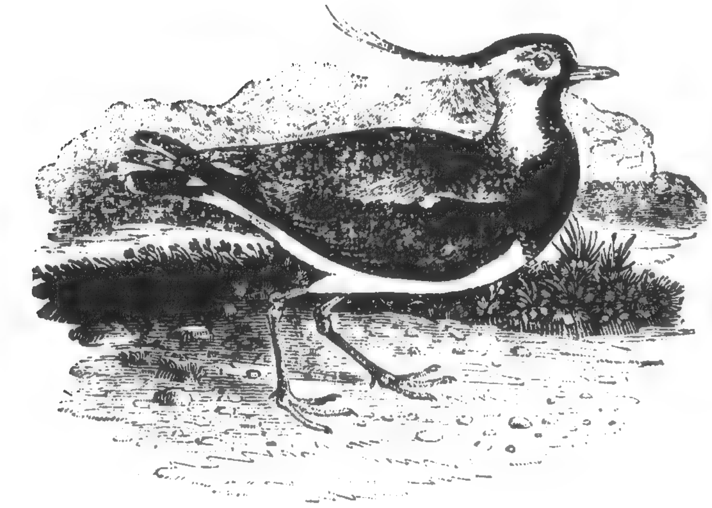
As poets commenced to observe with careful eye, so readers began to expect more accuracy and less poetic license. When in "Paracelsus" Browning carelessly introduced a Gannet nesting "amid the birch-trees by the lake," he was promptly corrected in an article in *The Ibis* (see Cunningham, 1866). When Tennyson in "In Memoriam" had innocently described gulls that "pipe and dive" and, elsewhere, swallows that feed upon bees, the eminent naturalist, J. E. Harting (1883), took him at once to task at some length, concluding, "Picturesque enough are these allusions, no doubt, and poetical, but too often, alas! inaccurate."

What, then, is the nature of true bird poetry? What elements beyond picturesque allusions to birds are expected of the poet? Though considerable qualification is in order—for the appeal of the printed word varies mightily with the reader—a tentative answer may be permissible. First of all, the best poets vividly, graphically recall the bird to memory. "Good bird drawing," Dr. Sutton (1962) remarks in a recent issue of *The Living Bird*, "is a creating of illusion to the end of bringing the bird to life." The artist works with line, color, and shading, the poet with words, with rhythm in all their subtle effects. Both enable us to see, to hear, to recall not only the physical appearance but the character of the subject; and both artists succeed insofar as they truly know and understand their subject, its unique individuality. But in addition to knowledge, imagination is required of both, or as Edward Thomas (1909) has said, "The power that sees a thing alive in the mind's eye, so that, were that thing outside to pass away forever, it would still be clear and with power of motion within the brain. To possess that power is to enjoy and suffer life intensely: to give that inward image another life, in words, in paint, in marble, in melody, is to be an artist."

What Thomas terms "that inward image" sometimes includes for the bird-poet, the meaning of experience, the sentiment prompted spontaneously by the ways of birds. This should be sharply distinguished from sentimentality, the inclination to see ourselves in birds, or merely to find amusement in their supposed quaintness (witness the tittering audience watching the marvels of Disney's photography). But persons really interested in birds not only see and hear but feel. As Hendy (1929) has observed, the poet makes these feelings articulate, for sometimes he expresses precisely our own private experience. At other times bird poetry is a matter of one man's meat. This happens when the sentiment precedes and the bird is merely a convenient peg to hang it on. When experience is balanced by thought or emotion, ornithology and poetry become truly united.

Clare and Keats

The imbalance of objective fact and subjective response is illustrated by extremes in the poems of John Clare and of John Keats. Clare, a self-educated Northamptonshire countryman with a passionate interest in birds, is the greatest of all naturalist-poets. According to a count by James Fisher (1955), Clare "knew from personal observation about 145 wild birds, of which 119 can be identified with reasonable certainty as county records—65 of them 'first records.' " Seventy-eight species appear in his verse, though he knew almost twice this number. With an incongruous dislike of "those matter of fact men, the Naturalists" (men like Thomas Pennant, for instance), Clare determined that verse was the proper medium of ornithology and that in his own writing "I will insert nothing but what has come under my notice." Fidelity to facts

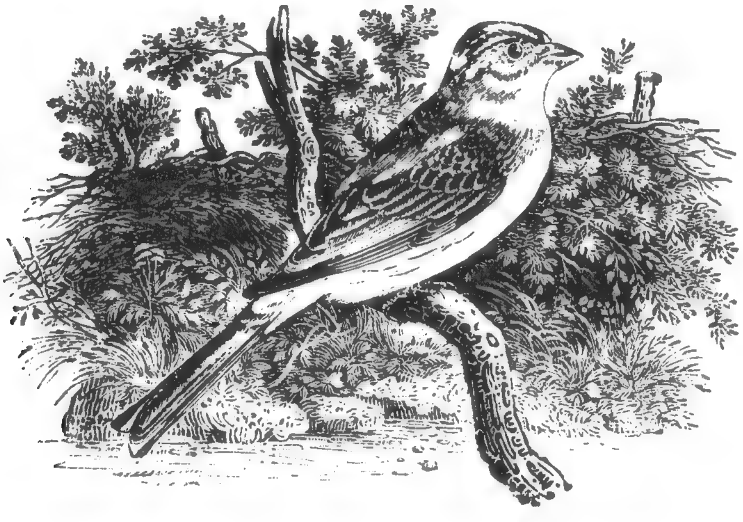


Lapwing

about living birds, not dead specimens, was to Clare a solemn duty. Take this, for example, from "The Spear-Thistle":

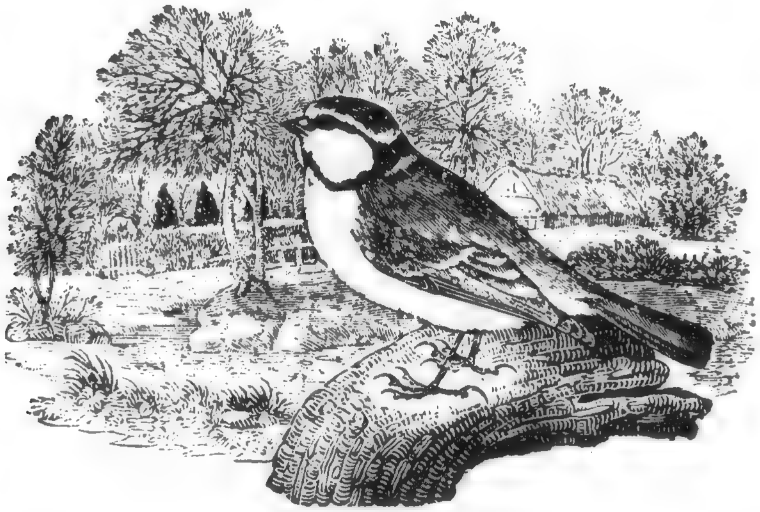
The pewit, swopping up and down
        And screaming round the passer-by,
Or running o'er the herbage brown
        With copple crown uplifted high,
Loves in its clumps to make a home
Where danger seldom cares to come.
The yellow-hammer, often prest
        For spot to build and be unseen,
Will in its shelter trust its nest . . .
And larks, though paths go closely by,
The partridge, too, that scarce can trust
        The open downs to be at rest,
Will in its clumps lie down, and dust
        And prune its horse-shoe circled breast,
And oft in shining fields of green
Will lay and raise its brood unseen.

Here are important notes on the habitat of ground-nesting Lapwing, Yellowhammer, a lark, and Partridge. Nesting materials fascinated Clare, who lines



Yellowhammer

his verse with them: Finches' moss green, Linnets' grey, Redstarts' "hair and moss and down and cobwebs very fine," and, the most marvelous nest of all, that of the "Bumbarrel" or Long-tailed Tit. But information by itself is only one ingredient of poetry. After sampling Clare, Keats with some restraint wrote "that your Images from nature are too much introduced without being called for by a *particular sentiment*." In other words, for Keats fact alone simply would not do. Clare in turn reacted with equal force to the poetry of Keats: "He keeps up a constant allusion or illusion to the Grecian mythology, and there I cannot follow. When he speaks of woods, Dryads and Fauns and Satyrs are sure to follow . . . He often described nature as she appeared to his fancies and not as he would have described her had he witnessed the things he describes." Both views are valid; each recognizes that the imbalance of fact and sentiment leaves imperfect the full effect. For one year, 1821, the rural verse of John Clare wholly eclipsed Keats's first volume; afterward, Clare lived on as the neglected poet-naturalist. In three years Keats was in his grave, but a new voice in English poetry had been heard.



Blue Tit

Immortality

But these two contemporaries were not always at odds in choice of theme. Like many another poet before and after, they were impressed by the sense of nature's eternity proclaimed in the song of birds. Clare's "Song's Eternity," prompted by the modest notes of a Blue Tit, thus begins:

What is song's eternity?
        Come and see.
Melodies of earth and sky,
        Here they be.
Song once sung to Adam's ear
        Can it be?
Ballads of six thousand years
        Thrive, thrive;
Songs awakened with the spheres
        Alive.

Throughout the six stanzas, as J. M. Murry (1922) remarks, "the bird-note begins, rises, dies away: and the poem is finished." Here the finest effects are in the simplicity of diction and in the rhythmic short lines which so plainly suggest the slight, staccato notes of the Tit. Clare has outdone himself. John

Keats, dying of tuberculosis, was rarely permitted to forget impending death and his own unfulfillment as poet. The thought of impending death pervades the "Ode to a Nightingale":

> Thou wast not born for death, immortal bird!
> No hungry generations tread thee down;
> The voice I hear this passing night was heard
> In ancient days by emperor and clown, . . .

and on through the well known lines—his own death so near beside the deathless bird. At the same time Keats recalls the actual song of the Nightingale. To human ears it has long seemed that the first sequences of this song express happiness and that a latter one, slowly uttered and in descending scale, is full of sadness. In the poem Keats conveys both moods. First the bird is "too happy in thine happiness," it can never have known human sorrow. Then with skillful transition, the song has become a "plaintive anthem" which may once have touched "the sad heart of Ruth when sick for home," now a fit "requiem" should he die,

> While thou are pouring forth thy soul abroad
> In such an ecstasy!

Having learned firsthand the two-fold quality of the Nightingale song, Keats carries this over into the movement of the poem.

In a poem on a dead canary, "Poor Matthias," Matthew Arnold expresses the idea that the bird world is completely sealed off from us, that there can be no communication:

> Birds, companions more unknown,
> Live beside us, but alone;
> Finding not, do all they can,
> Passage from their souls to man.

On the contrary, man's common delight in birds is the surest link of their life with ours, their ways reminding us that we can never understand them.

Migration

Their greatest secret, migration, remains despite the recent revelations of Jean Dorst. The ancients wondered at the annual flights of cranes and storks, whole populations perennially following the same routes, their loud cries likened by Homer and Virgil to the sounds of battle. And everywhere today people are strangely moved by flights of migrating Canada Geese. Yet this greatest of mysteries has not often served as poetic theme. In "The Passing of Arthur" Tennyson alludes to,

> wild birds that change
> Their season in a night, and wail their way
> From cloud to cloud.

And he is perhaps the only poet to record in verse the fatal attraction of light to migrants; in "The Princess" a lighthouse is described when,

> the crimson-rolling eye
> Glares ruin and the wild birds on the light
> Dash themselves dead.

In a different and facetious mood Browning, after reading Darwin on bower birds and others of the South Pacific, writes in "Mr. Sludge" of a prisoned crane which,

feels pairing time
In the islands where his kind are, so must fall
To capering by himself some shiny night,
As if your own back-yard were a plot of spice.

Song

If the migration of birds has prompted few poets, certainly their spring arrival is a different matter. In the far-distant past, when physical comforts could not be taken for granted, the arrival of birds signaled the end of bitter cold; the voice of the turtle was associated with relief from the rigors of winter. When Chaucer's "smale fowles maken melodye," the thoughts of men and women turned to dried roads and pilgrimages in happy companies. Pleasure in birds for their own sakes came later as did poetry celebrating their first notes. A rare exception is found in an anonymous poem of the fourteenth century entitled "The Flower and the Leaf." Unable to sleep, the poet, an unknown woman, goes abroad to enjoy the sights and sounds of early morning (ed. W. W. Skeat):

And I, that couth not yet, in no manere,
Here the nightingale of al the yere,
Ful busily herkned, with herte and ere,
If I her voice perceive coud anywhere.

She first watches and listens to a Goldfinch, then suddenly:

The nightingale with so mery a note
Answered him, that al the wodë rong
So sodainly, that, as it were a sot,
I stood astonied; so was I with the song
Through ravishèd, that, until late and long
Ne wist I in what place I was, ne where . . .

With such lines no wonder that "The Flower and the Leaf" was for a long time attributed to Chaucer. Later poets took up the theme of the Nightingale, most famous of European song birds. Clare noted the trial notes on its arrival:

When first we hear the shy-come nightingales,
They seem to mutter o'er their songs in fear, . . .
But when a day or two confirms their stay
Boldly she sings and loud for half the day.

The bird does indeed sing as much by day as by night, though, as Clare did not know, the singer is the male. In "The Marriage of Geraint" Tennyson finely expresses the human emotion awakened by the newly arrived Nightingale as he tells of,

a man abroad at morn
When first the liquid note beloved of men
Comes flying over many a windy wave
To Britain, and in April suddenly
Breaks from a coppice gemm'd with green and red,
And he suspends his converse with a friend, . . .
To think or say, 'There is the nightingale'.

One's emotion on first hearing a new arrival is easier to express than is the song itself in words. Late in life Tennyson attempted to suggest in words the loud, staccato effect of the Song Thrush:

> Summer is coming, summer is coming,
> I know it, I know it, I know it,
> Light again, leaf again, life again, love again . . .

Song itself may perhaps be conveyed more effectively by less obvious suggestion. The alternative is not poetry which merely *praises* but that which, without onomatopoeic attempt, conveys song *and setting.* For poetic purposes at any rate a tape of a bird's song is far from complete; even from the scientific standpoint, as Armstrong (1963) insists, song recordings should be accompanied by "a study of the song's setting in the context of the bird's life history." For the poet the impact of song is not alone upon the ear but upon the mind with its capacity for association with scene. After listening to the Nightingale, George Meredith has well succeeded in combining song with subtle hints of setting in "Night of Frost in May":

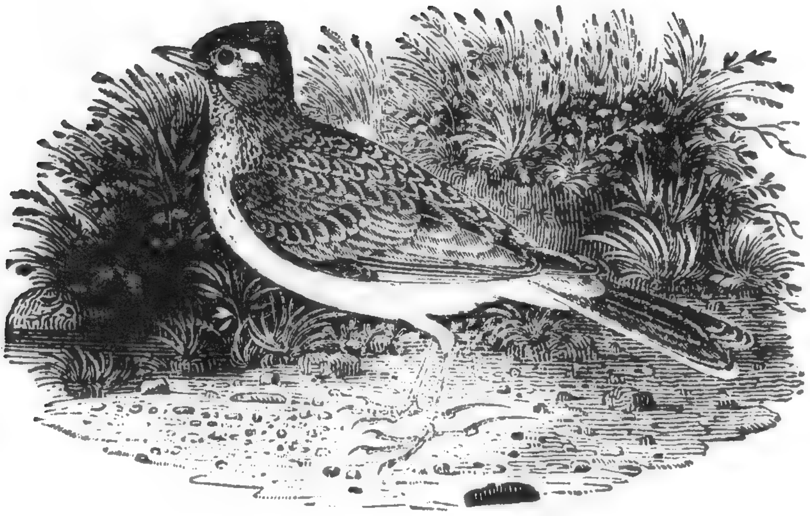
> In this shrill hush of quietude,
> The ear conceived a severing cry.
> It almost let the sound elude,
> When chuckles three, a warble shy,
> From hazels of the garden came,
> Near by the crimson window'd farm . . .
> Then soon was heard, not sooner heard
> Than answered, doubled, trebled, more,
> Voice of an Eden in the bird . . .
> It seemed a single harper swept
> Our wild wood's inner chords and waked
> A spirit that for yearning ached . . .
> A hand the magic might disperse:
> The magic swung my universe.

The full truth in these lines is felt only by one who has heard this song on a cold spring night. They are thus praised by G. M. Trevelyan (1954): "Chaucer, Milton, Wordsworth, Keats have written noble lines in praise of the nightingale's song, and of its historic symbolism to men. But this of Meredith's is not merely praise of the song; it represents the song itself. It is the most accurate description of what we hear when we listen to the nightingale, and of its emotional effect upon our poetic nerve." Clare had written:

> I've nestled down
> And watched her while she sung;
> Her wings would tremble in her ecstasy,
> And feathers stand on end, as 'twere with joy,
> And mouth wide open to release her heart
> Of its out-sobbing songs . . .

The Nightingale has inspired more verse than has any other bird. Readers of English poetry think next of the Sky Lark. Here again Meredith is superlative, in "The Lark Ascending":

> He rises and begins to round,
> He drops the silver chain of sound,
> Of many links without a break,
> In chirrup, whistle, slur, and shake,
> All intervolved and spreading wide,
> Like water-dimples down a tide
> Where ripple ripple overcurls
> And eddy into eddy whirls . . .



Sky Lark

Whereas the Nightingale's song comprises many sequences, each new and separated by pauses, the Sky Lark's is all one, "intervolved," "a chain of sound"; Meredith's short, swift, rhyming lines enhance this effect.

For its careful artistry as for fullness with which it reflects the mind of its maker, Shelley's "To a Skylark" is universally admired. As a bird poem, however, it falls short because the bird is lost. Writing on the same bird Wordsworth produces a different effect chiefly because he does not forget his theme,

Ethereal minstrel! pilgrim of the sky! . . .
A privacy of glorious light is thine,
Whence thou dost pour upon the world a flood
Of harmony, . . .

Compare the quatrain of Blunden on the Sky Lark:

A singing firework; the sun's darling;
Hark how creation pleads!
Then silence: see, a small gray bird
    That runs among the weeds.

These scattered passages illustrating song in verse may be concluded with lines from "Home" in which Thomas expresses a quiet sense of kinship with birds:

'Twas home; one nationality
We had, I and the birds that sang,
One memory . . .
The April mist, the chill, the calm,
Meant the same thing familiar
And pleasant to us, and strange too,
Yet with no bar.
The thrush on the oaktop in the lane
Sung his last song, or last but one;
And as he ended, on the elm
Another had just begun
His last; they knew no more than I
The day was done.

Such a passage combines a keen, objective awareness and a modest, unaffected response—the meaning to the poet of one moment at evening.

Nesting

Wordsworth and Clare are the poets of nests. The Wren's is here Wordsworth's theme:

> No door the tenement requires,
> And seldom needs a laboured roof;
> Yet is to the fiercest sun
> Impervious and storm-proof . . .
> These find, 'mid ivied abbey-walls,
> A canopy in some still nook;
> Others are pent-housed by a brae
> That overhangs a brook . . .

And, elsewhere, he observes that:

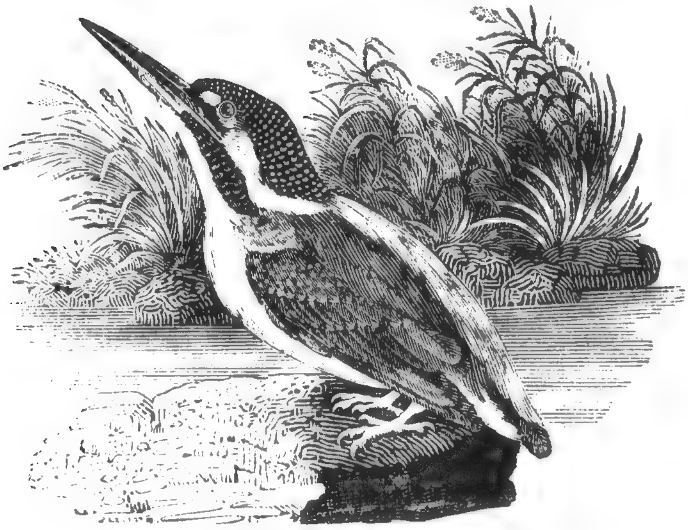
> the very nest
> In which this child of Spring was reared
> Is warmed thro' winter by her feathery breast.
> To the bleak winds she sometimes gives
> A slender unexpected strain . . .

The Long-tailed Tit also finds winter refuge in its far more elaborate nest. Clare's interest in this bird has been referred to. Note his careful description of the Nightingale's nest:

> How curious is the nest! no other bird
> Uses such loose materials, or weaves
> Its dwelling in such spots; dead oaken leaves
> Are placed without and velvet moss within,
> And little scraps of grass, and — scant and spare,
> Of what seem scarce materials — down and hair; . . .
> Snug lie her curious eggs in number five,
> Of deadened green or rather olive brown;
> And the old prickly thorn-bush guards them well.

Here is a naturalist presenting his data in verse form; one can imagine the reaction of a Keats. With equal accuracy Clare describes the Kingfisher's nesting habits:

> Sandmartin-like, they make a hole
> A steepy headlong bank beside.
> As well as ever did a mole,
> And there their many eggs they hide . . .



Kingfisher

Places more hard to reach than find
They choose, a safe and quiet home.
Their hole a full arm's length is made,
Turned at the last with sudden bend,
Where lots of fishes' bones are laid
Close to the large and furthest end;
Their eggs are white as wrynecks' be
And much about that middle size . . .

"Lots of fishes' bones" is hardly a lyric phrase; but Clare was determined to set down "only what I have seen." Nest like a Sand Martin's, eggs like a Wryneck's (and other woodpeckers'), the telltale bones, and the account is complete. Omitting the Mallard's tree nest and the Moorhen's "shelved nest hung just to touch the stream," we find a summer rain thus described by Clare:

The blackbird's wing was drabbling wet
With the shower so sudden coming . . .
The young ones in a nest of love,
Where the hedge the bramble hopples,
Cree'd, cawed and stretched their necks above
With their down all hung with dropples . . .
And magpies where the spinney was
Noised five and six together . . .

The scene fairly reeks with wet as archaism and coinage combine to give added effect. Both Wordsworth and Clare are content with objective description. As a final example, a poem in a different mood may be cited—"Birds' Nests" by Edward Thomas:

The summer nests uncovered by autumn wind,
Some torn, others dislodged, all dark.
Everyone sees them: low or high in tree,
On hedge, or single bush, they hang like a mark.
Since there's no need of eyes to see them with
I cannot help a little shame
That I missed most, even at eye's level, till
The leaves blew off and made seeing no game.
'Tis a light pang, I like to see the nests
Still in their places, now first known,
At home and by far roads. Boys knew them not
Whatever jays and squirrels may have done.
And most I like the winter nests deep-hid
That leaves and berries fell into:
Once a dormouse dined there on hazel-nuts,
And grass and goose-grass seeds found soil and grew.

None but implicit sentiment is here. This is the manner, too, of Clare, to which Keats objected, a particularizing art which yet reflects a love of the thing described.

Flight

Next after song the flight of birds seems greatly to have engaged the interest of poets, as of course this theme includes the flight-songs of Sky Lark and, as will appear, of Wood Lark and Tree Pipit.

The poetry of flight is marked by sharp contrasts of tone and effect. Sometimes the reader is arrested by a single word, a line, or a couplet, as, for example, in "Ambition," by Edward Thomas, who depicts a March scene:

Jackdaws began to shout and float and soar
Already, and one was racing straight and high
Alone, shouting like a black warrior
Challenges and menaces to the wide sky.
With loud long laughter then a woodpecker
Ridiculed the sadness of the owl's last cry.

By a skillful combination of verbs both flight and note come alive. So elsewhere with the Swift, where simile replaces emphasis upon the single word:

with wings and tail as sharp and narrow
As if the bow had flown off with the arrow.

Of the Swallow, Clare had written:

And mark the nimble swallow jerk and fling
Its flight o'er new-mown meadows happily,
And cuckoo, quivering upon narrow wing,
Take sudden flitting from the neighboring tree . . .

And Meredith's evening scene includes Swallow flight:

Swift as the swallow along the river's light
Circling the surface to meet his mirrored winglets,
Fleeter she seems in her stay than in her flight . . .
Lovely are the curves of the white owl sweeping
Wavy in the dark lit by one large star.
Lone on a fir-branch, his rattle-note unvaried
Brooding o'er the gloom, spins the brown eve-jar.

The evening advances from the Swallow drinking to the Barn Owl setting out to hunt, to the rattle of the Nightjar.

Let us turn to other birds as depicted by another poet, Father Hopkins, a keen student of flight and a master of words. Sky Larks and, less widely known, Wood Larks both engage in flight song. In Hopkins the wistful notes of the latter join those of sheepbells:

Thus they dingle, thus they chime,
While the woodlark's dimpling rings
In the dim air climb;
In the dim and dewy loneness,
Where the woodlark sings.

The quiet simplicity of the song suggested here distinguishes it from the intricate and longer climb of the more celebrated Sky Lark. Only Clare has written unmistakably about another similar flight song, that of the Tree Pipit:

Silent while up, then coming down she sings
A pleasant song of varied melody,
Repeated oft till some sudden check
The sweet-toned impulse of her rapture stops,
Then stays her trembling wings and down she drops . . .

The two larks sing during the ascent; the Tree Pipit, which never rises to such heights, begins singing near the peak and continues during its fluttering descent.

Father Hopkins often writes difficult verse, but he cannot be dismissed without brief reference to his most celebrated and most widely discussed sonnet, "The Windhover." Much nonsense has been written about the bird, a Kestrel, which prompted this poem, for the meaning becomes clear only if the habits of this bird are taken into account. Our concern fortunately is only with the morning picture of a hunting Kestrel, the first eight lines:

I caught this morning morning's minion, king-
dom of daylight's dauphin, dapple-dawn-drawn Falcon in
his riding
Of the rolling level underneath him steady air, and striding
High there, how he rung upon the rein of a wimpling wing
In his ecstasy! then off, forth on swing,
As a skate's heel sweeps smooth on a bow-bend: the hurl
and gliding
Rebuffed the big wind. My heart in hiding
Stirred for the bird,—the achieve of, the mastery of the thing!

How this Kestrel has been tortured to become some other bird "soaring in glorious rhythmic circles, ever driving upward with the thrill of achievement, of gratifying approach to its goal in the heights" (Schoder, 1949) when its actual goal is an insect or mouse below! Difficulties in Hopkins' lines disappear when the reader recalls the Kestrel's characteristic habit of hovering, then sweeping downwind, then turning again into the wind to hover. The poet knew precisely this because he had witnessed it.

It is fitting to conclude the poetry of flight with the simplicities of John Clare in a passage marvelous for its single words which capture the individuality of flight:

The crow goes flopping on from wood to wood,
The wild duck wherries to the distant flood,
The starnels hurry o'er in merry crowds,
And overhead whew by like hasty clouds; . . .
The pigeon suthers by on rapid wing, . . .
Whizz goes the pewit o'er the plowman's team,
With many a whew and whirl and sudden scream;
And lightly fluttering to the tree just by,
In chattering journeys whirls the noisy pie;
From bush to bush slow swees the screaming jay,
With one harsh note of pleasure all the day.

Elsewhere Wood Pigeons "smacked their clapping wings" and "the small wren twits with tail cocked o'er his back." In his eagerness to fit bird with word Clare is a master of ingenuity and novelty.

Future Bird Poetry

Recently Aldous Huxley (1963) has advanced his belief that poets today should take advantage of new scientific knowledge about birds. For men of letters, he states, "the new facts about nightingales are a challenge from which it would be pusillanimous to shrink." The new facts: that it is the male, not his mate, that sings; that song is territorial; that he sings at night because his digestive system requires him to feed every four or five hours throughout the twenty-four. "Between caterpillars, . . . he warns his rivals to keep off his private property." Huxley knows the work of Eliot Howard and Conrad Lorenz but apparently not that of Edward A. Armstrong (1963) and Charles Hartshorne (1958), both of whom present evidence that birds sing for reasons other than territorial defence. Besides, the biological utility of song is one thing; how the bird feels is another. Do people make love merely to continue the race? Analyses of the songs of many birds point to the conclusion that birds are pleased by their own performance, that they possess an aesthetic sense. Moreover, as Professor Hartshorne says, "there is a measure of congruity between the birds' feeling for sound patterns and ours." When Keats describes the Nightingale as "too happy in thine happiness," he thus anticipates the findings of today.

But generally speaking, what can be said for Huxley's thesis? For most persons the verse quoted in this essay will imply an answer. It has been long since recognized that poetry about birds cannot admit violence to fact; in his effort to bring the bird to life in words, the poet is duty-bound to observe correctly. But is there any need that he know the bird's life history? His endeavor is rather to evoke image, individuality, and perhaps to add his own response. The balance may shift either way, as illustrative passages have shown. Perhaps more descriptive of the role of the bird poet, future as well as past, are the words of Canon Raven (1927) who writes of his hours upon hours of watching a single familiar bird: "Such simple joys have a peculiar aesthetic quality: one is not exploiting the bird to one's own advantage; one looks to make nothing out of her; only one enters into and rejoices in her life." In some measure the best of bird poets share this very intimate pleasure and in words convey something of its nature.

Acknowledgments

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Browning, Robert, 1812-1889
Clare, John, 1793-1864
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Drayton, Michael, 1563-1631
Hopkins, Gerard Manley, 1844-1889
Keats, John, 1795-1821
Meredith, George, 1828-1909
Shakespeare, William, 1564-1616
Shelley, Percy Bysshe, 1792-1822
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EVOLUTION IN THE AFRICAN PARROT GENUS *AGAPORNIS*

William C. Dilger

To conduct investigations in behavioral and structural evolution, one should have a group of species that are closely related and yet have a strong divergence among homologous features. A group of related species has a common ancestor and the variability among its present sets of homologous features represents various departures from ancestral conditions. The arrangement of these departures in graded sequences, when it is possible, gives us some idea of the steps involved in attaining the greatest departures from the most "primitive" conditions. Once we have established such sequences, we then try to determine the direction of the changes and for this we seek information on close relatives of the group of related species. The features shared by the two groups probably represent features found in the common ancestor. I chose *Agapornis,* a genus of African parrots, as the group on which to work. This genus contains several species demonstrating ample variability among homologous features.

The Asiatic genus *Loriculus* (hanging parrakeets) most closely resembles *Agapornis* and is probably its closest living relative. The several species of *Loriculus* range eastward from western India and Ceylon across tropical southern Asia, the East Indies, and New Guinea to the Philippines. They are small, short-tailed parrots, able to eat a variety of foods—small seeds, berries, nectar, and flowers. They are sexually dichromatic and, although non-colonial breeders, may form small flocks during the non-breeding season. They inhabit the light forest or forest edges, never open country or deep forests. They sleep upside down, carry bits of nest material tucked amidst the feathers of the entire body, hold food in the foot, and scratch over the wing. They have an elaborate and varied system of agonistic (attack-escape) displays but no highly ritualized fighting. Their newly-hatched young have white down.

Unfortunately, this information, most of which we have garnered in tantalizing fragments from the avicultural literature, is about all we know of the behavior of *Loriculus.*

The parrot fauna of Africa is relatively poor. There are only four genera (*Psittacus* — 1 species; *Poicephalus* — 7 species; *Psittacula* — 1 species; and *Agapornis* — 9 species). I have taken these figures from Peters (1937) but I feel, as do others, that we should consider *Agapornis* as having only six species—that we should combine the white eye-ringed forms as subspecies under *personata,* the oldest name (Dilger, 1960). The species and diversity of parrots increase toward the Australo-Papuan area where they are most

Figure 1. Ranges of the species of *Agapornis* (after Moreau, 1948).

abundant. It seems likely that the African parrots came from Asia—probably in more than one invasion. The ancestor of *Agapornis* was probably *Loriculus* or a *Loriculus*-like species which underwent subsequent adaptive radiation.

The species of *Agapornis* are presently distributed from the northern savannas just south of the Sahara south to the north bank of the Orange river; *Agapornis cana* is found only in Madagascar. (See Figure 1.) This genus is obviously more diversified than *Loriculus*—probably a reflection of the fact that *Agapornis* occurs over a wider variety of habitats than does *Loriculus,* all the species of which seem to be fairly similarly adapted.

We can assume that most or all of the features, shared by *Loriculus* and at least by some of the *Agapornis* species, probably were also present in their common ancestor. Some of the features they share are: small size and similar body proportions; sexual dichromatism; white-downed young; sleeping upside down; cutting small bits of nest material and carrying these, several at a time, amidst the body feathers; broad diet of seeds, fruit, insects, nectar, flowers, etc.; non-colonial breeding; inconspicuous cere; lack of contrasting eye-ring; elaborate and varied agonistic displays; holding food in foot; strong nest-defence displays; similar habitats; and generally similar body posture. Of course, other parrots may share one or more of these features with *Agapornis* but none share nearly as many as does *Loriculus. Loriculus,* generally speaking, represents the common ancestor more than does *Agapornis. Agapornis cana, taranta,* and *pullaria* have more of these ancestral features than have the others of the genus. *A. roseicollis* is somewhat intermediate and *personata,* particularly *p. lilianae* and *p. nigrigenis,* represent the greatest departure from the ancestral type. Tables 1, 2, 3, and 4 and Figure 2 summarize some of the features, ancestral and others, shared by *Loriculus* and *Agapornis.*

Let us examine a few of the trends within the genus *Agapornis* in more detail. For additional information and illustrations, consult Dilger (1960).

TABLE 1

Habitat, Diet, and Social Organization at Breeding in *Loriculus* and *Agapornis*

Species	*Habitat*				*Diet*				*Breeding*			
	Open woodland and edges	*Wooded savannas and edges*	*Rain forest*	*Dry, wooded savannas*	*Seeds*	*Small fruits*	*Nectar*	*Insects*	*Solitary pairs*	*Semi-colonial*	*Colonial*	*Unknown*
Loriculus	X				X	X	X		X			
Agapornis cana	X				X				X			
A. taranta	X				X	X			X			
A. pullaria		X			X				X			
A. swinderniana			X		X	X		X	?			X
A. roseicollis				X	X					X		
A. personata personata				X	X						X	
A. p. fischeri				X	X						X	
A. p. lilianae				X	X						X	
A. p. nigrigenis				X	X						X	

Maintenance Behavior

All *Loriculus* regularly sleep and rest by hanging upside down. (See Table 2.) Only *A. pullaria* does this and then not regularly. *A. taranta* sometimes rests during the day in this fashion but sleeps in the usual upright position. We know of no other parrots that sleep upside down.

We have seen *taranta* holding food (pieces of fruit, berries, and honey-soaked bread) in the foot. However, they rarely use the foot to bring the food to the bill. More commonly they stand on the food while eating bits of it, or, less commonly, they hold the food in the closed foot while keeping the foot on the perch. *Loriculus* species do all of these things but frequently bring the foot holding the food to the bill. No other species of *Agapornis* has been observed holding food in the foot. In the wild, *A. taranta* eats juniper berries and *swinderniana* eats a variety of foods including green corn, wild figs, and insects. We might also expect *swinderniana* to hold food in the foot but have no observations on this point.

TABLE 2

Behavior in Certain Activities of *Loriculus* and *Agapornis*

Species	*Sleeping*		*Bathing*		*Holding food*		*Agonistic behavior*		*Fighting*	
	Upside down	*Upright*	*Standing water*	*Rain*	*Bill*	*Foot*	*Highly ritualized*	*Not highly ritualized*	*Not ritualized*	*Highly ritualized*
Loriculus	X		?	?	X	X	X		X	
Agapornis cana		X	X	X	X		X		X	
A. taranta		X	X		X	X	X		X	
A. pullaria	X	X	X	X	X		X		X	
A. swinderniana	?	?	?	?	?	?	?	?	?	?
A. roseicollis		X	X		X			X		X
A. personata personata		X	X		X			X		X
A. p. fischeri		X	X		X			X		X
A. p. lilianae		X	X		X			X		X
A. p. nigrigenis		X	X		X			X		X

All *Loriculus,* when walking, keep the body well raised from the substrate and have a curiously "round-shouldered" appearance, especially when bringing the head down. *Taranta* is the only *Agapornis* observed to share this feature.

All *Agapornis* may bathe in a manner similar to most small birds but *cana* has been seen bathing in light rains by stiffly hanging upside down with wings and tails spread and *A. pullaria* was seen bathing this way once. We have no information on bathing in *Loriculus. A. roseicollis, taranta,* and the four subspecies of *personata* are avid bathers; the others much less so.

Agonistic Behavior

A. cana, taranta, and *pullaria* have an elaborate system of agonistic displays (see Table 2) indicating varying degrees of probabilities for attack or escape (Dilger, 1960). These displays involve ruffling and fluffing various areas of the plumage, tail-spreading, and (in males only) showing the black wing-linings. They also show these black wing-linings during sexual encounters. *A. taranta* males show the black wing-linings by flicking the carpal areas out and back without displacing the primary tips. *A. pullaria* males expose the same area except that they hold the wrists out stiffly for some seconds before assuming the normal resting position. *A. cana* males have black wing-linings but we have not seen the birds use them during agonistic encounters. All three of these species have the Aggressive Walk—a peculiar, rapid walk toward an opponent that may be associated with feather erections in various combinations, depending upon the amounts and durations of conflicting attack and escape motivations. All three species may also spread the tail widely as an agonistic signal. The tails of *cana* and *taranta* are almost identical in color and pattern but the tails of *pullaria* are quite different. (See below and the color plate in Dilger, 1960 or 1962.)

Toward intruders both *cana* and *taranta* give strong displays in defense of the nest-cavity. One portion of the display is a loud, rasping vocalization as well as a sharp *yip*. This display is most complete and has the lowest threshold of response in *cana*. No such display exists in *roseicollis* and *personata*. Species of *Loriculus* have not nested in the laboratory but our experiences with closely-confined ("trapped") individuals indicate that their responses are similar to those of *A. cana* and *taranta*.

In response to potentially-dangerous intruders, strong mobbing—composed of shrill, rapidly-repeated vocalizations plus synchronous wing-beating—occurs in *roseicollis* and *personata*. The whole flock, being highly mimetic, engages in this behavior. The birds also engage in many intention movements to approach and retreat during mobbing. These two species, both colonial nesters, apparently have evolved mobbing as a predator deterent and rely on it rather than on displays within the cavity itself.

Also, *roseicollis* and *personata* have no threat displays although, being colonial breeders, they have many more agonistic encounters than do the non-colonial *cana, taranta,* and *pullaria*. Both *roseicollis* and *personata* usually resolve their differences by simple, unritualized intention movements to attack or escape. If this does not suffice, the birds actually fight but the fighting itself is highly ritualized—both in its form and in objective. We call such display-fighting—in which the combatants parry and thrust with their bills—Bill-fencing. The object is to nip the opponent's foot. Apparently the young are hatched with the propensity for Bill-fencing and toe-nipping, and with very strong inhibition against biting an opponent anywhere else. Although Bill-fencing appears to be "innate," the birds must practice to do it well and young birds are often painfully nipped, particularly when contesting an adult. Many, if not all, parrots have this built-in inhibition for biting each other whether they engage in display fighting or not. They retain this inhibition for their own kind and extend it to humans if they have been hand-raised. Thus it appears that, although Bill-fencing is innate behavior, it can be extended as a result of experience, to include other species.

An elaborate attack and escape display system, along with the low probability of encounters, seems to minimize sufficiently the chances of biologically-harmful combat in *cana, taranta,* and *pullaria* (and probably *Loriculus* as well). Unfortunate combinations of motivational states leading to fighting rarely result. However, when actual fighting does occur in these species, the results are disastrous—with one or both birds killed or severely injured. Unritualized intention movements for attack or escape coupled with highly-ritualized fighting in *roseicollis* and *personata* render actual combat virtually impossible in these species.

Reproductive Behavior

Pair Formation

We know little about pair formation in any of these species. Pair bonds last for extended periods, probably for the life of one of the partners. In *A. cana* and *taranta* pair formation seems to coincide with the assumption of adult plumage—at about four months of age. This may be true for *pullaria* as well. In *roseicollis* and *personata* the young form pairs as soon as they are independent of their parents yet still in juvenal plumage at about two months of age. The roots of these pair formations may start even earlier and, as might be suspected, siblings commonly pair. We know nothing of pair formation in *Loriculus,* but it is probably similar to that in *cana* and *taranta.* The birds maintain their pair bonds by sharing many activities. Of these, aside from simply always being together, "courtship feeding" and reciprocal preening are probably the most important.

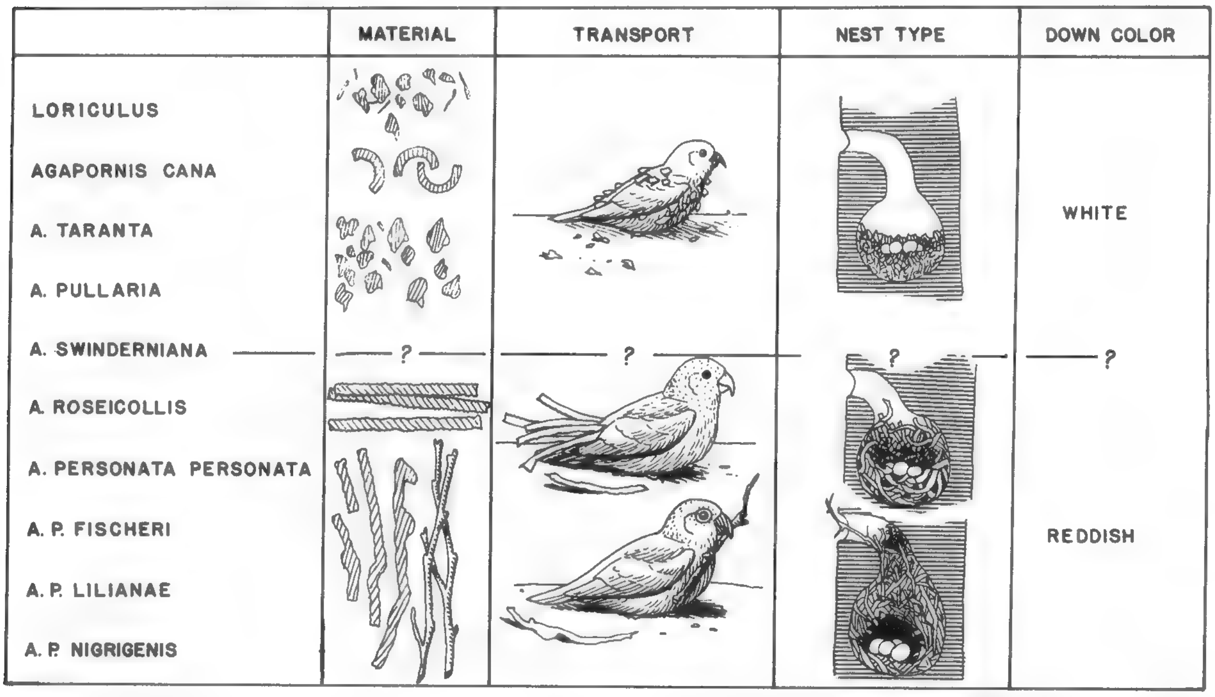

Figure 2. The type of nest material, method of transportation, type of nest built, and the color of the natal down in *Loriculus* and species of *Agapornis*. The type of material cut by *A. cana* actually represents a stage somewhere between *A. pullaria* and *A. roseicollis*. Note that the white eye-ringed forms carry twigs and fashion a completely-domed chamber within the nest cavity.

Nesting

All *Agapornis* and *Loriculus* species carry nest material to the cavities in which they nest. (See Figure 2.) Some simply provide a soft pad for the eggs and young, others build an elaborate, covered chamber with a tunnel leading to the entrance hole. All *Loriculus* species as well as *A. taranta* and *pullaria* cut small pieces of bark, leaves, and similar materials and tuck them, one piece at a time, amidst the feathers anywhere on the body the bird can reach except for the flight feathers. When several such pieces are tucked, the bird flies off to the nest-cavity where it pulls out the material and incorporates it into the nest. *A. cana* uses similar materials but cuts the strips in short arcs, not irregular bits. Like *pullaria* and *taranta* it tucks them in the feathers, but most often in the rump feathers. *A. roseicollis* cuts straight, long strips of material of uniform width and tucks them only amidst the feathers of the lower back and rump. *Loriculus* and *A. pullaria, taranta,* and *cana* arrange their materials into a soft pad in the bottom of the cavity although *cana* frequently manages to form a rather deep cup. *A. roseicollis* constructs a well-made cup with its long, straight strips. The four subspecies of *personata* never tuck nest material amidst their feathers but carry it, one piece at a time, in the bill. In addition to cutting strips of rather irregular widths, lengths, and straightnesses, they carry small twigs. This material is built into elaborate covered chambers with a tunnel leading to the cavity entrance.

The contour feathers of all *Agapornis* and *Loriculus* have special microscopic hooklets, especially around the tips and distal margins (Sick, 1938, and pers. obs.). These hooklets apparently do not grip the bits of nesting material but, rather, grip the feathers more firmly to each other, and thus prevent the tucked material from slipping out.

Agapornis and *Loriculus* are the only Old World parrots that build nests. One South American parrot, *Myiopsitta monachus,* builds large twiggy nests among tree branches. In over three hundred species of parrots only these three genera *(Agapornis, Loriculus, Myiopsitta)* are nest builders. We must regard parrots as a group of primary hole nesters—like the woodpeckers, barbets, motmots, and kingfishers, for instance. Nest-building among parrots must be an independent acquisition that is quite unrelated to similar activities by other kinds of birds. The evolution of nest-building of *Myiopsitta* on the one hand and nest building by *Loriculus* and *Agapornis* on the other must also be independent. These genera are thousands of miles apart geographically and the types of nests are entirely different.

There is a clear trend from cutting small bits of material, which the bird tucks over the entire body, to cutting long strips, which it tucks only in the rump, to the abandonment of tucking and the acquisition of carrying material in the bill.

Gamopractic Behavior

We use the term gamopractic behavior to replace the more limited term, precopulatory behavior. The term precopulatory leaves out copulation which is an integral part of this functional complex and the terminal appetitive activity before the consummatory sexual act or stimulus ending a bout of gamopractic activity. In other words, copulation belongs with all of the other behaviors functioning in precopulatory behavior. The function of gamopractic behavior is to raise the immediate probability of a male and female gamete meeting to form a zygote.

Again, in *Agapornis* there are two main types of gamopractic behavior correlated with two basic types of male-female relationships. In *cana, pullaria,* and *taranta* neither sex clearly dominates the other. (See Table 3.) Either member of a pair may supplant the other and either may feed the other during courtship feeding although the male usually feeds the female. (The internal states responsible for this activity are not clear. See Dilger, 1960, for further discussion.) In *roseicollis* and *personata,* the female is clearly dominant over the male. Therefore the motivational states of the sexes are more predictable. The male is mostly dominated by fear of the female and by sex—this being his basic conflict of drives during gamopractic activities and giving rise to the typical gamopractic displays of these species. In addition, *cana, taranta,* and *pullaria* are sexually dichromatic so that there is never any doubt as to the "maleness" or "femaleness" of any individual regardless of what it is doing. On the other hand, since *roseicollis* and *personata* lack sexual dichromatism,

TABLE 3

Courtship Activities in *Loriculus* and *Agapornis*

Species	*Courtship feeding*			*Squeak-twitter*	*Head-bobbing*	*Display of carpals*		*Displacement scratching*
	Present, type unknown	*Reciprocal*	*Male to female*	*Direction of ritualization*	*Direction of ritualization*	*Absent*	*Present*	*Direction of ritualization*
Loriculus	X			?	↓	?	?	?
Agapornis cana		X		↓		X		↓
A. taranta		X					X	
A. pullaria		X					X	
A. swinderniana	?	?	?			?	?	
A. roseicollis			X			X		
A. personata personata			X			X		
A. p. fischeri			X			X		
A. p. lilianae			X			X		
A. p. nigrigenis			X			X		

sexually specific behaviors must signal sexual "identity." These non-dichromatic species have, therefore, what has been termed "compensatory diethism" (Dilger, 1960).

A female *roseicollis* or *personata* must, by her behavior, indicate that it is safe for her mate to feed or copulate with her. She does this by assuming the fluffed posture which indicates harmlessness or submissiveness in many species of birds. During copulation the female mainly fluffs the feathers of her wrists and face—the areas the male can see from his position. The females of the other species do not adopt this submissive fluffing during feeding or copulation.

The various gamopractic displays characteristic of *Agapornis* have already been described and discussed (see Dilger, 1960), so I will simply list them here and discuss those which show well-marked differences. The gamopractic displays recognized are: Switch-sidling, Carpal Flash, Carpals Held, Head-bobbing, Displacement Scratching, Squeak-twittering, and Displacement Preening. Tail-wagging and "pseudofemale" soliciting are probably not displays but need further investigation.

Carpal Flash *(taranta* males only) and Carpals Held *(pullaria* males only) are almost certainly homologous. (See Table 2.) These displays differ mainly in the duration of the exposure of the black underwing coverts and in the fact that a widely-spread tail is often associated with Carpals Held. Curiously, *cana* males lack this display although their wing-linings are also black. Similar displays are used during agonistic encounters.

Head-bobbing (Table 2) is a display clearly derived from regurgitory head-bobbing used during courtship feeding and in feeding the young. All species of *Agapornis* have this display but each in a different form. In general, the bobbing movements are more numerous and more rapid in *cana, taranta,* and *pullaria*—most numerous and most rapid in *pullaria.* There are fewer and deeper bobs in *roseicollis* and even fewer and deeper ones in *personata.* These last two species also incorporate feather ruffling of the back and scapulars. This is particularly strong in *personata.* We have seen two male *Loriculus galgulus* perform Head-bobbing with many rapid bobs—very much like *A. pullaria.* Although display bobbing has lost its original function associated with regurgitation, females often respond to it by soliciting feeding. A bout of Head-bobbing might then grade into true feeding or vice versa. (For a discussion of these transitional activities, see Lind, 1959.)

Displacement Scratching (Table 2), a display evolved from the head scratching, is characteristic of males thwarted during bouts of sexual behavior. Ordinary head-scratching (over the wing) furnishes the precursory motor patterns which have become ritualized to varying degrees in the different species of *Agapornis.* In *cana, taranta,* and *pullaria* this scratching shows little evidence of ritualization. The male typically has the foot nearest the female lifted or at least his weight shifted to the other foot preparatory to mounting. At this point thwarting commonly takes place. The foot is then employed in scratching the face rather than in stepping onto the female's back. In *roseicollis* there is evidence of changes in the motor patterns. The movements are faster, more "perfunctory," and the bird frequently scratches the bill instead of the feathered areas of the head. More important is the fact that the male often scratches when he is several inches from the female and no thwarting is obvious. Also important is the fact that now he frequently uses the foot farther from the female. The ratio of employment of the near foot to the far foot is 3:2 in this species. This trend continues in *personata:* the movements become faster and more perfunctory; the scratching is performed even more often when immediate thwarting is not apparent; and there is even less dependence upon the near foot. The ratio of employment of the near foot to the far foot in *p. personata* and *p. fischeri* is 7:6. This ratio in *p. lilianae* and *p. nigrigenis* is very close to 1:1. These four forms also scratch the bill more often than *roseicollis* does.

Displacement Scratching provides a particularly good illustration of the evolution of a display from an ordinary unritualized activity.

Squeak-twittering (Table 2) requires much more investigation but subjective data so far indicate that this vocalization (a repetitive and persistent series of squeaky sounds) becomes progressively more stereotyped, shriller, and more rhythmical through the series from *cana* to *p. nigrigenis.* Since all vocalizations are displays by definition (Moynihan, 1955), the non-display precursor is lost in vertebrate antiquity. Vocalizations probably evolved from air-gulping of aquatic vertebrates (Spurway and Haldane, 1953). Consequently, vocal displays proliferate from one another. Squeak-twittering, judging from the sounds incorporated and from the situations in which it occurs, seems to indicate submissiveness with a strong element of thwarting. The activity with which it is most closely associated now is Displacement Scratching, most commonly occurring immediately before, during, or immediately after this behavior.

Displacement Preening is highly ritualized in *cana,* consisting of an alternate series of quick nods of the head to the right and left. High motivations sometimes prompt more complete movements and the true nature of this activity then becomes apparent—the bill actually reaching the feathers of the left and right upper breast where a few quick and perfunctory preening movements are sometimes made. This display apparently does not occur in the other species which utilize Displacement Scratching, tail-wagging, or pseudofemale soliciting in similar circumstances.

Tail-wagging, an ordinary comfort activity, frequently occurs during gamopractic bouts in *roseicollis* and *personata.* We see it often particularly during highly-motivated bouts when the male is thwarted. There is no evidence of ritualization. The birds seem to use this unritualized behavior instead of the ritualized Displacement Scratching during moments of particularly strong sexual thwarting. It is as if, at the moment of very strong thwarting, the unritualized behaviors are more useful than the ritualized activities, now more under the control of the physiological states underlying gamopractic displays. This seems to provide evidence for the rather strong competition among related displays (see Dilger, 1960).

Pseudofemale soliciting frequently occurs in sexually-thwarted male *roseicollis* and *personata.* The sexually-specific motor patterns of vertebrates are often seen in either sex. Some of these pseudofemale or pseudomale behaviors are very common and performed so frequently that we must think of them as normal (see Morris, 1955). Female *Agapornis,* like other birds, adopt a stereotyped posture indicating readiness for copulation. She crouches horizontally, raising the head, tail, and wings. During strong gamopractic bouts the male, when he turns his back toward her, may adopt this female soliciting posture. Females will then often make intention movements to mount and sometimes actually do so. We have not seen females of normally heterosexual pairs perform male copulatory movements, however. Such activity is either very rare or absent in the sexually-dichromatic species.

It is apparent that through the series—*cana, taranta, pullaria, roseicollis,* and *personata* — Displacement Scratching, Squeak-twittering, and Head-bobbing become progressively more and more ritualized as signals. Displacement Preening in *cana* may represent an end point in a history of progressively-ritualized preening, the earlier stages of which have been lost to us. Tail-wagging, if it can compete successfully with established gamopractic displays, may represent the beginning of a new gamopractic display. The occurrence of pseudofemale soliciting in *roseicollis* and *personata* males, though poorly understood, represents a common vertebrate pattern. The only other item of particular interest here is that in parrots, unlike most birds, copulations may be of very long duration—five to six minutes or more. Most are of much shorter duration but these do not result in sperm emission. It seems that copulation serves several functions: pair-bond maintenance, arousal and synchronization of sexual physiologies, and, of course, initiating the proximities of male and female gametes.

Parental Care

All species of *Agapornis* incubate for about the same period (roughly three weeks) and take about the same time to fledge their young (about forty days). Both parents feed the young by regurgitation and gradually the male seems to take over the larger share of this behavior. However, although the young of all species fledge in about the same time, their developments—particularly the plumage development—differ. Plumage development, retarded in these species as it is in many hole-nesting birds, is presumably an adaptation preventing the feathers from being soiled with feces, thus reducing undesirable consequences. Through the series *taranta, cana, roseicollis,* and *personata* there is a progressive increase in the efficiency of nest-sanitation and a corresponding increase in the early development of the juvenal plumage (see Figure 2 in Dilger, 1960). *Agapornis* species do not remove feces, dead young, broken eggs, and other debris but simply cover them with new nest material.

Morphological Features

There seems to be a general increase in size but there are apparent irregularities. *Loriculus* and *A. cana* and *swinderniana* are all small; *taranta* and *roseicollis* are quite large. On the other hand, *p. lilianae* and *p. nigrigenis* are also quite small. Size may be either a secondary or primary condition. It seems reasonable that the large size of *taranta* is a secondary condition since its closest relatives *(Loriculus, A. cana* and *pullaria)* are all rather small. Because the highlands of Ethiopia—the range of *taranta*—are quite cool, the large size of *taranta* may simply be an example of Bergmann's rule.

The presence of blue in the lower back and rump follows an interesting pattern. In *pullaria* the lower back, but not the upper tail coverts, is blue. In *roseicollis* and *swinderniana* the entire lower back and upper tail coverts are blue. Both *p. personata* and *p. fischeri* have only a tinge of blue in the upper tail coverts. The entire back is green in *p. lilianae* and *p. nigrigenis.* It seems that *Agapornis* evolved a blue rump but that selective pressures are against it in the most recently-evolved forms. *Agapornis*' blue rump may have developed in connection with specializing in tucking nest material amidst the feathers of the back. I would be interested in knowing how *swinderniana* carries its nest material.

There is a tendency to develop a contrasting eye-ring. This is a ring of red feathers against a green background in *taranta* males; blue and white feathers against a mostly-red background in *pullaria;* white feathers in a mostly-red background in *roseicollis;* and a wide area of naked white skin against either a red or a black background around the eyes in all subspecies of *personata.* Both sexes and all ages of *cana* and *swinderniana* lack a contrasting eye-ring and the same is true for adult female and all juvenile *taranta. Loriculus* do not have contrasting eye-rings.

The tail patterns and colors also demonstrate a gradual change from *A. cana* and *taranta* through to *personata* (see the color plate in Dilger, 1960 and 1962). The tails of *cana* and *taranta* are remarkably similar — yellow tipped with green with a subterminal black band. There is little melanin at the base. The tail feathers of *pullaria* are similar except that there is a bright red area between the subterminal black band and the yellow and there is considerable melanin in the base. The tail of *swinderniana* is similar except that there is much more red between the black band and the base and the base contains much melanin. In *roseicollis* the subterminal black band is faint

TABLE 4

Morphological Features in *Loriculus* and *Agapornis*

Species	*Sexual dichromatism*			*Color of bill*			*Melanin in bill of young*			*Clavicle*		*Juveniles resemble*			
	Marked	*Weak*	*Absent*	*Red*	*Black*	*Whitish*	*Extensive but weak*	*Extensive and strong*	*Restricted but strong*	*Present*	*Absent*	*Male parent*	*Female parent*	*Neither parent*	*Both parents*
Loriculus	X			X	X		X			X			X		
Agapornis cana	X					X	X				X	*X	**X		
A. taranta	X			X			X				X		X		
A. pullaria		X		X			X				X			X	
A. swinderniana			X		X			X			X			X	
A. roseicollis			X			X		X			X			X	
A. personata personata			X	X					X		X				X
A. p. fischeri			X	X					X		X				X
A. p. lilianae			X	X					X		X				X
A. p. nigrigenis			X	X					X		X				X

*Juvenile *cana* males resemble adult males.

**Juvenile *cana* females resemble adult females.

along the outer edge; there is even more melanin in the base and the red is not as pure—more of a rusty red. The tails of all four subspecies of *personata* are practically identical. The outer portion of the subterminal black band is nearly gone; there is even more melanin in the base and the red portions are quite dull. There seems, therefore, to be a trend from yellow to red; from a strong subterminal black band to an incomplete one; and toward increasing melanin in the base.

Juveniles of *taranta* resemble the adult female but sometimes a young male will have a red feather or two in the forehead or orbital ring. (See Table 4.) Young *cana* males resemble their fathers except for a greenish wash on the nape. Young female *cana* resemble their mothers. Young of *roseicollis* and *swinderniana* resemble neither parent, and the young of *pullaria* have yellow faces instead of orange, like adult females, or bright red, like adult males. To this extent they resemble neither parent. The young of all forms of *personata* resemble their non-dichromatic parents very closely.

Juveniles of all species have more or less melanin in the bases of their bills. (See Table 4.) This melanin is widespread but diffuse with a brownish appearance in young *cana, taranta,* and *pullaria.* In juvenile *roseicollis* and *swinderniana* the melanin is also widespread but very dense, appearing black. Melanin may be absent in the bill bases of all *personata* forms, but when it occurs, it is very restricted, yet still dense. The condition for *Loriculus* is the same as for *cana, taranta,* and *pullaria.*

In Summary

The *Agapornis* ancestor probably spread into Africa millions of years ago across the once damper Arabian peninsula, adapting to and colonizing across the northern savannas and south in the east to the southern savannas. A population somehow managed to reach Madagascar rather early and became the present *cana.* Similarly, a population managed to adapt to rain forest and became *swinderniana.* The northern savannas eventually produced *pullaria* and its relative, isolated on the Ethiopian plateau, *taranta.* The southern savannas gave rise to *roseicollis* and the East African grasslands (between *roseicollis* and *pullaria*) gave rise to a *p. fischeri*-like form probably derived from *roseicollis* or a proto-*roseicollis.* This *fischeri*-like form evolved into a northern and southern form which became the present *fischeri* (northern) and *lilianae* (southern). Next, the *fischeri*-like form evolved into *fischeri* and *personata.* Last, the *lilianae*-like form evolved into *nigrigenis* and *lilianae.* The sources of the interruptions of gene flow in the East African populations may very well have been the conditions imposed by the development of the Rift Valley systems. The behavior of *p. lilianae* and *p. nigrigenis* is so similar, even quantitatively, that we have been unable to distinguish them on this basis. They are probably of very recent origin.

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LIFE HISTORIES AND THE EVOLUTION OF MEGAPODES

George A. Clark, Jr.

The generally dark-colored gallinaceous fowls, commonly called megapodes, of the family Megapodiidae are similar in proportions and foraging methods to pheasants. The megapodes are found only in the Australian region (Figure 1), where similar-sized pheasants, such as reside in adjacent southeastern Asia, are absent. The situation is apparently analogous to the presence of marsupial mammals in the Australian region in contrast to the placentals dominant in adjacent southeastern Asia.

Just as marsupials and placentals differ strikingly in reproductive habits, so do pheasants and megapodes. Members of five of the six megapode genera incubate their eggs by means of fermentation of organic matter in mounds scraped together by the birds (Figure 2). In one of these five genera, *Megapodius,* some populations use sun-warmed sand or volcanically-heated ground as an incubator, while the sixth genus, *Macrocephalon,* incubates its eggs in sun-warmed sand.

Also unique among birds is the great precocity of young megapodes which at hatching kick open the shell, breaking it into numerous pieces (cf. Bergman, 1963), and then dig upwards through sand or organic matter to the surface. Juvenile megapodes, unlike the young of other warm-blooded animals, receive no parental care and are independent of the adults. For example, Frith (1962: 121-122) observed an adult *Leipoa ocellata* (Mallee Fowl) that, while digging in the mound, uncovered a newly-hatched chick and promptly kicked it out of the mound as though the young bird were merely a piece of unwanted debris. Young megapodes can fly weakly on their hatching day (again unlike all other birds) and can forage successfully within a day or so after hatching.

These features contrast sharply with those of pheasants which build simple nests on the ground or in a tree and incubate their eggs in the usual avian way, by sitting on them. The embryonic pheasant, unlike the megapode, uses an egg tooth on its beak to break through the shell at hatching (Clark, 1961). Even the most precocious of young pheasants do not fly until a few days after hatching (Nice, 1962), and apparently all normally receive parental care.

This survey considers certain variations in life histories in relation to the probable evolutionary history of megapodes. Although the habits of two species of Australian megapodes, *Leipoa ocellata* (Mallee Fowl, see Figure 3) and *Alectura lathami* (Australian Brush Turkey, Figure 4), have been studied

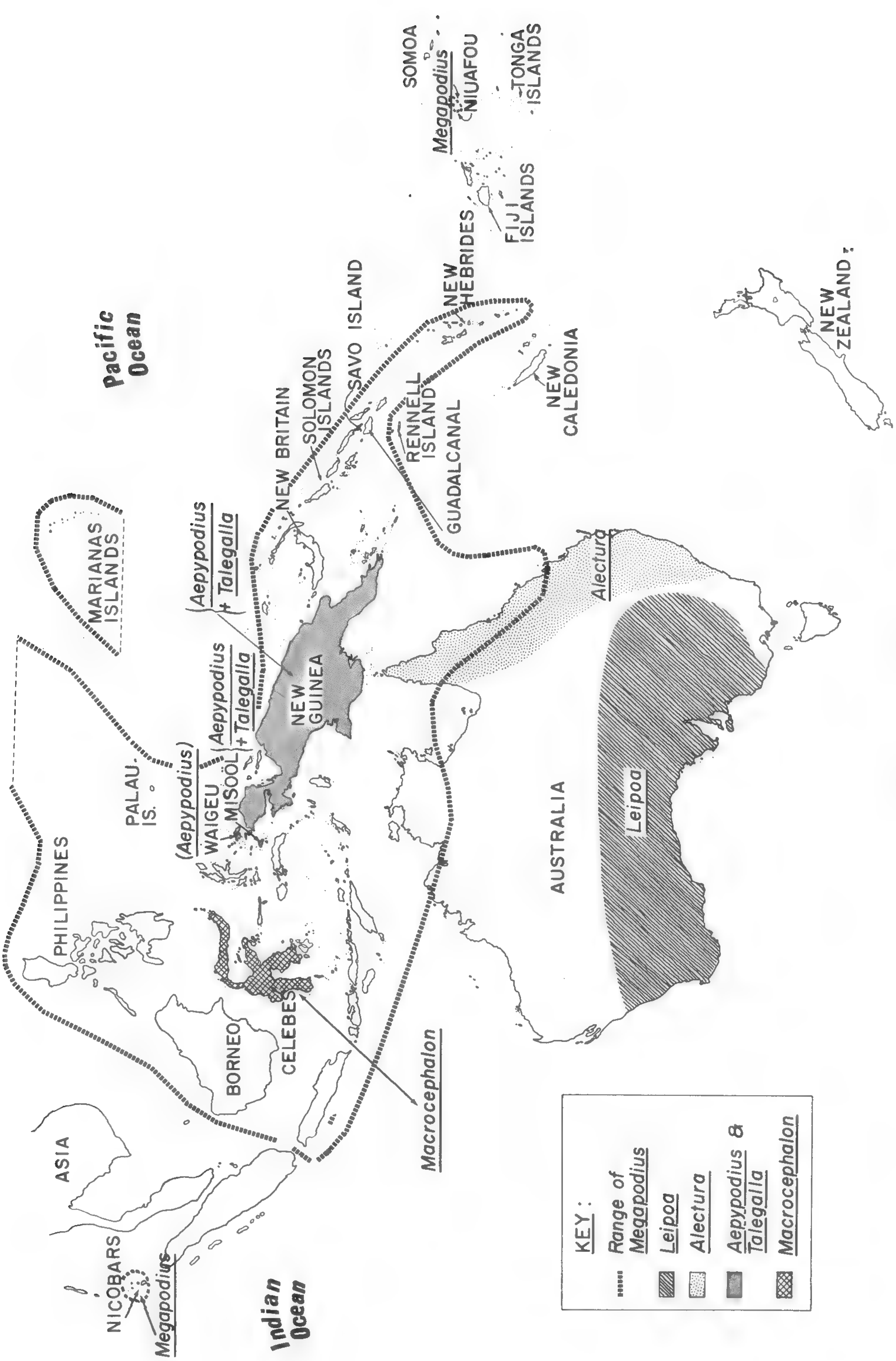

Figure 1. Ranges of the six genera of megapodes.

Figure 2 *(above)*. Nesting mound of the Scrub Fowl *(Megapodius freycinet)* at the edge of Kanganaman Village, Sepik River, Territory of New Guinea. Photograph by E. Thomas Gilliard.

Figure 3 (*below*). The Mallee Fowl (*Leipoa ocellata*), an inhabitant of arid scrub across southern Australia. The species, about the size of a small domestic turkey, is more brightly colored than most megapodes, a possible correlation with the comparatively bright illumination of the ground in the country where it occurs. Photographs by John Warham.

in detail by several investigators, the other ten species of megapodes are poorly known, which is unfortunate, especially since some populations either have been exterminated or are presently endangered by human activity (e.g., *Megapodius laperouse;* Greenway, 1958). Despite the deficiencies of life history data for much of the group, morphological evidence is sufficient to develop hypotheses on megapode evolution, thus providing one basic frame of reference for organizing information. As additional data become available, these phylogenetic hypotheses can be further evaluated for their accuracy.

Aspects of Megapode Distribution

Of the megapode genera (Table 1), *Megapodius* has the widest range, extending west of the Malay Peninsula to the Nicobar Islands, north into the Philippines and Marianas, east to the small island of Niuafou in the Tonga group, and south into northern Australia (Figure 1). There are, however, a few broad gaps in this range. For example, the populations of *M. freycinet* in the Nicobars are isolated, being about 1,000 miles from those of Borneo and Java to the east; within this hiatus lie the Malay Peninsula and Sumatra. The entire population of the species *M. pritchardii* is restricted to the small island of Niuafou and is separated by more than 800 miles from the nearest population of *Megapodius freycinet* to the west.

TABLE 1

Some Variations in the Family Megapodiidae

Genus	*Range in brief*	*Habitat*	*Body size*	*Egg-laying sites*	*Communal breeding*	*Heat source for incubation*
Megapodius	Widespread	Jungles and beaches	Small	Holes or mounds	Yes	Fermentation, sun, or volcano
Macrocephalon	Celebes	Jungles and beaches	Large	Holes	Yes	Sun
Aepypodius	New Guinea and nearby	Mainly upland jungles	Large	Mounds	No?	Fermentation
Talegalla	New Guinea and nearby	Lowland jungles	Large	Mounds	No	Fermentation
Alectura	Australia	Jungles and rain forest	Large	Mounds	No	Fermentation
Leipoa	Australia	Dry scrub	Large	Mounds	No	Fermentation and sun

Lister (1911) suggested that the extensive range of *Megapodius* was due to transport by prehistoric man. In some areas (e.g., the Solomon Islands and parts of New Guinea), megapodes and particularly their eggs are consumed by human populations (cf. Frith, 1956; Gilliard, MS). If man was responsible for the wide distribution of *Megapodius,* then the evolutionary differentiation of the small insular populations of *M. laperouse* (Palau and Marianas Islands) and *M. pritchardii* may have occurred in relatively recent times. In general, medium-sized Galliformes do not make long transoceanic flights, but, where broad gaps occur in *Megapodius* distribution, intermediate land areas might have served as historical stepping stones. Also perhaps relevant are observations that some *M. freycinet* regularly fly short distances from island to island, and that others make long cross-country treks at the time of egg-laying (cf. Ripley, 1960).

New Guinea is central in the present distribution of megapodes as all but two *(Leipoa ocellata* and *Megapodius pritchardii)* of the 12 species occur within 1,000 miles, and seven of the 12 species are found either on New Guinea or nearby smaller islands (cf. Ripley, 1960). The megapodes and their immediate ancestors apparently have evolved primarily within the Australian and southwestern Pacific area where changing geological and ecological barriers have doubtlessly influenced the evolution of the family through geological time.

The ranges of certain New Guinea megapodes illustrate the geographic replacement of closely-related species. Three allopatric species of the genus *Talegalla* are distributed around the island along the coast; this genus is replaced in the interior above 3,000 feet by *Aepypodius arfakianus* (Ripley, 1960). Curiously, *Aepypodius* also occurs at lower elevations on two islands off the west coast of New Guinea. These groups are the seldom-seen *Aepypodius bruijni* of Waigeu Island and a rare, subspecifically distinct, population of *A. arfakianus* on Misool (Ripley, 1960). Also present in the New Guinea area, generally at lower elevations, is the widespread *Megapodius freycinet.*

As Ripley (1960) has pointed out, the smaller size and shorter bill of *Megapodius,* relative to the larger megapodes, appear to be correlated with foraging differences sufficiently great to permit the widespread distributional overlap of *Megapodius* and the larger megapode genera. It would be interesting to know if intergeneric territoriality or hostility has developed where *Megapodius* and the other genera meet. Only one clear example of distributional overlap of two of the large species of megapodes has thus far been reported. Ripley (1960) discovered and analyzed this remarkable case of four species of megapodes (small ones: *Megapodius freycinet* and *M. wallacei;* large ones: *Talegalla cuvieri* and *Aepypodius arfakianus)* on the relatively small island of Misool west of New Guinea. He has hypothesized that intense predation may keep the populations of the four species so small as to prevent elimination of any one species of either pair through interspecific competition. (Ripley, 1964, has shown that the form *Eulipoa wallacei* should be included in the genus *Megapodius.)*

Alectura lathami (Figure 4) of the rain forests of Queensland and New South Wales, Australia, and *Leipoa ocellata* of the dry scrub areas across southern Australia are southern representatives of the megapodes of large body size.

The megapodes, like many other taxonomic groups, show an increase in number of species from the temperate zone into the tropics; in megapodes this greater number of tropical species appears to be more a result of proliferation of geographically separated species of similar foraging habits than of

Figure 4 (*above*). The Australian Brush Turkey (*Alectura lathami*), an inhabitant of the rain forests of Queensland and New South Wales, Australia. It is darkly colored in apparent correlation with its environment. Photograph by John Warham.

Figure 5 (*below*). A mound of the Mallee Fowl under construction (background). Scratching with their feet, Mallee Fowls gather leaves, twigs, and sand to make the mound from over many square yards of ground. Photograph by D. Havenstein.

Figure 6. While the female (right) stands by, the male Mallee Fowl checks the temperature in the mound's egg-chamber by plunging his beak into the sand. Photograph by H. J. Frith.

the development of foraging diversifications which would permit a greater number of species occurring together over a wide area. However, *Megapodius* coexisting with the brush turkeys appears to illustrate the latter condition.

Some Variations in Reproductive Habits in the Megapode Genera

Leipoa (Figure 3): Most of the following discussion of this monotypic genus is based on the excellent studies of Frith (1956, 1959, 1962).

Considerable variation in the reproductive ecology of *Leipoa* depends to a great extent on marked differences from year to year in rainfall in the arid regions where this species lives (Frith, 1959); reproductive activity may be much reduced in years of extended drought.

The birds spend as much as 11 months per year working around the mound. In a representative season, work on the mounds begins in winter. In the mound-building process, the birds scratch vegetable material (leaves, twigs) and sand from the ground over many square yards into a pile forming the prospective mound (Figure 5). With favorable weather during several months, fermentation develops and then recedes. When the mound cools internally to temperatures suitable for incubating the eggs (often in the range 90 to 96°F), the birds excavate an egg chamber centrally in the fermenting layer of the mound. The eggs are layed in this chamber through the breeding season (Figure 6), and the adults, especially the male, regularly attend the mound to dig in order to check and regulate the mound temperature. Frith (1959, 1962) has found that *Leipoa* can hold the temperature in the egg-chamber at a relatively constant level through the greater part of the egg-laying season. Apparently the tongue is the site of the temperature receptors (Frith, 1962).

Figure 7 (*above*). In the fall the Mallee Fowls scratch open their mound on clear days so that it may receive heat from the sun. In the background are seen the xerophilic eucalyptus trees known as mallee from which the species' vernacular name is derived. Photograph by H. J. Frith.

Figure 8 (*below*). While the male Mallee Fowl stands nearby, the female expels an egg into the chamber. Photograph by H. J. Frith.

Figure 9 *(above)*. The male Mallee Fowl inspects the newly-laid egg as the female leaves. Another egg, partly exposed when the chamber was scratched open, can be seen under the male's neck. Photograph by H. J. Frith.

Figure 10 *(below)*. The male Mallee Fowl, after inspecting the newly-laid egg, proceeds to scratch soil over it. Photograph by H. J. Frith.

Figure 11 (*above*). Eggs of the Mallee Fowl. The eggs are incubated together in the central chamber of the mound. Here they are shown dug out from the chamber deep in the mound. Photograph by H. J. Frith.

Figure 12 (*below*). A remarkable picture of a juvenile Mallee Fowl emerging at the surface of the mound after digging its way up from the hatching site. Photograph by H. J. Frith.

In spring and early summer the birds often open the mound during daylight in good weather to allow excess heat to escape from the inner portions of the mound. In cold or rainy weather the mound is often heaped high with sand and debris to aid in retaining heat. Later in the season as fermentation fails, the mound is opened on clear days to receive heat from the sun (Figure 7).

Eggs are laid one at a time, rarely as often as only two days apart, but usually four or more days apart. An average weight for eggs is between 180 and 190 grams or about 10 per cent of the adult female weight (Frith, 1959). The laying of the egg (Figures 8, 9, and 10) often appears laborious (Frith, 1962), which is interesting partly because the *Leipoa* egg, although large in absolute size, is not exceptionally large relative to the adult female size when compared with birds in general (Heinroth, 1922). For example, many small passerines produce, in relatively rapid succession, a clutch of eggs each weighing about 10 per cent of the adult female weight, and some birds such as Wilson's Petrel *(Oceanites oceanicus)* lay eggs weighing more than 20 per cent of adult weight.

There are many unusual aspects of the incubation of megapode eggs (Figure 11). *Leipoa,* like other megapodes, but unlike other birds, do not turn their eggs during incubation (Frith, 1959; Clark, 1960). The eggs in the mound are often situated with the blunt end upwards and the pointed end down, the position in which the eggs are laid. The orientation of the eggs in the incubating chamber of the mound has little, if any, effect on their hatching success (Frith, 1959: 40). Although some investigators have reported regular patterns in the spacial distribution of eggs within the *Leipoa* egg-chamber, such claims appear to have been exaggerated.

In partial association with intermound variations in incubating temperature from 80 to 96°F (Frith, 1959), natural incubation periods vary from 50 to 96 days (Frith, 1959), which is perhaps the greatest range in incubation period reported for any avian species. Furthermore, two chicks have been prematurely hatched under artificial incubation at 100°F in only 44 days (Frith, in Nice, 1962) while in captivity successful hatching has taken as long as 99 days. The young at hatching dig upwards a distance varying from several inches to a few feet, and the trip to the surface may last from two to 15 hours (Frith, 1959). The repeated diggings of the adults to check and regulate mound temperature apparently also function in keeping the contents of the mound loose, thus aiding the escape of the young (Figure 12). Juveniles on emergence from the mound appear tired (Frith, 1962). Nevertheless, after resting, they are sufficiently precocious to fly weakly on the day of hatching and to begin foraging within a day or so after hatching. There is no reliable evidence that the young of *Leipoa,* or any other megapode, receive parental care. Frith (1959) has observed that captive juveniles show no inclination to gregariousness and to repel each other with threat displays.

Adult male *Leipoa* are strongly territorial and have associated calls and displays (Frith, 1959). The male is generally dominant over the female and does the majority of work concerned with mound construction and temperature regulation. Evidence from color-banded birds indicates possible pairing for life (Frith, 1962). During the non-breeding season the pairs cease holding territories for a few weeks and may gather in small groups. With the resumption of reproductive activities, the pairs re-adopt a territory, although not necessarily that held during the previous breeding season. Mound-sites are generally traditional; the same site is often used for many years, although the same pair may not occupy it from one breeding season to the next. Not every

Figure 13. The leafy nesting mound of the Australian Brush Turkey (*Alectura lathami*) in a rain forest, New South Wales. Photograph by D. Havenstein.

mound-site is used each season, and new mounds are occasionally started. The end of the breeding season is often marked by the male digging up and destroying the mound (Frith, 1959).

Leipoa, and perhaps other megapodes, show little or no direct care for eggs once they have been laid and initially covered in the mound (cf. Frith, 1959:40; 1962:48). It appears, in *Leipoa* at least, that an object of primary concern at the mound is the regulation of the temperature in the egg chamber. The eggs themselves are sometimes destroyed by the birds either during temperature regulation or in cleaning out the mound at the end of the breeding season. The behavior of megapodes appears in this respect rather different from that of birds which incubate by sitting on their eggs.

Leipoa is generally considered to be evolutionarily specialized, adapted to the dry scrub and derived from an ancestral, jungle-dwelling brush turkey (cf. Frith, 1962).

Alectura (Figure 4): Brush turkeys of this monotypic genus also construct mounds of organic materials which, before egg-laying begins, are allowed to ferment until the internal temperatures drop to levels suitable for incubation. In this genus as well as *Aepypodius, Talegalla,* and *Megapodius,* the eggs are not laid in a central egg chamber, being instead buried individually in the mound (Figure 13). *Alectura* has not yet been studied in detail in the wild, but several reports cover the maintenance and breeding in captivity. The male shows strong territoriality and works to regulate the internal temperature of the mound by removing or adding materials. In this genus as in *Leipoa,* the male dominates the female in regulating the mound temperatures. Fleay (1937) has briefly described *Alectura* displays which are apparently similar to the hostile displays of *Leipoa.*

Talegalla: The three species of brush turkeys comprising this genus construct mounds similar to those of *Alectura* and apparently have similar habits of territoriality and temperature regulation of mounds (cf. Mayr, 1930; Gilliard, MS). According to native reports in an area where eggs are regularly harvested from the mounds, only one pair of birds attends a mound and the incubation period lasts between 60 and 90 days (Gilliard, MS).

Aepypodius: Of the three genera of brush turkeys, this genus of two species is the least well studied. The mounds resemble those of *Talegalla,* and periodic adjustment of the mound materials indicates that the birds regulate the mound temperature (Mayr, 1930). As Ripley (1960:637) has suggested, *Aepypodius* and *Talegalla* should possibly be included in a single genus, since only relatively minor morphological differences are known to distinguish the two presently-recognized genera.

Macrocephalon: This genus, restricted to the island of Celebes, appears highly specialized in possessing a helmet-like structure on the back of the head and in the pinkish coloration on the underparts in the living bird. These birds live mainly in the forested interior regions but are known to make long treks to the coastal regions where the eggs are deposited in holes dug in the sand near the shore (Fairchild, 1943). The heat for incubation of the eggs apparently comes from the sun. There is no indication that these birds regulate temperatures in the egg-laying holes and the communal nature of the egg-laying areas is apparent (Fairchild, 1943). This species has, however, been studied relatively little in every respect.

Megapodius: This genus of four species shows great variation in reproductive ecology. On Savo and Simbo Islands of the Solomons and on coastal New Britain, volcanic heat is used by *M. freycinet* in incubating the eggs which are placed in holes (Frith, 1956). *M. pritchardii* of Niuafou apparently relies entirely on volcanic heat for incubation. In contrast, *M. laperouse* of the Palau and Marianas Islands deposits its eggs in mounds as do populations of *M. freycinet* from the Nicobars, coastal northern Borneo, Celebes, the Philippines, Moluccas, New Guinea (Figure 14), northern Australia, New Britain, the Solomons, and New Hebrides. The largest known mounds are those of *M. freycinet* in northern Australia, where in some cases the birds have added materials to the mounds over many years, eventually producing giant mounds as large as 60 feet long, by 15 feet wide, by 10 feet high (Frith, 1962: 15); if these structures can be called nests, they are perhaps the largest known for birds. Another method of incubation is the burying of eggs in holes where heat is provided by the sun such as done by the population of *M. wallacei* of the Moluccas. Similar incubating methods are recorded for populations of *M. freycinet* as on Dunk Island, Queensland, Australia, where some of the population also use mounds (Frith, 1956).

The egg-laying sites of *Megapodius* in sand or volcanic fields are often clearly communal (e.g., on Savo). Furthermore, there are persistent reports that more than one pair of *Megapodius* may use a single mound at the same time (cf. Gilliard, MS). Some populations (e.g., *M. wallacei*) make treks for many miles from the interior foraging areas to the shore for egg-laying (cf. Ripley, 1960) in a manner analogous to the trips made by *Macrocephalon;* the lack of territoriality and temperature regulation in such forms is obviously correlated with the great distances between foraging and egg-laying grounds.

Figure 14. The seldom-photographed Scrub Fowl (*Megapodius freycinet*) at its mound. Among all the megapodes this species probably has the greatest variation in breeding habits. Photograph by John Warham.

Megapodius is not known to regulate the temperature of either mounds or holes (Frith, 1962:18); the birds appear to rely on picking an area with a suitable temperature for an egg-laying spot. In areas lacking marked seasonal changes, *Megapodius* may lay eggs throughout the year (Frith, 1956).

Additional comparative life history data on megapodes, including aspects such as clutch size, breeding seasons, and predators, have been ably reviewed by Frith (1956).

A Basic Evolutionary Division within the Megapodes

The Megapodiidae are clearly monophyletic in origin as shown by great similarities among the genera in structure (e.g., in the natal down; Clark, 1964), and in habits (e.g., mound-building, lack of parental care for young, etc.). The presence of a non-functional egg tooth (Clark, 1961, 1964; Bergman, 1963), unique, vestigial natal-down feathers preceding the juvenal flight feathers, and other lines of evidence (Clark, 1964) demonstrate that megapodes have evolved from gallinaceous birds which, although very likely of similar adult size, were smaller at hatching. This suggests that the ancestors of megapodes possessed somewhat more conventional nesting habits such as would be associated with the smaller body size and lesser precocity at hatching.

A fundamental division within the megapodes lies between the three genera of brush turkeys and *Leipoa* versus *Megapodius* and *Macrocephalon*. The proportions of *Megapodius* chicks at hatching are remote from those found in the brush turkeys, *Leipoa*, and especially non-megapode Galliformes (Clark, 1964). Furthermore, *Megapodius* has a rather specialized pattern of foot webbing. Hence it appears most likely that the brush turkeys, despite certain specializations, are somewhat more primitive than *Megapodius*.

Ecological and behavioral evidence appears entirely compatible with this interpretation of megapode evolution. It is simpler to visualize the territoriality of the brush turkeys as evolved directly from that of an ancestral group rather than as a secondary evolutionary appearance of territoriality. Furthermore, it is simpler to conceive of incubation in mounds evolved from a simple nest rather than from the burying and abandoning of eggs in the ground. Insofar as can be deduced from living representatives, the megapodes appear to be derived from an ancestral jungle-nesting group rather than from birds nesting in sandy, open areas. Thus, contrary to some opinions, it appears most likely that the habit of incubating eggs in holes by heat of the sun or volcanic activity has secondarily evolved in the megapodes. The simplicity of the hole-nesting is not primitive, being somewhat analogous to evolutionary loss of nest-building in the history of certain brood-parasitic birds such as the North American Brown-headed Cowbird *(Molothrus ater).*

In *Leipoa* at least, eggs are occasionally deposited away from the mounds (cf. Frith, 1962). Such procedures yielding successful hatching of eggs in an ancestral megapode population might have initiated the evolution of populations using exclusively sun or volcanic heat for incubation. Or, possibly, the rather complete gradation from mounds to holes found in living *Megapodius* (Frith, 1962) represents in part the kind of phylogenetic sequence that led to the incubation of eggs in holes.

Megapodes differ from other birds in having a very high ratio of yolk weight to egg-white weight. For this character, limited available data (Meyer and Stresemann, 1928; Mayr, 1930) indicate that *Megapodius* has a higher ratio than *Talegalla* which in turn has a higher ratio than non-megapode Galliformes. Further study may possibly show that this character has potential significance in interpreting evolution within the megapodes. Also the ratio of egg weight to adult weight may prove to have similar importance. Very limited data (Heinroth, 1922) suggest that *Megapodius* lay a relatively larger egg (17 per cent of adult body weight) than do the brush turkeys (12 per cent for *Alectura);* pheasants of similar sizes often lay eggs weighing 5 per cent or less of adult hen weight.

Evolution of the Basic Megapode Stock

There is no convincing evidence that the megapodes are evolutionarily primitive either among birds as a whole or among the Galliformes (Clark, 1964), despite the occurrence of certain reptile-like features secondarily evolved in the megapode reproductive biology (see Table 2).

The kinds of changes which presumably occurred in the evolution of megapodes are indicated by comparing the columns in Table 3 which summarizes some behavioral and ecological differences between megapodes and more conventional gallinaceous birds.

It seems likely that, in at least some cases, species recognition is inherent in the development of megapodes, since in populations whose eggs are simply abandoned at the start of incubation (e.g., *Megapodius wallacei*) there might be no opportunity for offspring to hear or see adults. Precise recognition of the species would presumably be especially important for mating where two or more species coexist, as on the island of Misool. Species recognition in non-megapode Galliformes frequently, if not always, involves learning by the young (imprinting). Hence, in the evolution of megapodes a learned species recognition may have been converted into an inherent one. An analogous behavioral evolution has presumably been involved in the history of certain brood-parasitic species (Mayr, 1963:109).

TABLE 2

Some Reptile-like Features of Megapodes

1. Incubation of eggs essentially underground.
2. Long incubation period.
3. Relatively low incubating temperature.
4. Large size of yolk relative to egg.
5. Highly precocious young.
6. Lack of parental care for young.

TABLE 3

Some Differences in Reproductive Biology Between Megapodes and Other Galliformes

Non-megapode Galliformes	*Megapodes*
Eggs often laid in rapid succession.	Eggs generally laid less frequently.
Generally smaller eggs.	Generally larger eggs.
Thicker egg shell?	Thinner egg shell (Frith, 1959).
Eggs normally incubated by body heat of adult.	Eggs not incubated by body heat of adult.
Incubation above ground.	Incubation essentially underground.
Often a higher incubation temperature.	Often a lower incubation temperature.
Often rapid early embryonic development.	Often slow early embryonic development (Clark, 1964).
Shorter incubation period.	Longer incubation period.
Smaller yolk supply.	Larger yolk supply.
Generally a small, simple nest.	Often a large nest (mound); sometimes no nest.
More adult care directed specifically towards eggs.	Less adult care directed specifically towards eggs.
Turning of eggs during incubation.	No turning of the eggs.
Temperature detection often by brood patch.	Temperature detection by mouth region (Frith, 1959).
Young of clutch hatch about the same time.	Scattered time of hatching.
Functional egg tooth.	Non-functional egg tooth.
Less precocious and generally smaller young at hatching.	More precocious and generally larger young at hatching.
Parental care for young.	No parental care for young.
Imprinting in at least some forms.	No imprinting? (Inherent species recognition?)

TABLE 4

Some Correlations in Megapode Reproductive Biology

(1) Gradual hatching is correlated with gradual laying of the eggs and the start of incubation at the time of laying of the egg.

(2) Gradual laying of the eggs is correlated with large egg size.

(3) Precociousness of the young and absence of parental care for young are correlated with gradual hatching.

(4) Methods of incubation are correlated with large eggs, (sometimes) large clutch size, and gradual laying of the eggs.

(5) Large eggs are correlated with great precociousness of the young and with the size of the juveniles at hatching.

(6) Slow early embryonic development is correlated with low incubation temperatures.

(7) Long incubation period is correlated with slow early development and the great precociousness and size of young at hatching.

(8) Temperature detection by the mouth region is correlated with methods of incubation.

(9) Large yolk supply is correlated with large egg and chick size.

(10) Non-functional egg tooth is correlated with the size of the young at hatching and the kicking out of the shell.

In analyzing the evolutionary history of a group it is important to investigate the many interrelationships between the various life history features (see Table 4).

To reach any definite conclusions about influential environmental features in the evolution of megapodes is at best difficult. Perhaps strong selection favoring change of any one of the many co-adapted features would have been sufficient to yield the evolution of the megapode stock, but perhaps more likely it is possible that megapodes have evolved through varying selection pressures on different features of their reproductive physiology and behavior.

An initial step might have been the covering of the eggs with organic matter on leaving the nest in the way that grebes do. Then, gradually, could have evolved the trait of adding more and more organic matter and returning less and less frequently to check the nest temperature. Initially the brood patch might have been used for thermal detection, and then gradually could have evolved the use of thermal receptor's in the mouth region. With less continuous attention given to the nests, selection would favor increased precocity of the young which might then hatch at times when adults were away from the nest; this in turn could lead, through selection, to a larger egg size (hence larger young at hatching) and the various specializations associated with the greater precocity of juveniles (Figure 15).

Many kinds of factors might have influenced the early evolution of the megapodes: (1) Predation on adults, eggs, or chicks, (2) location of nests remote from feeding grounds, (3) advantages of more precocious young, (4) physiological changes leading to a loss of adult broodiness, etc. Definitive statements as to the roles of such factors are not yet possible.

Modern hypotheses on evolutionary mechanisms (Mayr, 1963) would indicate that the evolution of megapodes from more conventional ancestors

Figure 15. A juvenile Mallee Fowl shortly after hatching. It is similar in body weight and in length of the folded wing to adults of the Coturnix Quail (*Coturnix c. japonica*). Photograph by H. J. Frith.

was a gradual process and that throughout the transition a co-adapted balance of reproductive ecological features was maintained. No clear advantage of the megapode reproductive habits relative to those of other Galliformes have yet been suggested. It appears that the megapodes and other Galliformes have evolved, through quite different evolutionary histories, into alternate but equivalent patterns of reproductive biology.

Summary

Aspects of the distribution and life histories of megapodes are briefly reviewed from the standpoint of probable evolutionary history. A major division within the megapodes is that between the three genera of brush turkeys and *Leipoa* versus *Megapodius* and *Macrocephalon*. The occurrence of territoriality and temperature regulation of the mounds appear to characterize the brush turkey-*Leipoa* group. The incubation of eggs by sun or volcanic heat as found in *Macrocephalon* and some *Megapodius* is considered to be secondarily evolved within the megapodes.

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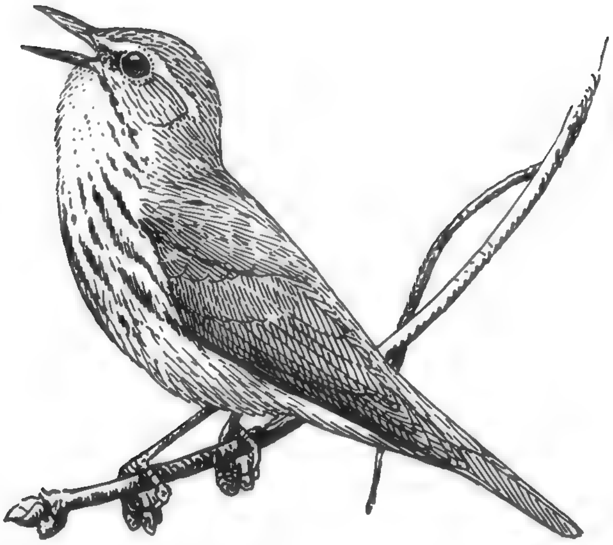

Northern Waterthrush

THE NORTHERN WATERTHRUSH IN VENEZUELA

PAUL SCHWARTZ

Many species of birds that nest in North America spend a considerable portion of each year in South America. Since that phase of their life cycle that is important to the preservation of the species takes place in North America, we think of them as North American birds. Few people realize that many such birds are away from North America the greater part of each year and that a number of individuals reside in their winter homes twice as long as in their summer homes.

We know a great deal about the nesting of most North American species but relatively little of the winter life of those that winter in the tropics. This is not surprising when one understands that resident field ornithologists in the tropics are few and those few concentrate on the birds nesting in their regions. Visiting ornithologists are naturally too interested in the fascinating local species to pay much attention to the familiar migrating or wintering birds.

My position is a bit peculiar. Although resident in the tropics most of my adult life, I still feel an attachment to the birds I knew as a boy in my native Pennsylvania. The sight of a familiar American Redstart *(Setophaga ruticilla),* flitting in the foliage above me as I lolled in a hammock beside a lazy tropical stream, re-awakened a dormant interest in birds.

Although I too became absorbed primarily with the birds that nest in Venezuela, miscellaneous observations of wintering and migrating North American birds soon aroused my curiosity and resulted in the field work that forms the basis of this paper. Strangely enough, Redstarts were again the prime factor.

For several years I lived in a house adjacent to a wooded ravine on the north side of the Caracas Valley. Among the birds close to my doorstep in winter were American Redstarts. Frequently I stood on my porch completely entranced as one flitted about the vines at arm's length or searched for food in the cracks and crevices of the moss-bearded concrete floor at my feet. Once the fall migration was over, the Redstart that I continued to see near my house during the winter was always the same one—or so it seemed. Furthermore, if one year it was a female, the next year it was too. The illusion that the same individual returned in successive years was heightened when one year I had a young male as my guest, the following year a beautiful mature-plumaged male and the third winter the same male—according to a peculiar pattern of color on his breast.

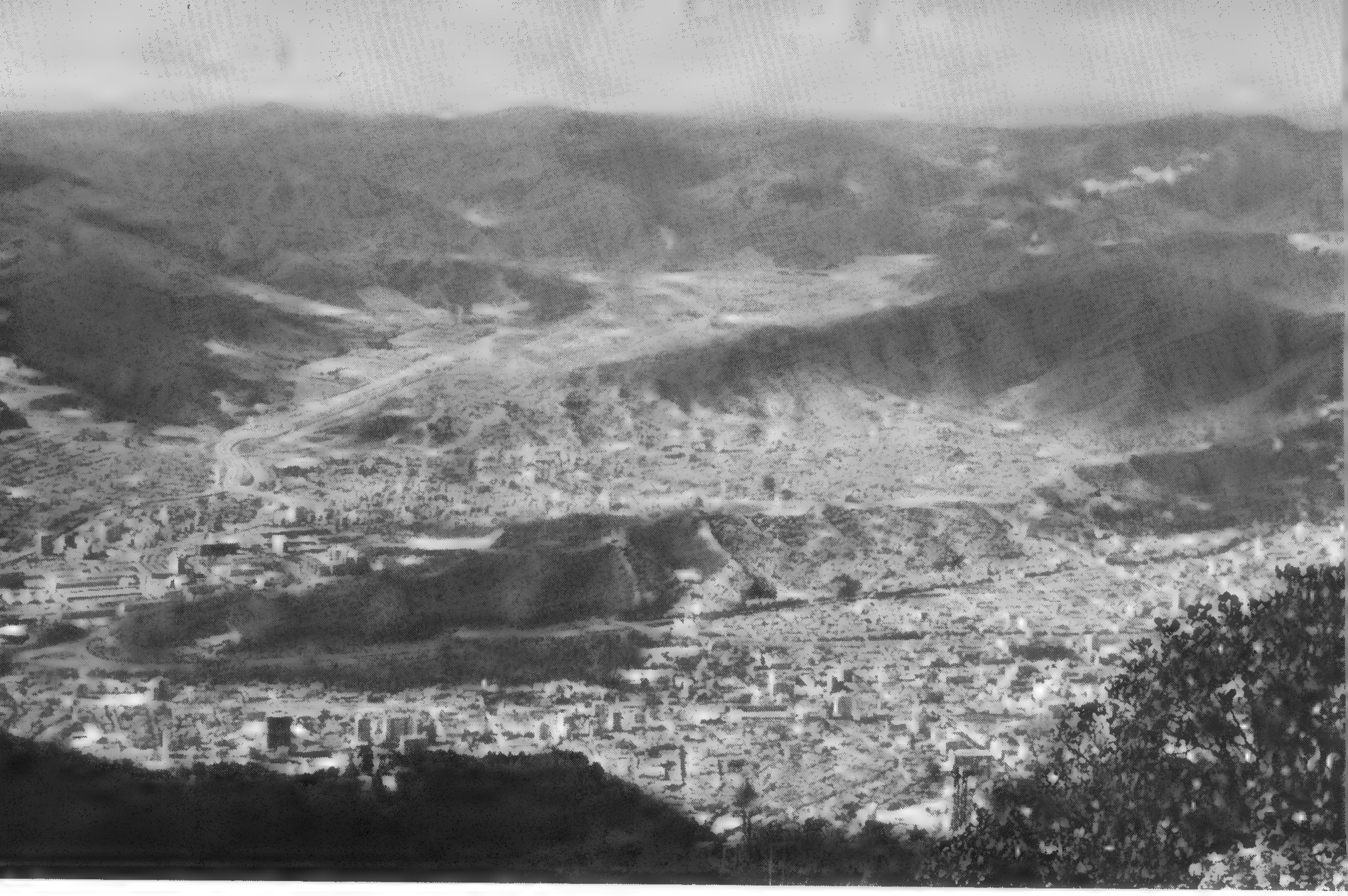

Figure 1. Caracas, Venezuela. The Botanical Garden of the Universidad Central de Venezuela is the dark "island" in the lower left-central part of the picture.

Scattered observations of other winter residents indicated that individuals of other species also seemed to lead solitary lives each within a fairly restricted area. But such observations lacked substantiation. I am suspicious of circumstantial evidence for in my many years of working with wildlife I have seen it break down more than once. Therefore, to make observations of greater validity, I started in April 1956 a program of color-banding Northern Waterthrushes *(Seiurus noveboracensis)* in the Botanical Garden of the Universidad Central de Venezuela in Caracas. I chose the Northern Waterthrush, hereinafter referred to as "Waterthrush" (the Louisiana Waterthrush, *S. motacilla,* is exceedingly rare in Venezuela), because it was relatively easy to capture and observe. I occasionally caught other migrants, especially Redstarts, and banded them also.

Place and Season of Observations

The Botanical Garden was appropriate for my observations because it was: (1) An ecological island much favored by Waterthrushes. (2) Close to my office. I could indulge in this avocation without wasting time in travel. (3) Of manageable size. I could cover the most important sections every day or two. Starting with 1958-59, I covered the whole area every week while the Waterthrushes were present.

Catching, banding, and noting the weights of the birds absorbed much more of my time in the field—several thousand hours—than pure observation. I banded nearly 400 Waterthrushes and caught a number of individuals repeatedly with the intention of making a more complete "clinical" chart of their weights, molts, etc. While many transients no doubt passed through without being banded, I believe that, starting with the season of September 1958 to May 1959, I caught the majority of those that remained in the area a couple of days or longer. During the seasons of 1957-58 through 1961-62 I banded all resident birds.

A brief description of the study area will clarify this last statement which may sound a bit presumptuous. The Botanical Garden (elevation about 860 meters) extends east and west for about 1,400 meters and averages about 150 meters across. (See Figure 1.) On the north it is bounded successively by a six-lane highway, the Güaire River (cleared of all vegetation and lined with concrete), Los Caobos Park (devoid of shrubs and undergrowth), and urban construction. To the south and east is the campus of the University (unsuitable habitat for Waterthrushes) and beyond the campus and on the west is urban construction. A ridge, about 60 meters higher than the garden and campus and covered mostly with deciduous, second-growth woods, runs parallel to the long axis of the Botanical Garden and separates it for its full length from the campus.

The arrival of the Waterthrushes in the fall coincides with the last part of the rainy season. Actually September and October are two of the rainiest months. At this time transient birds may settle on the wooded ridge. However, with the advancing dry season when the ridge becomes as barren as a northern deciduous forest in winter and bone dry as well, the birds that remained there must move. They either descend to the Botanical Garden and force out territories there (this explains the appearance of unbanded birds in late December and January) or, if the Garden is saturated, they depart in search of other suitable areas. Thus, after about 1 January the Waterthrush population of the Botanical Garden is all contained in and limited to those areas which, because of artificially-supplied water, provide the moist earth and low-growing vegetation required by the species.

In addition to my concentrated efforts in the Garden I have made numerous observations elsewhere in Venezuela. I have also checked the specimens and records of the Phelps Ornithological Collection in Caracas, the Carnegie Museum in Pittsburgh, and the U. S. National Museum in Washington.

One derivative of this work—a paper concerning the orientation abilities of wintering Waterthrushes—was presented at the XIIIth International Ornithological Congress at Cornell University in 1962 (see Schwartz, 1963). The present paper treats general aspects of the life history of Waterthrushes in Venezuela. A future paper will cover specific aspects of this life history—weights, molts, "anatomy" of migration movements, etc.—all related to that portion of the life cycle that occurs in Venezuela and especially in the Botanical Garden.

Method of Capture

All birds were caught with mist nets. On days of a large influx during the fall migration I sometimes caught from two to four birds at one net position by circulating constantly to keep the birds moving. Also, a net or two placed strategically beside one of the few bathing spots (a late afternoon bath seems to be a ritual for both the Waterthrush and the Redstart) usually produced good results for a day or so in the dry season. But the birds that came to the pool quickly changed from the subconscious use of approach and escape paths that had become habitual through frequent safe experience and became aware of possible hazards in the course. As a result, although the nets by the bathing pools could be used again with some success a month or two later, they worked really well only once each season.

Except for these cases, I had to concentrate on catching each individual separately. If the species' strong territoriality made this necessary, its territoriality and its ground-foraging habits also made it possible. Capture was not left to chance. A net was placed in a location where my experience indicated it would be most effective and the bird was kept active and herded toward it. First captures were usually easy; subsequent attempts frequently provided contests between me and the bird that were sometimes amusing and often taxed my wits to the extreme. In a few cases the bird won. Especially difficult to capture were the individuals that learned to fly straight up to the overhead trees rather than keep to the lower levels. If I could invent no new trick and were determined to recapture a certain bird, I placed a speaker near the net and played a tape recording of *call notes* of the Waterthrush. Although when trying to capture local nesting birds I frequently use play-backs of their recorded songs, I used only the call notes for the Waterthrush for a reason I shall explain later.

Once captured, a bird was weighed, otherwise examined, and—if it was the first capture—banded. I used both colored and U. S. Fish and Wildlife Service numbered bands in combination, with a maximum of three bands on one bird. There is no evidence that the use of three bands had any adverse effect on the birds. I sometimes had to replace colored bands that were worn by abrasion and dampness.

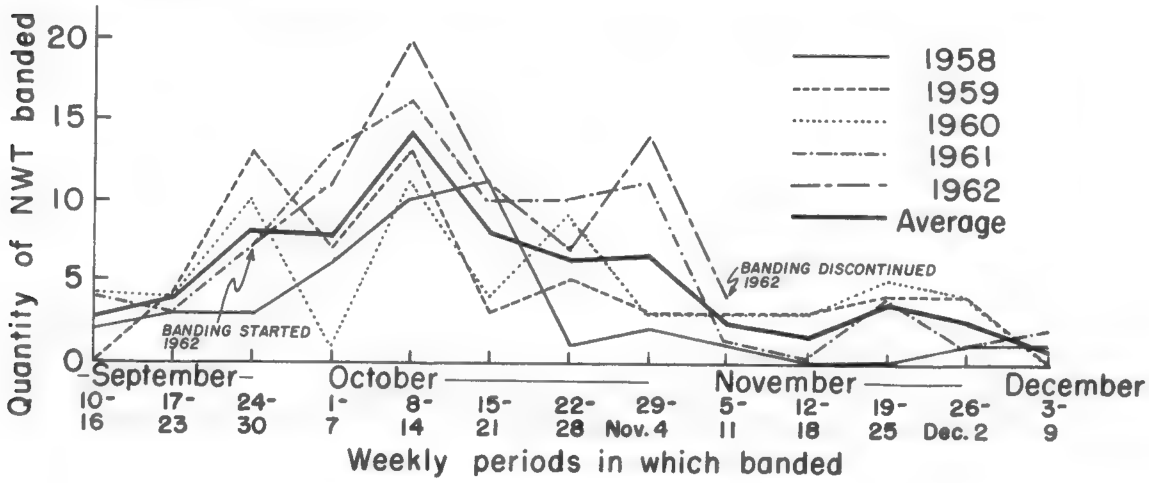

Figure 2. Northern Waterthrushes banded during the fall migration in Caracas, Venezuela.

Arrival and Departure

The earliest record of the arrival of the Waterthrush on the South American mainland is 5 September—from my own notes. The Phelps Collection has a specimen taken 7 September in the state of Sucre. No doubt this species arrives on some of the offshore islands a few days earlier.

Regular arrivals in the Botanical Garden begin about 15 September, but do not achieve importance in numbers until the end of September. From then until about 1 November, the great bulk of birds appears, sometimes steadily, sometimes in waves separated by as much as a week with hardly any new arrivals. After 1 November the rate of arrival is much less although there may be isolated minor spurts and there is a tendency to a small peak in the last half of November.

A chart of the number of birds banded each week (see Figure 2) shows the preponderance of new arrivals during October with a definite peak in early mid-October. Figure 2 errs on the conservative side and also involves some lag. A curve of my notations of new arrivals would show more birds arriving during each period, especially in October, but would no doubt also err due to the kinetic nature of the situation when there is a large influx. A lag occurs if there was a large influx on the final day of one of the arbitrarily-chosen weekly periods and not all the birds were caught that day. Those banded the following days would thus count in the succeeding period. Also, during this lapse some individuals would slip through without being banded.

Although many of the waves coincide with local heavy weather, others do not and I have found no conclusive relationship between local weather and the arrival of migrants. So far I have made no attempt to correlate the arrivals with weather conditions in southern United States or the Caribbean area.

I have at times been impressed with the large numbers of Waterthrushes that suddenly appear in the Botanical Garden in times of heavy weather but I have never observed such concentrations as those indicated by Arthur T. Wayne (in Bent, 1953), and repeated by Griscom, Sprunt, et al. (1957), of "hundreds in the area of a hundred square feet." "Hundreds" implies at least 200. It is difficult for me to imagine two or more Waterthrushes on every square foot. Nevertheless, the occasional arrival of considerable numbers does indicate that, although this species is solitary in most of its habits, it probably migrates in loosely-associated flocks. Furthermore, these flocks are apparently rather homogeneous because mass arrivals of Waterthrushes do not coincide with mass arrivals of other species.

The great majority of birds banded each fall are transient in the Botanical Garden and, after remaining for a period of from a day or two to several weeks, they move on. Unfortunately there are no recoveries as yet to give any idea of their direction or final destination.

Starting in mid-October occasional individuals remain as winter residents. (Throughout the whole study no more than three per cent of the birds that remained as first-year winter residents arrived before 18 October.) In November more birds remain than leave. Meanwhile the birds that spent the previous winter in the Botanical Garden, and have survived, return to reoccupy their former territories. These always arrive a little earlier their second season (see Table 1).

After mid-April the resident Waterthrushes begin to depart for the north. Most of them leave during the last week in April and the first week in May. Old residents leave earlier than first-year birds but there is some overlap. The population decreases gradually; there is no mass departure. Whether individuals take off on their own or fly up to join birds overhead is unknown. It is rare to find a resident bird in the area after the first week of May.

Although there are a few transients, the spring migration through the Botanical Garden is insignificant. One year I banded an unusual number—eleven; on the average between two and five stop off on their way north. In 1954 a Waterthrush appeared on 15 June and remained until 21 June; that too was unusual. Based on my research and observation, the latest date that I consider normal for any Waterthrushes in the Botanical Garden or the South American mainland is 20 May.

According to my records, winter-resident Waterthrushes remain in the Botanical Garden for an average of slightly over six months. (See Table 1.) The dates in the Arrival column show (1) *banding* of a new bird, or (2) *sight identification* of a returning resident. Note that Bird 71 spent five winters in the Botanical Garden. I have parentheses around its first date because it may have been there two weeks before I banded it. Bird 71 was always a difficult bird to catch and its astuteness seems to have been rewarded for it has lived far longer than any other Waterthrush I have banded—nearly five years when

TABLE 1

Duration of Northern Waterthrushes in the Botanical Garden, Caracas, Venezuela

Individual number	*Date of arrival*	*Date of departure*	*Months and days in Botanical Garden*
62	21 October	5 May	6/14
	10 October	23 April	6/13
64	21 October	6 May	6/15
71	(6 December)	(25 April)	(4/19)
	4 November	23 April	5/19
	2 October	(8 April)	(6/6)
	14 October	(21 April)	(6/7)
	13 October	(23 March)	(5/10)
73	(25 December)	5 May	(4/10)
	4 November	30 April	5/26
	29 October	(22 April)	(5/24)
77	25 October	30 April	6/5
130	12 October	23 April	6/11
	1 October	(16 February)*	(4/15)
151	28 October	3 May	6/5
157	1 November	30 April	5/29
162	4 November	30 April	5/26
283	28 October	(5 May)	(6/7)
289	5 November	(5 May)	(6/0)
294	13 November	(5 May)	(5/22)

*Presumably this bird fell to a predator.

last seen, a remarkable age for a small, ground-foraging bird. Bird 73 was not present more than a week before being banded. It may have resided previously in a territory that became unsuitable with the coming of the dry season or it may have been a "late" bird in its life cycle. This latter explanation seems possible when we note that even in its third year of residence it was not found before 29 October. Since its territory was one of the easiest to observe, I could not have missed it by more than a day or two.

The dates in the Departure column in Table 1 show the last time an individual was identified positively. The dates in parentheses indicate: (1) A bird was seen in that territory later but not positively identified, or (2) the area was not checked for several days or longer after the last positive sighting. Thus the Arrival and Departure dates in Table 1 give the minimum period that each numbered bird was a resident in the Botanical Garden and indicate that six months is typical.

I have not found any specific data on how long the Waterthrush remains in its nesting area but from general information in various publications it appears to be about three months in the southern part of the breeding range and probably less farther north. Accordingly, the Waterthrush resides in its winter home at least twice as long as in its summer home.

A similar comparison for the American Redstart shows the proportion to be the same or even greater. I have found banded Redstarts present in the winter for as long as seven months.

Habitat

Although Waterthrushes may be found in strange situations during migration, the resident birds seem to require the same habitat in Venezuela as in North America.

They generally occur between sea level and 1,200 meters with some exceptions. During the fall migration I have seen them as high as 2,100 meters, and there is a specimen in the Phelps Collection taken at 2,060 meters near Villa Paez on 12 February. The date indicates that this bird was a winter resident.

Waterthrushes are found among the mangroves along the coast and offshore islands and along the edges of streams, rivers, lakes, ponds, and puddles where there is low-growing vegetation for cover nearby. Although they sometimes occur near swift-flowing mountain streams, they apparently prefer quieter waters, just as they do in their summer homes. Surprisingly enough, they do not require bodies of water or marshy woodlands in their territories. Many birds reside in gardens in urban areas; in public parks if they are suitable and there is not too much disturbance by human activity; in plant nurseries and plantations of various kinds. If these areas do not have natural streams or ponds—and most of them do not, they do have frequent sprinkling or irrigation systems of some kind to keep the earth relatively moist and provide occasional puddles of water. The minimum requirements for suitable habitat appear to be: (1) Earth that is damp enough to provide the proper food. (2) Vegetation that grows close to the ground yet leaves space underneath for foraging. (3) Higher vegetation—small trees or large bushes—that provides refuge.

Having observed their fondness for baths, particularly the bath at the day's end, I believe that an area that supplied the three minimum requirements yet did not provide a place for a bath within reasonable flying distance would not be inhabited very long.

In the Botanical Garden practically none of the Waterthrush territories have permanent water in them. However, no territory is more than 400 meters from one of the three or four spots suitable for bathing, and at sunset the birds frequently travel to one of these spots.

A curious incident involving Bird 71 illustrates the almost ritualistic nature of the evening bath. Within its territory was a tiny, artificially-fed stream that at one spot formed a pool, favored for drinking and bathing by many birds, both winter and year-round residents. Number 71 frequently foraged in the area and occasionally took a short bath at the same time. But even if it had bathed as late as 4:00 PM, it usually returned again about a half hour before dark for its evening ablutions.

One afternoon I was observing and photographing from a blind beside this pool when, because of water rationing due to a severe drought, the pseudo-stream stopped flowing about 5:30 PM. At 4:30 PM, Bird 71 had foraged there but left without bathing; at 6:00 PM it returned, foraged a bit, and then

Figure 3. Northern Waterthrush, one of 400 banded in the Botanical Garden in Caracas. This individual led a charmed life. It made five trips to Venezuela from North America and in a homing experiment returned to its winter territory from a release point 300 kilometers southwest of the Botanical Garden. In this photograph it is crouched—trying to bathe in its accustomed place even though the bathing pool, at the moment, is empty.

walked to where the pool had been and tried to bathe. Finding no water the bird was obviously confused and walked out of the depression, looked around, walked back in and again tried to bathe. After repeating this performance several times, it finally walked in, settled down, and went through the complete bathing motions in the damp waterless "pool."

Unfortunately by that time the batteries of my equipment were so depleted that I could manage only one photo and that one did not coincide with any active bathing movements. However, the crouched position of the bird in Figure 3 illustrates the act.

Food

No Waterthrushes were taken for examination of stomach contents but there is nothing to indicate that their food in Venezuela is of essentially different character from that reported elsewhere (Bent, 1953; Eaton, 1957).

Many birds referred to as leaf-tossers are only leaf-flickers; the Waterthrush is a leaf-tosser in the true sense. From numerous observations I can say that be the leaf large or small the bird grasps it in its bill and tosses it or places it to one side. Due to rain, some large leaves are at times rather thoroughly anchored to the ground and it is consequently amusing to see the birds work to pull them from position.

Although Waterthrushes customarily forage on bare ground, among fallen leaves, under low-growing plants, or in shallow water, I have noted cases of fly-catching (both in the air and from the surface of the water) and leaf-gleaning. Occasionally I have seen them forage over the semi-horizontal fronds of fan palms.

I have been surprised at their almost complete disdain of the thick schools of tadpoles that choke the shallow pools during the rainy season just as the birds are arriving from the north. Occasionally a bird picks at one and then continues walking about with no further interest.

One spring-migrant Waterthrush indulged in a rather unusual foraging behavior. It had apparently discovered a rich food supply about eight meters above the ground in the crevices of the rough bark of a large tree and moved actively over the trunk and branches, picking up something I could not see to identify. When the trunk or branch slanted less than an angle of 60 degrees above the horizontal, the bird walked up and down. On the steeper or more nearly vertical surfaces it moved up and down by a series of sideways hops, using its wings only if, in changing position, it failed to get a good grip and started to slip. Normally Waterthrushes walk (see Bent, 1953) but I have seen individuals that both hop and walk and a rare one that used hopping as its only method of locomotion.

Figure 4. Northern Waterthrush foraging on the trunk of a tree.

Although as a rule its food consists of small bits, I have occasionally seen a Waterthrush working on a fairly large moth and I once watched a bird feasting on the internal contents of a tropical cicada so large that the bird's head almost disappeared inside the cicada's abdominal cavity. Although I did not witness the beginning of the banquet, I suspect that the bird found the monster dead. When the Waterthrush visits bird-feeding stations provided with seeds, fruit, and bread soaked in milk or water, it limits itself to the bread.

Voice

The only time I ever heard the true song of the Waterthrush given spontaneously in Venezuela was about 4:00 PM, 7 April 1962, by a first-year resident. When the bird, which was foraging, became aware of my presence it started calling, flew to a small tree and from there to a clump of bamboo, still calling. A moment after it alighted on a bamboo stalk, one call note was prolonged into a partial song. Then with no further call notes, it gave three complete songs at intervals of from 15 to 30 seconds. After that it flew into a neutral wooded area, calling as it flew.

The usual vocalization is the call note, a typical metallic or stone-like *tink*. Used to express uneasiness or alarm this call also takes the place of song as the signal of territorial possession. The frequency of repetition and the intensity of the notes seem to indicate the degree of excitement. Beyond this I could detect no difference in the calls regardless of the motives that inspired them.

Occasionally an individual will give a raspy squeak when being handled but usually the birds are silent, invariably so when in the net or a paper bag for weighing or "temporary storage." The American Redstart usually chips constantly under such conditions.

That the "tink" call note replaces the song as the territorial signal on the wintering ground is demonstrated by play-backs of recorded vocalizations. On 19 April 1956 I played the song of the Waterthrush from one of the Kellogg-Allen records ("American Bird Songs," Vol. 2, Cornell Laboratory of Ornithology). There was no observable reaction from the Waterthrushes in the vicinity; those I could see continued foraging without pause. In subsequent seasons I played additional songs from the Borror-Gunn record ("Warblers," Sounds of Nature Series, No. 4, Federation of Ontario Naturalists), always with negative results.

After hearing the spontaneous song mentioned above, I tried the play-backs of songs again on 20 April 1962. Trials at several places in the morning gave negative results. When I played the song at noon in the territory of the Waterthrush that had sung two weeks before, the bird started calling, flew up in a tree, and sang once; another playing at 5:30 PM brought a similar response. In neither case did the bird approach the loud speaker.

Play-backs of songs in six other territories in the late afternoon between 5:00 and 6:00 gave negative results in four (in three of these territories I saw the birds). In the other two the birds were not visible when I started the play-back but soon appeared and started calling, obviously attracted by the song. One of the two gave a single "half-hearted" song but could not be induced to repeat it.

By contrast, a play-back of call notes, recorded in the area, usually brought immediate response. The Waterthrushes flew about looking for the intruder in a reaction as active and excited as one expects from most nesting birds when the true song is played in their territory.

Territory

Those individual Waterthrushes that do not continue their migration within a day or two after arrival tend to remain in a limited area that presumably has adequate food and with which they have become familiar. These familiar foraging areas become territories in that they are defended against intraspecific intrusion. And they are defended constantly and, when necessary, violently.

Sometimes, after an influx of birds in the fall, two Waterthrushes may be seen foraging quietly and peacefully two or three meters apart. Such tolerance, probably possible at the moment because both birds are primarily interested in eating after their long, energy-consuming flight, is of short duration. I have observed numerous cases where such peaceful situations terminated suddenly when one bird, without calling or giving any other advance notice, flew at the other and chased it away.

Territories are maintained not only by the birds that remain as residents but also by transients, many of which stay in the area for several days or weeks before continuing their journeys. Their size is determined by the area a bird can defend successfully and further governed by two somewhat interdependent factors: (1) Environmental variety and (2) intraspecific pressure. Environmental variety refers to the relative suitability of the various parts in the entire area under consideration. Intraspecific pressure refers to the number of individuals of the same species that are trying to stake out territories in a given area.

If a Waterthrush has no competition from others of its kind, it will tend to roam and forage over an area larger than it actually needs to sustain itself. The poorer the food supply within the area, the farther the bird roams. In the strict sense this is a foraging area, not a territory. If other birds appear within this foraging area and claim portions for themselves, the part that each can defend for its own use becomes its territory.

Population pressure is seldom so light that a bird can have a territory as large as it would normally tend to roam in. An individual can defend a territory against one competitor easier than it can against several. As the population pressure increases, the territories become smaller and the least successful birds may find their territories so reduced in size that they cannot survive and must go elsewhere. A balance among the successful birds determines the minimum size of the territories. Assuming equal population pressure, the size of the territory will vary inversely with the available food supply. The more suitable is the habitat, the more food there is available and the smaller the territory required to support an individual bird. Stenger (1958) demonstrated this in her study of the Ovenbird *(Seiurus aurocapillus).* In the present study I have seen this relationship amply illustrated.

The normal size of a territory varies from 1,000 to 2,500 square meters and averages 2,000 square meters. In relatively open places as opposed to wooded or park-like areas the territory is often a disjointed series of clumps of vegetation stretching over 200 to 300 meters. The largest effective territories I found were about 5,000 square meters. These were noted in the Botanical Garden during the season of 1957-58 when, for some unexplained reason, there were very few resident Waterthrushes, and in marginal habitats during other seasons. The smallest area noted was about 400 square meters in a very rich section of the Botanical Garden during a season of heavy population pressure.

Eaton (1957) considered the normal size of the Northern Waterthrush nesting territory near Ithaca, New York, to be about 10,000 square meters. On this basis the average size of the winter territory is about 20 per cent that of the nesting territory. This proportion of 1:5 is similar to the proportion of 1:4 in the Louisiana Waterthrush (deduced from Eaton, 1953, 1958). Both ratios are logical, considering that the winter territory provides food for one adult and the nesting territory for two adults plus nestlings.

As with other animals the territories of the Waterthrush are not completely static although, with properly-established birds, the core areas remain pretty much the same throughout the season. An individual will encroach on the territory of a neighbor whenever it can. When a bird disappears, the neighbors quickly include portions of the vacated territory within their own. Although a number of first-year residents that from the start settle in suitable areas remain until their departure in the spring, many others make major changes before finally settling because:

(1) More aggressive new arrivals displace them.

(2) Changes in environment, such as those resulting from the advancing dry season, may make their areas unsuitable.

(3) Exploratory flights may disclose other areas that are more suitable. Such cases are rare. I have records of two birds which, after making a change, apparently found that "the grass wasn't greener" after all and returned to their original territories.

There were a few birds that, so far as I could determine, spent the entire season wandering about and never settled for long in one area. Presumably there was some eccentricity in their behavior.

Actually the Waterthrush displays a very strong attachment to its territory (Schwartz, 1963). First-year residents and even many transients return to their territories if removed and released at distances that permit their return by use of local orientation. (Apparently they have not yet taken the bearings that enable them to return from greater distances.) Birds that complete the second fall migration return to the territory they occupied the previous year. The shape or periphery of the territory may alter and it may expand if there is less population pressure but it is always anchored about the same points. Having been selected in the process of elimination the previous year, the territory is not likely to deteriorate under natural conditions and age seems to reinforce the bird's defensive ability. The old residents even tolerate considerable alteration by man and cling to what territory remains, moving only if they are left with practically nothing.

Although the birds spend most of their time in the territory, the majority of them are obliged to leave periodically for water, and, if unmolested, may forage in the vicinity of the water supply. There is indication that they also make occasional forays to neutral areas for supplementary feeding.

A certain amount of time each day is spent resting on perches from a meter to 10 meters above the ground with the higher elevation preferred. One finds resting birds only by accident for their flagging tails are still and they are silent.

During the last few weeks before they start northward most of the Waterthrushes become very shy and more difficult to find. They call less, the calls are weaker, and they are somewhat indifferent about the defense of territory. When some have departed, the territories of those remaining may change radically and even tend to dissolve. The birds still maintain their solitary ways but may forage regularly in new places. In some cases they may even abandon the territories they have been occupying all winter.

Territorial Defense and Display

The "tink" call note is the most common means of indicating possession of a territory and intimidating intruders. A bird staking out a new territory or reinforcing its claim to a former one will move about the territory and its borders, possibly on the ground or in low bushes but also often in trees up to six meters, and call constantly. This often brings a reaction from a neighboring Waterthrush, and, if in their movements the two come togther at the border, there will ensue a calling duel that may last a number of minutes. Since there are no fences marking the borders and each bird feels it owns more than its neighbor allows, there is sometimes a brief chase. At other times one or both may tire of the stalemate of the calling duel and either fly to other parts of its territory or start foraging. The calls lessen in intensity and finally cease.

Since the territories are usually rather small, there is an ever-present tendency to extend the foraging areas into the territories of others. These intrusions are frequent and, if the invading bird remains silent, nothing happens. If the owner spies a silent intruder, it usually starts to call. If the intruder fails to withdraw in a reasonable time, it is chased. Occasionally it is chased without any preliminary calling. If, instead of remaining silent, the intruder calls back or, if it attracts the attention of the owner by calling first, it is usually chased at once. During the fall migration there tends to be a greater tolerance to a silent invader. Nonetheless, when birds already present are suddenly confronted by an invading horde, chases are frequent. I could usually tell, upon arriving at the Botanical Garden, whether there had been an influx of birds that day by the amount of calling on all sides.

The birds arriving in fall migration are usually silent for the first day or two unless alarmed. Even then they often flee silently. There is an obvious advantage in silence because by not attracting attention to themselves they can replenish their depleted reserves quickly before having to compete for territories. Similarly, birds that are obliged to invade another's territory for water usually do so in silence. If, as often happens, several Waterthrushes, all out of their own territories, meet at the bathing place for the evening bath, conflicts are limited to maintaining an individual distance of several meters and establishing a "peck order" or priority of bathing.

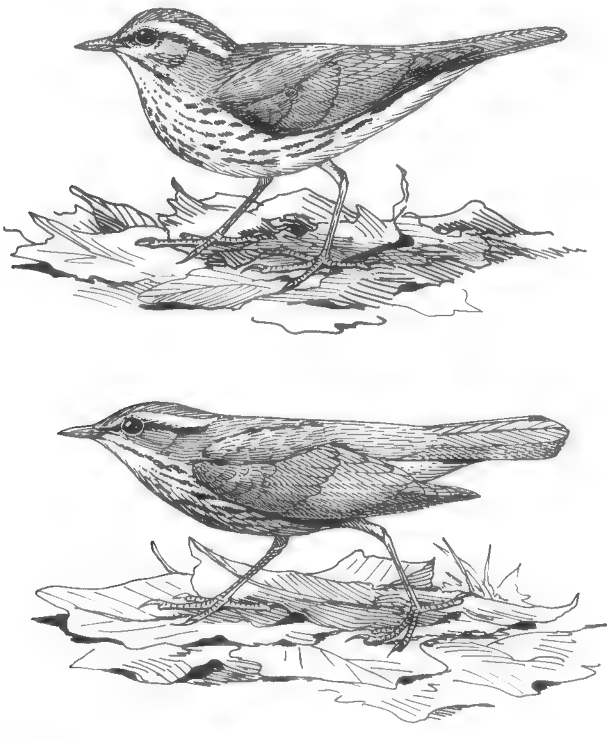

Figure 5. Top, Northern Waterthrush walking normally. Bottom, Northern Waterthrush crouch-walking.

If a bird invading another's territory refuses to be driven out by calls and attempted chase, the owner tries the "crouch-walk." The bird crouches lower to the ground than normally. (See Figure 5.) Its bill, back, and tail are pretty much in a straight, horizontal line as it walks toward the opponent with its tail slightly spread and its wings quivering. During the crouch-walk the bird is almost always silent. It may toss some leaves and pick at things on the ground, apparently ingesting some. If the intruder still remains passive, the owner, once it is within two meters of the intruder, flies in attack and is usually successful unless the intruder is actively trying to capture territory. In that case it responds to the owner's crouch-walk by doing the same and the two opponents walk back and forth or round and round about two or three meters apart. The more aggressive keeps edging closer; if the other does not retreat, attack, "cock-fighting," and sometimes locked combat follow. If one of the birds still does not retreat, the contest may continue for some time. Some first-year birds are thus displaced from their territories. I have never seen a second-year or older bird displaced entirely, but I have known one now and then to cede a part of its territory—especially if the area was larger than it could defend well.

These fights do not usually result in serious harm to the birds but that they may is suggested by the following incident: Bird 130, a second-year resident, was caught in the late afternoon of 1 January 1961 and released the next morning 65 kilometers away in a homing experiment. Its neighbor, Bird 231, a first-year resident, quickly moved into the vacant territory. At 1:30 PM on 13 January, Bird 231 was still in possession of this territory and there was as yet no sign of Bird 130. On my next visit, 1:00 PM, 14 January, Bird 130 had returned and reclaimed its old territory; Bird 231 had vanished and was never seen again. It seems unlikely that it left the Botanical Garden. Presumably it died in combat or was so injured that it fell prey to an enemy.

Figure 6. The attitude of a Northern Waterthrush when encountering a snake.

Waterthrushes conflict very little with other species. In occasional chases with Redstarts, usually females or young males, most often the Redstart appears to be the aggressor. I have never observed a territorial dispute between a Waterthrush and a Redstart or between a Waterthrush and any of the "local" birds. Although several of the latter, including the Rufous-fronted Thornbird *(Phacellodomus rufifrons)*, have call notes similar to those of the Waterthrush, such calls usually do not cause conflicts. Once I saw a Waterthrush foraging on the ground on one side of a tree and a Rufous-fronted Thornbird foraging on the other. When the Thornbird started to call, the Waterthrush jumped up on an exposed root, spied the small, brown-backed bird, and chased it—obviously a case of mistaken identity. Actually, in the Botanical Garden there are no species, local or migratory, that occupy the same ecological niche as the Waterthrush.

Apart from the attitudes used in defense of territory I have noticed only one other display—if it may be called a display—and have seen this just twice. Both times the curious attitude of the bird attracted my attention. The Waterthrush was stretched to full height, almost as if standing on tip-toe, and its neck was extended although the head was horizontal and the bill was not pointed upward. (See Figure 6.) In this position it walked back and forth in front of a crawling snake. In both cases the snakes were small racers, not large enough to consume the bird yet one of them was nearly so. The bird showed no sign of fear and could easily have flown away; it made no maneuver to attack the snake. The snake showed no intention of attacking the bird. Both encounters ended when I disturbed them by moving to get a better view, but in one case, with the snake already out of sight, I saw the bird suddenly retreat. I suspect that the snake feinted toward it.

I have been unable to interpret this action of the Waterthrush toward the snake but confess I have a mental picture of the confusion of the small boy suddenly confronted by a sleeping tiger or a gigantic strawberry shortcake. If Waterthrushes behave this way in the presence of all snakes, it may account for the bird I found dead with a hole, one-half inch in diameter, in its left breast and for the disappearance of some of the other birds.

Summary

Between April 1956 and November 1962 I color-banded nearly 400 transient or winter-resident Northern Waterthrushes in the Botanical Garden of the Universidad Central de Venezuela in Caracas and observed the species elsewhere in Venezuela.

The earliest arrival in the fall was 5 September, but the main migration occurs during October. Most of the fall birds are transient in the Botanical Garden. First-year residents arrive after mid-October, the majority in November. Returning residents arrive earlier in subsequent years than in the first year. They stay in the Botanical Garden about six months, apparently twice as long as in their nesting areas in North America. Resident birds depart the last week of April and the first week of May. Spring migration is insignificant through the Botanical Garden. A few spring transients may pass through as late as 20 May.

Although their habitat requirements in Venezuela are basically similar to those in North America, many Waterthrushes reside in gardens, parks, and plantations with only an artificial supply of water. They do seem to require suitable bathing spots within reasonable flying distance of their territories. Waterthrushes occur as high as 2,000 meters but most of them occupy areas from sea level to 1,200 meters.

The food of the Waterthrush in Venezuela resembles that reported elsewhere.

I heard only one true song given spontaneously. The normal vocalization is the "tink" call note, used for both alarm and possession of territory. Play-back of tink calls produces excited reactions; play-back of true song is usually ignored.

The Waterthrush lives alone in a territory defended against intraspecific intrusion. The territories, varying in size from 400 to 5,000 square meters, are normally about 2,000 square meters. The size varies inversely with the suitability of the habitat and the population pressure. All birds are strongly attached to their territories but first-year residents may change territories for one reason or another; returning birds reoccupy their former territories.

Waterthrushes chase intruders not intimidated by call notes. If the intruder remains, the owner uses the crouch-walk display and then attacks. Fights occasionally cause serious consequences.

The Waterthrush has no competition in its ecological niche from other species; thus there are few interspecific conflicts.

Twice I saw a Waterthrush assume a curious attitude when encountering a snake.

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THE SOLAR ECLIPSE AND BIRD SONG

Peter Paul Kellogg and Calvin M. Hutchinson

Photographs courtesy of Hutchinson Photography

The shades of night which accompany an eclipse of the sun have always intrigued mankind and caused him to pause, if only for a moment, to contemplate the mystery, the magic, the grandeur, and the extent of the universe of which he is a part.

Although this interest in solar eclipses has a long history and has given rise to fantastic tales, it is probable that no eclipse ever had as much publicity and public interest as did the eclipse which was total on a narrow path across the State of Maine on 20 July 1963 at about 5:30 PM, EDT. For weeks and even months before this eclipse, scientific, semi-popular, and popular magazines and newspapers devoted space to its occurrence. The government of Maine quite outdid itself in taking advantage of a unique opportunity to attract scientists wishing to make a serious study of the phenomenon, as well as vacationing tourists who were urged to spend their mid-summer holiday in Maine and to observe with millions of others one of the greatest natural spectacles of the twentieth century to occur in or near a densely-populated area and at a time when many people would be out-of-doors.

Light and Its Relation to Bird Song

While it is well known that many birds respond to the light changes in early morning and in the evening by beginning or ending their songs, Armstrong (1963) in an excellent chapter on "The Influence of Light, Weather and Temperature on Song" reminds us that many factors influence song and that it is the total effect of these several factors which we must consider.

A solar eclipse causes variation in light intensity somewhat similar to that of approaching dusk or dawn and usually brings sudden changes in temperature. The eclipse does not influence many of the factors which affect bird song—for example, time of year, and physiological condition of the bird—and this no doubt accounts for many different reports of the eclipse by various observers. It is also probable that the sudden interruption of an established diurnal routine is more confusing to some species or individuals than to others. All these possibilities for variation in the cause and effect on the singing behavior of birds at the time of an eclipse tend to keep the value of any observation on response to an eclipse a strictly local affair and must lead us to expect very general conclusions rather than specific results which would enable us to predict with accuracy the response of a given species or individual.

Figure 1. At Corinna, Maine, in the afternoon of 20 July 1963 prior to the solar eclipse. The senior author points to his location on an eclipse map and makes preliminary notes into the microphone to test the sound-recording equipment.

Eclipse Versus Normal Dusk and Dawn

From past experiences with an eclipse we were aware of the tremendous pressure under which one must make observations in the sixty or so seconds of totality. Although, technically, all minutes are equal spans of time, our immediate reaction was that the event of totality lasted not more than twenty seconds.

Another factor, seldom appreciated, is that the natural response of the human eye, and the bird's eye too, tends to lessen the response to the approaching darkness so that, when totality comes, one gets more the impression of turning off a light rather than that of the gradual normal twilight. Totality comes, or did come to us, as more of a shock than we are accustomed to experience at dusk. It is probable that a part of our minute of totality was spent in accommodating our eyes to the sudden decrease of light. This experience suggests that, for a future eclipse, it would be wise to attempt to accommodate the eyes to very low light levels for at least a half-hour before totality by using very dark glasses, such as worn by individuals who work in darkrooms and then go out into bright light, and by removing the glasses at the instant of totality.

The partial explanation for this response which seemed to us to make the approach to darkness of the eclipse so different from the normal approach of twilight is the characteristic response of the eye to varying light intensities. All senses are approximately logarithmic rather than linear in their responses. This means, essentially, that in reducing the light intensity from a million candle power to a half-million our response would be evaluated as having approximately the same import as changing the intensity from one candle power to one-half. This type of response is not only important but is really an advantage because it greatly extends the range of light intensities in which we can see well. We can appreciate this readily when we recall our ability to perceive objects and even some details in a dimly-lighted darkroom, and yet not be blinded by the full light of the sun.

During a normal sunset the decrease in light intensity is gradual and fairly linear with respect to time. There is no sudden, sharp decrease in intensity even when the sun sinks below the horizon because the earth's atmosphere greatly modifies the intensity and acts as a diffusion medium or even a source of light after the sun has set. During an eclipse, especially when the sun is well above the horizon, conditions are very different. In the first place, the decrease in light intensity accelerates with time, and the final disappearance of the sun's disc behind the disc of the moon is one of the most strikingly sudden events in nature. Secondly, the earth's atmosphere, away from the horizon, has much less of a diffusing effect on the light because the thickness of the atmosphere which the light must penetrate is so much less. Nevertheless, it is true that much light is reflected to an observer from atmosphere outside the path of the eclipse. This light greatly modifies the darkness so that the total light intensity during totality is approximately twice that of a full moon.

From these considerations of the response of the eye to changes in light intensity, and the various factors which control and modify the decrease in the rate at which darkness descends during an eclipse, we can see that the twilight resulting from an eclipse, when experienced under perfect conditions, is much different from the twilight experienced at sunset. We must remember, however, that the presence of clouds greatly modifies both the phenomenon of the eclipse and of normal sunset.

Figure 2. An hour before the eclipse. The sound-recording equipment, with a non-directional microphone on top of the car, is ready. Clouds threaten to mar the view of the eclipse.

The 1963 Eclipse Expedition to Maine

Until about a week before the event it did not appear possible that we could get away to observe the phenomenon and even if we could we realized that we could spend only the one day (the day of the eclipse) in locating a station for the observations and in getting acquainted with the singing birds of the locality—specifically, those individuals within hearing range of our particular station.

The trip north from Brunswick, Maine, which we left in mid-morning was uneventful though hardly encouraging. Intermittent sunshine and cloudy weather, with occasional showers or even hard downpours, made us realize that only unusual good fortune would result in our having an unobstructed view of the sun in the late afternoon. The radio stations of the state carried almost nothing but news of the impending eclipse. Mostly, they made an effort to be hopeful about the weather but there was the realization that the possibilities were precarious. Big concentrations of meteorologists and other scientists were at Orono and on Mt. Desert Island, places selected by experts as having the best chance for fair weather.

Our requirements were considerably different from those of most observers. First, we wanted singing birds of as many species as possible. Second, we wanted as little man-made interfering noise as possible. Of course we, too, hoped for good visibility but this requirement was not paramount. Our needs ruled out all places where there would be crowds and for this reason we deliberately steered away from the much-talked-about centers of activity.

Shortly before noon on the day of the eclipse we were in the middle of the band of totality in the little town of Corinna about 30 miles west of Orono. A local hunter whom we met at a gas station suggested a wild area "with lots of birds"—a river bottom, crossed only by a dirt road on which he guaranteed there would be little traffic. The area was about two miles south of Corinna and we spent the next few hours exploring, listening for birds, and checking the natural openings through which we hoped to see the sun at the time of the big event. Our choice of spots could hardly have been better. Typical birds of the Canadian Zone were there and singing—Olive-sided Flycatcher *(Nuttallornis borealis),* Hermit Thrush *(Hylocichla guttata),* Swainson's Thrush *(H. ustulata),* Veery *(H. fuscescens),* Myrtle Warbler *(Dendroica coronata),* Slate-colored Junco *(Junco hyemalis),* White-throated Sparrow *(Zonotrichia albicollis)*—as were the Red-eyed Vireo *(Viveo olivaceus)* and American Goldfinch *(Spinus tristis).*

We found an old logging road running off the dirt road to the east. Although this was not intended for cars, we were able to make our way along it with care to an opening where we had a good view of the sky to the west when looking upward at angles of from 15 to 35 degrees. Here we set up our sound and photographic equipment with a non-directional microphone mounted above the center of the car and with the recorder on an improvised table at the side of the car. We tested, made vocal notes on the tape, and performed dry-runs exactly as we would do in the brief minute of totality. We noted the birds singing and even recorded a bit of song. Because we had decided not to use a parabolic reflector which picks up sound from only one direction, all sounds were weak and not of good quality although they were recognizable; and these recordings made before, during, and after the eclipse have given us the opportunity to re-live and re-evaluate our experiences many times. The important thing is that we can do this again without the feeling of pressure under which we worked at the time.

Figure 3. Using a 30-centimeter lens to project the bright image of the partly-eclipsed sun on a box of magnetic tape, the senior author follows the progress of the eclipse.

The results of our recordings are somewhat disappointing if viewed only from an entertainment point of view. As the darkness descended, bird song fell off noticeably but some species, according to our recordings, never did stop completely. The *per-chic-o-ree* of the Goldfinch was heard clearly in the middle of totality; the Hermit Thrush and Swainson's Thrush sang weakly during the darkness; a Veery called.

Other observers, in more open areas, reported flocking activities. A radio report said that Starlings *(Sturnus vulgaris)* flew towards established roosts.

Miss Marjorie Rusk of Syracuse, New York, who was south of Mt. Katahdin, Maine, where the eclipse was 98-99 per cent total, reported the Common Nighthawk *(Chordeiles minor)* calling and a White-throated Sparrow singing throughout the eclipse, and the Swainson's Thrush giving scold notes.

Mr. Carl Hiller of Marblehead Neck, Massachusetts, reported that, as it got dark, gulls left their feeding grounds and headed for their roosting or nesting areas but turned around as soon as the light returned.

Mrs. Margaret H. Hundley (1964), reporting her observations on the reactions of birds to the eclipse, included a list of four species we recorded. She writes: "For about three or four minutes during the time of least light, except for an occasional call, all songs ceased except for *Turdus migratorius* [Robin] and *Hylocichla ustulata* [Swainson's Thrush]. The latter continued singing as loudly as before darkness."

Figure 4. Totality. The foreground is lighted by photoflash.

No one with whom we talked reported Whip-poor-wills *(Caprimulgus vociferus)* singing but it would seem natural to expect that they would do so.

Perhaps no two lists of birds heard before, during, and after the eclipse would be anywhere near similar. Certainly the lists I have seen are very different. There is no question but that song was greatly reduced during totality, and considerably reduced in the period 15 minutes before and 15 minutes after totality. On our list the first voice we heard after totality was the little peeper, *Hyla crucifer*. This was unexpected and was heard only once. Among the birds, the White-throated Sparrow songs, the Hermit Thrush calls and songs, and the Swainson's Thrush songs were soon back to normal frequency.

Perhaps the most profitable results of our brief expedition were some ideas as to how to conduct such a study in the future. The next total solar eclipse in North America will be visible in Florida, Georgia, and the Carolinas on 7 March 1970. Ideally one should start well in advance of this eclipse by selecting an area known for its quietness and abundance of bird life and song and, for at least a week before the eclipse, make observations and recordings there. If possible, a number of good observers should take part and, for several days before the eclipse, hold discussions based on bird songs recorded under normal conditions. Then, following the event, they could compare the results, heard immediately before and after and during the eclipse, with conditions observed under similar light (measured by a photometer) at dawn and dusk on the days immediately preceding and following the eclipse.

Such a study, requiring both time and care, would presumably have to be done by enthusiasts rather than by paid observers. However, it would be exciting and would repay the observers by enabling them to add a bit more to our knowledge of birds during the phenomenon of a total eclipse.

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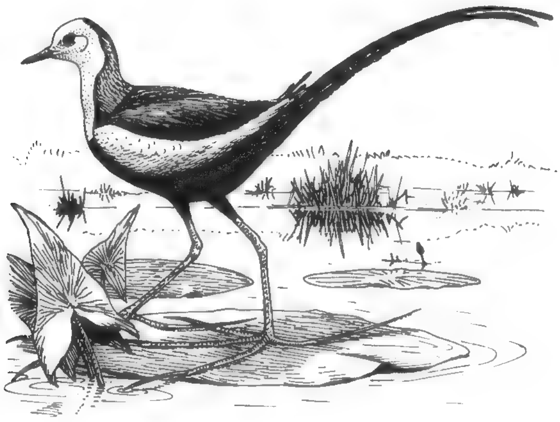

Pheasant-tailed Jacana

Ferruginous Pygmy Owl. Drawing by Don R. Eckelberry.

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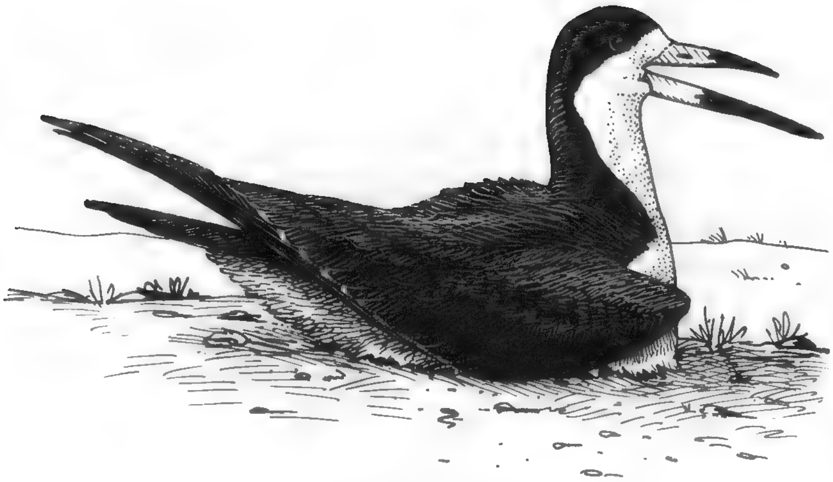

Black Skimmer

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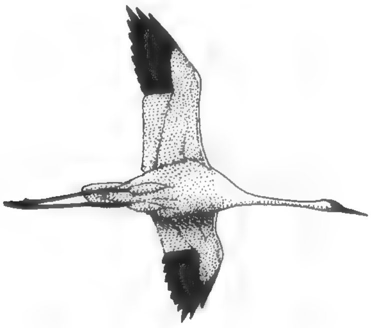

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Male Canada Warbler at the Nest

Photographed in northern Michigan by Betty Darling Cottrille.

NESTING OF A PAIR OF CANADA WARBLERS[1]

HERBERT KRAUSE

In the mid-afternoon of 21 June 1957, Dr. O. S. Pettingill, Jr. and I found a nest with eggs of a pair of Canada Warblers *(Wilsonia canadensis)* not far from the shore of North Fishtail Bay, an extension of Douglas Lake in Cheboygan County, northern Lower Michigan. The next day we set up a blind approximately 10 feet from the nest-site. On the morning of June 23, I began daily observations.

A preliminary search of the literature revealed that the Canada Warbler is one of the Parulidae which has received little attention. To cite one instance, Bent (1953:649) says that it is not known "how long the young remain in the nest." Cordelia J. Stanwood (*in* Bent, 1953:648) seems to have been the first to put up a blind and study this species in some detail, though apparently only for a short time during the nestling period. Except for notes by Kendeigh (1945a, 1945b, and 1952), by Walkinshaw (1956), and by Middleton (1957), all of which provide excellent data, the literature does not include a comprehensive study of the Canada Warbler. Even reports on behavior during the nesting period are limited to brief notes.

From the morning of 23 June until 9 August, I spent the major portion of each day, a total of 207 hours, in the blind or on the territory in the adjacent areas. The following remarks deal merely with the data recorded during the period of incubation from 23 June to 1 July in 39 hours and 39 minutes of observation.

The Nest-Site

The nest was in the middle of a small opening in a dry, mixed pine-maple-cedar community. White pine was the dominant growth; bracken grew rankly on the forest floor. A road, paralleling the lake shore, ran past the site, providing additional "edge effect" to that which was formed by the perimeter of the open space. According to the literature, the Canada Warbler seems inclined toward boggy or swampy situations, heavily shaded, but this nest was 400 feet or more from a spruce bog and an alder swale—places that would meet any such habitat requirements.

The nest itself was built under the fronds of dead bracken which had fallen about the foot of a small red maple. The fronds formed a projection over it. Some 15 feet away grew a small white cedar, apparently the favorite resting haunt of this pair of Canada Warblers. The undergrowth surround-

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[1] Contribution from the University of Michigan Biological Station

ing the nest included wintergreen, wild lily-of-the-valley, blueberry, sarsaparilla, and the ever-present bracken. Above the bracken rose sapling red maple, aspen, beech, alder, pin cherry, and paper birch. And beyond the opening were mature white pine, aspen, birch, red maple, alder, and white cedar.

Forty-one species of birds were noted in the nesting area. The American Redstart *(Setophaga ruticilla)* and the Ovenbird *(Seiurus aurocapillus)* were the most common. Other birds regularly present included the Veery *(Hylocichla fuscescens),* Blue Jay *(Cyanocitta cristata),* Common Crow *(Corvus brachyrhynchos),* Yellow-shafted Flicker *(Colaptes auratus),* and Robin *(Turdus migratorius).* Occasional visitors were such birds as the Black-throated Green Warbler *(Dendroica virens),* Pileated Woodpecker *(Dryocopus pileatus),* and Wood Thrush *(Hylocichla mustelina).* The mammals included the red squirrel, gray squirrel, eastern chipmunk, short-tailed shrew, and white-tailed deer. A red fox was reported in the vicinity but I did not see it. The only reptile was a garter snake which I caught sight of sunning itself about 200 feet from the nest. However, I saw no activity which suggested any interaction between the Canada Warbler and these faunal forms.

The Nest

A statement that the Canada Warbler uses a variety of materials for nesting purposes but "appears not commonly to use any parts of evergreen trees" (Kendeigh 1945b:431) met an exception here. The nest under observation was made of white pine needles mixed with the needles of red pine rounded into shape. Woven into these materials were bits of dead cedar leaves, rootlets, small plant stems, and several long strands of the dried inner bark of aspen. All the materials were brown in color so that in appearance the nest was dead-leaf brown. The forest floor, thickly strewn with layers of fallen white pine needles, was also brown, as ripe-acorn brown as the dead bracken that curled over the nest. There were four eggs, creamy-white and freckled rather heavily with reddish brown spots especially at the large end.

Incubation Period

Though Kendeigh (1945a) considers 12 days to be the normal period for incubation in the Parulidae generally, Forbush's (1929:308) bleak words, "No data," seem to sum up what is known about the exact length of the incubation period of the Canada Warbler. Since the nest was found on 21 June and two eggs were found to be hatched by 7:35 AM on 1 July, the portion of the incubation period under observation approximated nine days. If Kendeigh's 12-day period is used as a yardstick, the beginning of incubation must have occurred on 18 June or shortly before. The third egg hatched at 2:00 PM on 1 July. The fourth egg unaccountably disappeared without a trace on the morning of 26 June.

Female on the Nest

On the nest the female was often remarkably quiet. Frequently for periods of from 10 to 20 minutes she would remain stone-still. Sometimes her eyes closed and she appeared to doze, though for short periods only. At such times she appeared to lose a certain alertness and to relax—the quiescence of sleep. But a noise or a distraction, so faint it escaped my eye and ear, brought her to instant and guarded wakefulness. After such a period her eyes seemed to glint with renewed intensity.

At other times, more restive, she would yawn, swallow repeatedly, stretch her neck, rise in the nest, poke at what I thought must be the eggs, push them closer to her, then, shifting her position, settle back and waggle down into sitting position. Sometimes watching her try to lift a wing slightly as if to stretch it I felt a sympathetic achy twinge in my own cramped legs—cramped from hours of being draped over a camp stool in my blind.

Female off the Nest

Seldom did I hear her voice except as *chep* often repeated. Once or twice, however, she uttered low *trep* notes as she left the nest. Once off she usually flew via an under-bracken route to the white cedar tree, apparently a favorite resting, loafing, and feeding place. Here, on a number of occasions especially during the early brooding period, I saw her come, hurrying in the rush of her wings. Once in the tree, she almost always raced up branches, darted from limb to limb, plunged from one elevation to another below, flipped her tail, fluttered her wings.

This violent activity finished, she sometimes rested, perched motionlessly perhaps for a minute or two, yawned, rubbed her mandibles against the branch on which she perched, defecated, ruffled her feathers and shook them. Sometimes she stretched wing and leg, one wing and one leg at a time. Sometimes she preened vigorously, especially on the breast, at other times lightly. She might nibble the bend of the wing, poke at the abdomen, pull at the base of the rectrices and prod at a spot under the wing.

Then for a space she fed. One moment she was perched, motionless as the wood on which she sat. The next instant she was a bundle of restless activity, dashing up a branch to snatch something from a leaf or grab up an insect from a bud scar. Sometimes she tore a worm from the bark and, if it was wriggly, slammed it against the side of a limb. Often she fluttered under a cluster of leaves or darted out to snap up a fly or mosquito or other insect with a *whirr* of the wings and a loud snap of the mandibles. This snapping of the bill, flycatcher-like, noted by Samuels as early as 1883, is probably responsible for the old names given this species—Canadian Flycatcher and Canadian Flycatching Warbler. In fact, the female's quick movements and unpredictableness while feeding remind one of the American Redstart, and the snapping of the bill of both the Redstart and many of the tyrannids.

Occasionally she went beyond the white cedar. Now and then she disappeared into the bracken and out of my view. At such times she may have gone some distance, perhaps out of sight of the nesting place, for often when I stepped out of the blind, no "cheps" of protest came from bush or tree. Perhaps she went to bathe or drink. One rainy morning I saw her beak lifted, nibbling the drops of moisture on the tip of a Juneberry leaf.

Frequently on her "off-the-nest" period the male would join the female in the white cedar. While she frisked animatedly among the branches or rested or fed, he was in attendance, sometimes only a few inches away but generally several feet. Now and again he seemed to be stimulated by her activity and preened or ran up a slanted branch when she did, but it seemed to be at a slower pace and was done as if he did this because she did and not because he was urged by necessity. At such times I half expected him to burst into a swelling aria, but beyond a few throaty "treeps," he remained silent. Several times after a resting period, there were chasing episodes, one bird following the other in quick flashes among the branches. It seemed to me that the male began the pursuit but at times I felt that the chase began with the female.

I noticed that when feeding or other activities took them out of the white cedar, the female usually led the way, the male immediately following and frequently entering into pursuit flight. Weaving and turning the two would disappear from view.

Female Attentive and Inattentiveness

During the nine days that I watched the nest, the female alone was involved in actually sitting on the eggs. Kendeigh (1952) believes this to be true of wood warblers in general, although he does not mention the Canada Warbler specifically. Her periods of attentiveness averaged 32 minutes and were longer than Kendeigh (1945a:163) found for the Parulidae generally—9 to 28 minutes. During my observations she was on the nest 85 per cent of the time. The longest period was 84 minutes on 29 June and the shortest, one minute on 23 June.

Her inattentive periods averaged about 7 minutes, well within the limits of from 2 to 11 minutes given by Kendeigh (1945a:163). Her longest period away from the nest was 17 minutes on 24 June and the shortest was one minute that same day. Most frequently she was gone for about 4 minutes.

The Female's Return to the Nest

The female's approach to the nest seemed to be on two different levels of elevation. If intruders had been about—crows, jays, or man—she perched on the aspen or maple sapling, "chepping" sometimes, silent other times, always peering about before she dived into the bracken and climbed into the nest. However, if the way seemed clear, she came in under the bracken and went directly to incubate or brood. Rarely did she perch on the nest or even near it. She was either on it or off it. Sometimes, after a longer-than-usual rest stop, she fairly tumbled along the ground, and up the little incline to the nest as if in a hurry to get back to the eggs.

She clung to the nest with remarkable tenacity. When I checked the eggs or young she would let me come to within three feet of her and once my hand was within twelve inches of her before she "exploded" into the bracken.

Male Attentiveness

During my observations, the male came to the nest-site only nine times. On many occasions though I caught him in attendance in the white cedar tree. And he may have been silently present more often than I know. Usually, however, I would hear a soft *trip* or *treep* or a series of such notes (like the buzz of a Cedar Waxwing, *Bombycilla cedrorum,* only lower in pitch and less musical). I would see him either in the white cedar or the white pine in back of the blind or across the road in a red maple or white pine. He was, as far as I know, in attendance about three per cent of the time during incubation. His longest period of attentiveness was 10 minutes on 27 June and the shortest one minute on 26 June.

As far as I could see, the male never approached the nest as if he were about to join the female while she incubated the eggs, or to come close to her. Not once did I observe him perched on the edge of the nest while she was on the eggs. There was no sign of such behavior as touching of bills or even close proximity one with the other. Once, however, for a short period he sat under the bracken back of the nest-site.

As he approached the nest, the male uttered a rather sharp *threep* which seemed to be a kind of command. At any rate, on its utterance, the female left the nest immediately, almost as if in a hurry. On only one occasion did I see her remain on the nest at the appearance of the male. Usually she perched nearby among the bracken, although several times she flew as far as the white cedar. There she remained while the male came to the nest. Not once during incubation did I see her return to the nest while he was there.

Singing of the Male

Even when he was not in actual attendance either at the nest or in its immediate vicinity, the male presumably kept in communication with the female by a generous and full-throated amount of singing. I did not hear him singing at or near the nest-site until the nestling period began but always at some distance—anywhere from approximately 75 to 300 feet away. Although Kendeigh (1945a:159) reports that in the Canada Warbler the male sings "at a rate of 6 times per minute" and that "Soon after a mate is secured they [the males] usually become very quiet," I found no cessation of song in the white cedar male during that portion of the incubation which I observed. On 23 June, he sang 13 times, each song period averaging nine minutes; on 27 June he sang eight times, each interval of song approximating 4.6 minutes per period; and on 1 July, the day of the hatching and the inception of feeding, he sang seven times, lengthening the intervals of song to an average of 5.3 minutes.

So far as I could determine, the delivery of song was not confined to a selected perch or a particular locality or even a given area in the foraging range. I could not determine the extent of his territory. It seemed to me that when the desire to vocalize came on, the male sang where he happened to be.

Male Comes to Nest with Food

When the male did come, he came in the most striking fashion. I became aware of this remarkable behavior the first day in the blind. My notes for 23 June read: "3:32 PM. Female left the nest as male came in. Male appeared with green worm; approached the nest, hopped on the edge, and leaned forward as if offering food to young birds in nest; uttered 'run-together' series of Junco-like notes but duller with less carrying power; turned away from nest, still holding worm; returned to nest cavity, repeated his actions, stood on the nest edge, turning this way and that as if not sure what to do with the worm, flew to nearby aspen, swallowed the worm."

On this as well as on subsequent occasions I took careful note of his behavior. On four of the seven days of the incubation period I observed, in the forenoon as well as the afternoon and on one day (27 June) twice in the afternoon, I saw him repeat this. Each time he followed the same behavior as if it were a ritualized act—the approach to the nest with food in the mouth, the offering of the food to something in the nest which was here symbolized by the eggs, the *treep* call-notes, the turning about on the nest edge, the coming away from the nest, and the return to the cavity and finally the swallowing of the food.

At first I wondered whether this might be an example of "delayed" courtship feeding. Such display behavior akin to this has been reported in species of the genus *Dendroica* by Linsdale (1938), Harding (1931), and Mendall (1937). Lack (1940), summarizing the subject of courtship feeding in birds, has noted (page 170) that "In many species in which courtship feeding occurs, the male also feeds the female on or near the nest during incubation."

The question needs further study but it would seem, in this instance at least, that the male's attempt to feed the eggs may have been a kind of "anticipatory feeding" of the young. Since food offering occurred on the first day of the observation—23 June (probably the third day of incubation)—there is no reason to believe that the male did not exhibit the same behavior earlier. Perhaps there is a kind of anticipatory building up of tension, an innate drive to feed the young which grows in intensity during the incubation period. Perhaps there is present the instinctive urge to feed: there is at hand the nest but as yet there are no young to receive the food. Perhaps the urge is heightened by the deferments and failures to feed. It may be significant that the male offered food to the nest twice in the afternoon, 27 June, near the end of the incubation period. It may also be significant that during the nestling period the male takes the dominant role in feeding the young. In fact, the female is relatively inactive as a provider until the end of the nestling period.

Although I watched with the utmost care to see if he would offer the food to the female and although the female was on several occasions perched on bracken nearby (once only five feet away), I did not see him bring or offer her the food. Instead after each failure to dispose of the morsel in the nest, he swallowed it himself. All told he swallowed the food eight times during the period under observation.

Only on one occasion, on 23 June, did the female remain on the nest at the approach of the male and this time she was fed. When the male came flying in, uttering the usual *threep* notes, she fluttered her wings and replied with run-together "cheeps" but remained sitting. However, her behavior suggested some kind of tension. When the male in his customary way offered food (to her instead of to the eggs) she did not accept. He backed up slightly, then moved forward again, offering food. Still she did not take it. He withdrew to the edge of the nest, shifted about and returned. This time she ate the food.

The above instance occurred only once, at the end of a 43-minute period of attentiveness. I can only think that he offered food as before and that the female just happened to be there. She took the place of the "eggs-young," and was given the food. The occasion, I believe, was purely fortuitous, but may add weight to the idea that this behavior is anticipatory feeding of nestlings.

Summary

A nest with eggs of the Canada Warbler was found in northern Lower Michigan in a dry forest opening. This paper deals with information recorded from a blind at the nest during the period of incubation.

Incubation was performed solely by the female, with attentive periods averaging 28 minutes, inattentive periods 7 minutes. Her behavior on and off the nest and her approach to the nest are described.

The male came to the nest nine times and was in attendance three per cent of the time. His approach to the nest is described. Each time he arrived with food and offered it to the eggs as a kind of "anticipatory feeding." Throughout the period of incubation the male sang without let-up from approximately 75 to 300 feet from the nest.

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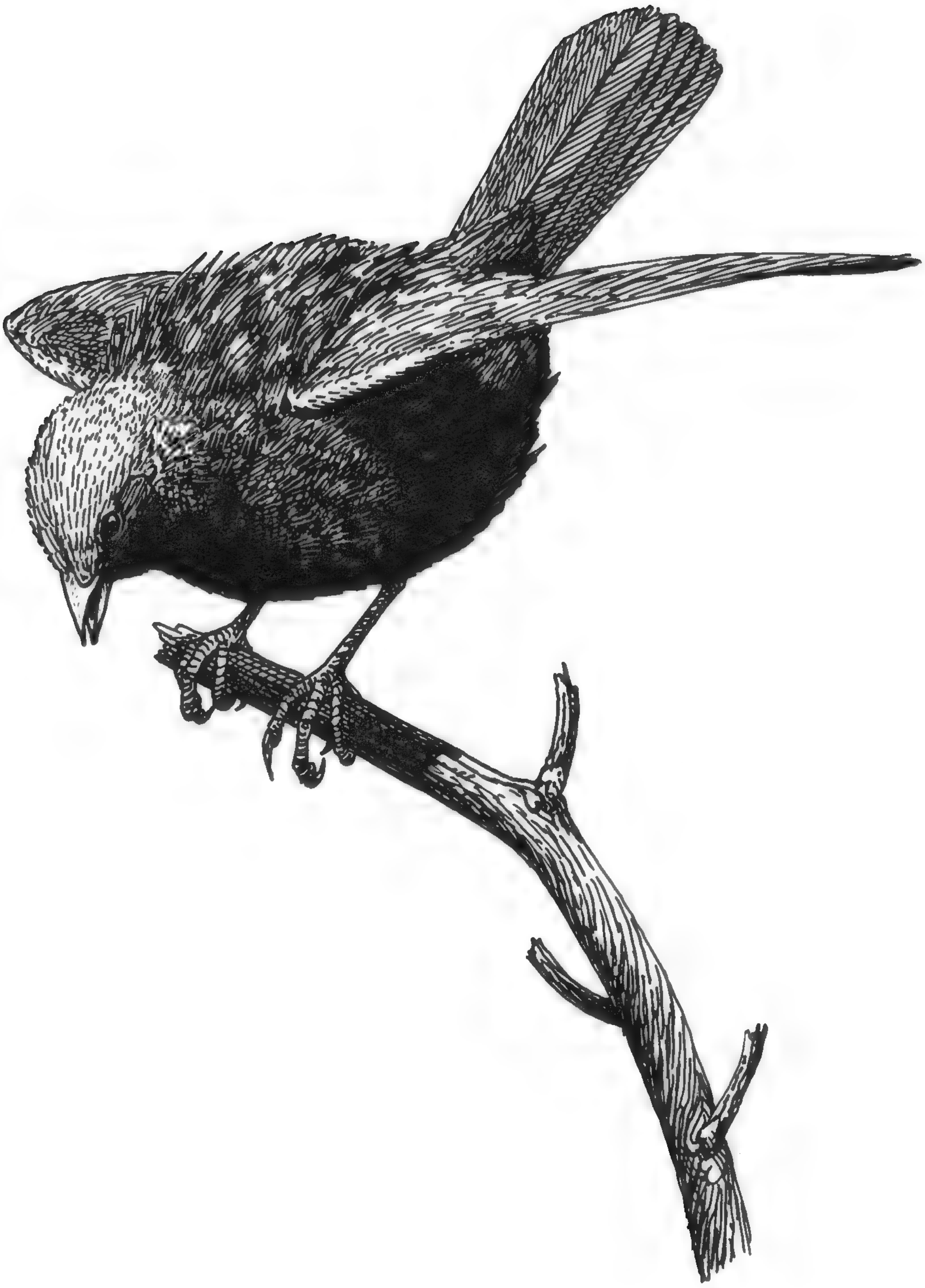


Brown-headed Cowbird

THE BROWN-HEADED COWBIRD, WITH OLD AND NEW HOSTS

HAROLD MAYFIELD

In contemplating the cowbird and its hosts, we tend vaguely to assume that all of these species have come down through the ages together and that, therefore, the parasitic relationship must be tolerable to the hosts or perhaps even beneficial in some obscure way, although the observations at a particular time and place often provide no such assurance. For the Brown-headed Cowbird *(Molothrus ater)* in eastern North America, I believe this assumption may be hasty. Rather, I believe, the opening of the forests by civilized man has allowed the cowbird to penetrate into new regions where it has access to host species that have had little or no ancestral experience through which to develop effective defenses against it. Here the cowbird is exploiting the new hosts with exceptional benefit to itself and with extraordinary potential for damage to them.

The Spread of the Cowbird Eastward

Before the coming of the white settler, the home of the Brown-headed Cowbird was the open grasslands of the mid-continent (see Figure 1), which are still the center of abundance of the species (Friedmann, 1929:151). The cowbird seems to have been completely missing from the unbroken tracts of forest in eastern North America. We might suppose this from its habits alone, but fortunately we have documentation from parts of the original forest last opened by the settler.

In Ohio, for example, the cowbird seems not yet to have become a regular inhabitant until nearly the middle of the nineteenth century, although human settlement had been in progress there already for more than 50 years and by 1840 the rural population had risen almost to one and one-half million people distributed at an average rate of more than six persons to the square mile in almost all counties (Brown, 1940:6-7). Kirtland, a long-term resident of the state, wrote in the first check-list of the birds of Ohio, "The cow-bunting is admitted into our catalogue on rather doubtful authority" (1838:180). Fifteen years later, Read (1853:397) said the cowbird had "recently greatly increased in numbers"; and 26 years after his 1838 check-list Kirtland pencilled in the margin of his copy of Nuttall's Manual of Ornithology, "abundant, formerly rare" (Christy, 1936:88).

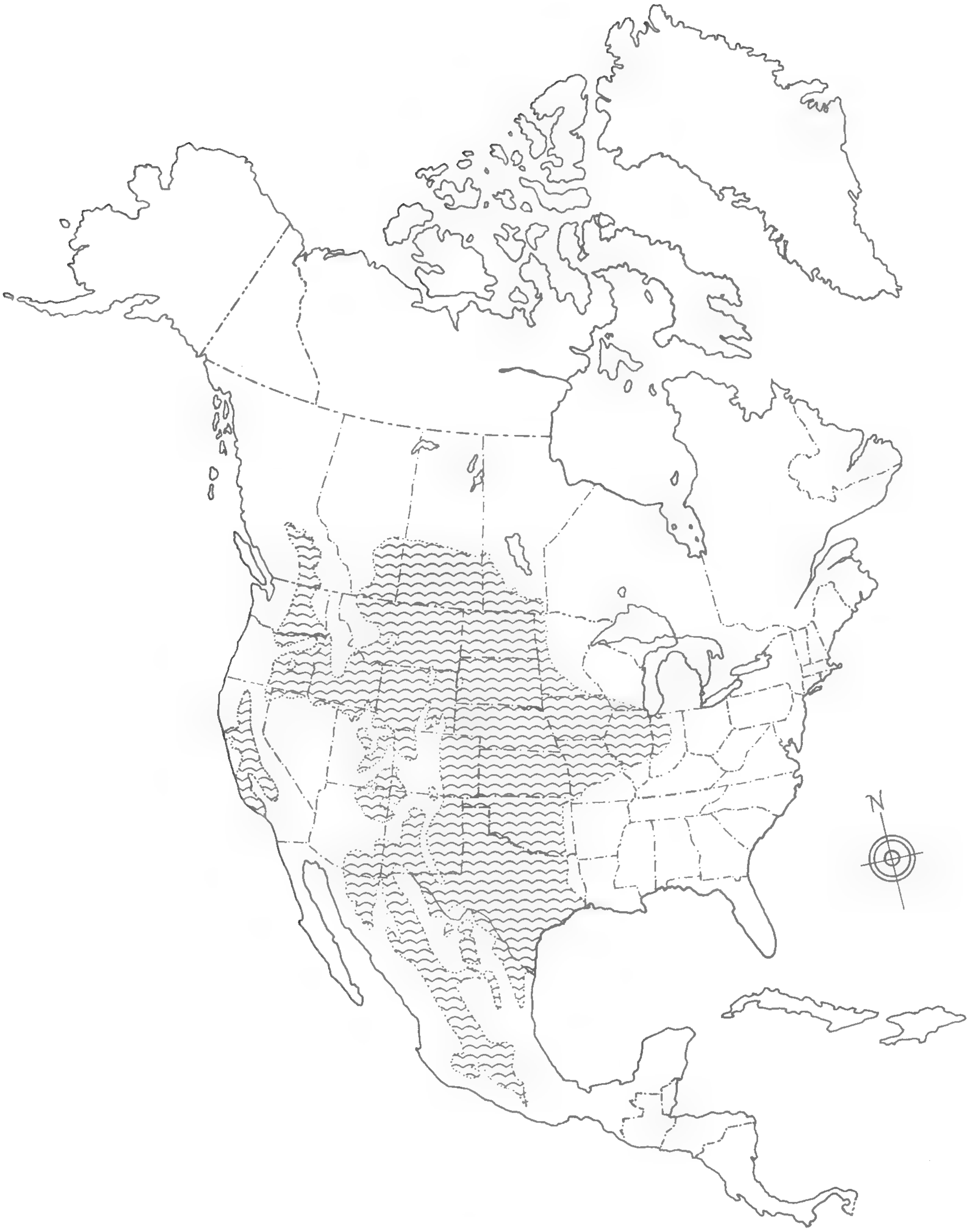
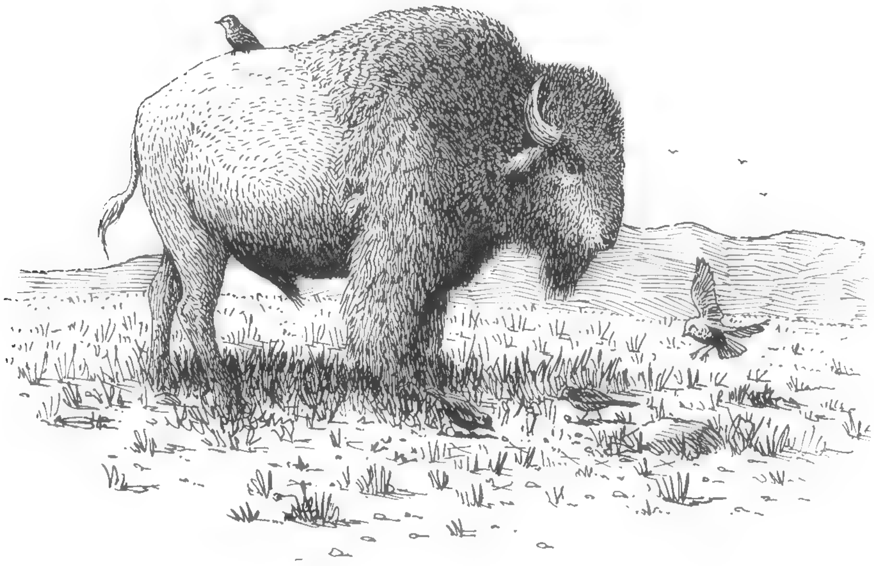


Figure 1. The grasslands of North America (based on a similar map in "The Ecology of North America" by Victor E. Shelford, published by the University of Illinois Press, Urbana, 1963).

In southern Ontario, Charles Fothergill was an active field observer from 1817 to 1840. Several volumes of his meticulous, hand-written notes (unpublished) have been preserved in the Royal Ontario Museum at Toronto, and they contain only one late and puzzled comment about the "brown-headed oriole," which I presume to be the cowbird.

The cowbird may enter the forest momentarily in its social flights and its nest searches, but I believe its feeding habit limits it to areas that provide at least some open plots of short grass. The cowbird gathers its food, both seeds and insects, principally by walking on the ground. It is adept at harvesting insects stirred up by grazing animals, whence its early name in the West "buffalo bird" and in the East "cowpen bird." Yet the cowbird's ability to thrive today suggests that such animals are not necessary as sources of food. Perhaps the buffalo or bison *(Bison bison)* on the Plains may have helped the cowbird more by beating down the tall grasses than by supplying insects.

The amount of grassy area needed to meet the minimum requirements of the cowbird may not be great. Enough may be supplied by roadside berms, lawns, gardens, and small fields scattered through a forested land.



Doubtless there are also other habitat requirements of the cowbird that are not pertinent to this account. For example, the social and breeding behavior of the cowbird causes it to make much use of exposed perches, and J. Frank Cassel of North Dakota tells me the cowbird is rarely found in wide expanses of grassland that are completely free of trees. Further, the cowbird is not found regularly in the more arid tracts of open country where the ground is mostly bare rather than grassy. Nowhere in the East, however, is there likely to be any considerable area with a shortage of perches or an excess of bare ground.

If short-grass feeding grounds are so important to the cowbird, regions of tall, dense grass (unless beaten down by bison) must have been unfavorable habitat for this ground-walking bird. These doubtful regions would include much of the original tall-grass prairies of the Midwest, savannas and marshes within the eastern forest, grassy borders of forest lakes and streams, and salt marshes of the Atlantic coast. Indeed, there must have been very little space suitable for the cowbird east of the Great Plains.

Consider, for example, the wet prairies near Lake Erie in Ohio. Samuel Brown (1815:137-141) described them as they appeared in October, "higher than our heads and as thick as a mat, confined together by a species of pea vine . . . thick enough to hold up a hat. Some places a cat could have walked on it. . . . To break a path four rods was as much as one could do at a turn." It is hard to believe that such a jungle of grass was suitable for the cowbird or, in fact, for many of the other birds we see on open grassy areas today—pastures, golf courses, roadsides, and lawns. The difficulty such vegetation may present to a bird that is accustomed to walking on the ground is illustrated by an incident witnessed by a modern observer in Kansas. Three Bobwhites *(Colinus virginianus)* alighted in a patch of tall prairie grass *(Andropogon hallii)* and became trapped momentarily, wedged between the converging stems near the ground, unable to run or fly. One of the birds was caught by hand before it could extricate itself (Robinson, 1957:68).

Not all of the eastern grasslands were as tall and dense as these, but other early descriptions of grassy openings in Massachusetts and New York mention stalks head-high or taller (Bidwell and Falconer, 1925:8,158), and very few of them could have resembled the cowbird's original home in the short-grass plains. There were probably not many places east of the Mississippi River, except very locally around salt licks and wallows, where the buffalo kept wide fields and broad trails beaten through the vegetation. Although scattered bands of bison wandered to the Atlantic watershed, and the numbers just west of the mountains seemed considerable to travelers from the East, the buffalo east of the Mississippi River were mere stragglers from the innumerable hordes of the Plains (Roe, 1951:256). On the Red River in southern Kentucky, Daniel Boone found "the buffaloes more frequent than I have seen cattle in the settlements . . . sometimes hundreds in a drove" (Garretson, 1938:22), and other settlers in Kentucky reported buffalo trails three teams wide; but these conditions were not general between the Mississippi and the Appalachians.

Because of a shortage of the right kind of habitat on the eastern seaboard, the cowbird must have existed there only in small numbers, if at all, before the arrival of the European colonists. The cowbird did not appear in the definitive tenth edition of Linnaeus' "Systema Naturae" in 1758, although the other common blackbirds, the Red-winged Blackbird *(Agelaius phoeniceus)* and Common Grackle *(Quiscalus quiscula)* were included, as were other conspicuous birds of the settled areas in the East. Mark Catesby (1731-1743, 1:34; Allen, 1951:466) published a picture and an account of the "cow-pen bird" based on his observations in the Carolinas between 1722 and 1725. The fact, however, that he pictured a female rather than the more striking male and that no other person to my knowledge mentioned the bird until late in the eighteenth century suggests that it may not yet have become well known, although its characteristic feeding habit was already recognized in the name for it used by Catesby. Another naturalist of the period, Peter Kalm, who visited Ontario, New York, and Pennsylvania in 1747-1750, gives a detailed account of the mixed flocks of blackbirds—Red-winged Blackbirds and Common Grackles—in the grain fields without mentioning the cowbird (Allen, 1951: 508).

In any case, the cowbird was certainly common in Pennsylvania and New York by 1790 (Bartram, 1791:240; Friedmann, 1929:153). To an ornithologist today, this seems an early date in history, but by 1790 the tidewater lands had been under cultivation for six generations. The population of the

Colonies was almost four million; Pennsylvania and North Carolina were the most populous states; and nearly all the land east of the mountains from North Carolina to Maine, as well as strips southwestward through southern Pennsylvania, Maryland, and western Virginia to the bluegrass region of Kentucky, had rural populations of six or more people per square mile (Bidwell and Falconer, 1925:148). By 1790 the forest had been opened substantially.

As we ask ourselves how the cowbird made its way from the grasslands of the West to the farmer's fields of the East, we are reminded that the original forest was not at all the unbroken woodland people tend to suppose. Instead, the earliest visitors found numerous "natural" clearings, some of them mere openings in the trees and others great meadows—variously called "plains," "prairies," "swales," and "savannas." They were common along the Atlantic coastal plain but more numerous west of the Alleghenies. They may have been kept open by the Indians who burned the woods regularly in late fall to improve conditions for game (Bidwell and Falconer, 1925:7, 157). The larger oases of grass marked the travel routes for men and game, and channeled the flow of settlers toward the West. They were ready-made for the herdsmen and their flocks.

Most of us are aware that the first wave in the westward tide of Europeans across America consisted of hunters and trappers. Also we have been amply reminded of the third wave, the farmers, who came to stay. But most of us are only dimly aware that there was a second wave, the herdsmen, following on the heels of the hunters and moving far ahead of the farmers. They left few monuments.

Always ahead of the permanent settler was the free range. In Virginia, for example, in the late 1600's it lay at the outskirts of the tidewater settlements; but in a few years it was on the Piedmont, and by 1750 officers of Braddock's army noted the "cowpen men" (but not, unfortunately, the cowpen birds) beyond the Cumberland Gap. Before long there were droves of swine, sheep, and cattle in Kentucky. The southern Appalachians remained largely free cattle range throughout the 1700's. Back and forth along pathways that followed the grass, across southern Pennsylvania and the Valley of Virginia to Kentucky, marched herds of cattle, sheep, and swine, the only crops that could walk themselves to market from the far frontier (*Fortune*, 1935:61). Almost certainly, the herdsmen broadened and improved the grazing lands along their route with fire and ax, while the hooves of their animals beat permanent swathes through the tall grasses. Although the blue grass and white clover were introduced plants, they became established in Kentucky so early that the first settlers found them already abundant (Bidwell and Falconer, 1925:159). Thus, long before 1790, wide pathways, trampled by streams of domestic animals, offered inviting routes for the cowbird across forest and mountain to the new agricultural lands opening up in the East.

Even if the cowbird made the trip originally without human help, its probable route was along the chain of grassy openings eastward from the blue grass region lying between the Tennessee and Ohio Rivers. Other birds of the open country of the West did not make their way east until the intervening lands were more completely cleared. The Horned Lark *(Eremophila alpestris)* came to New York and New England as a nesting bird shortly before 1900 (Pickwell, 1942:343), and the Lark Sparrow *(Chondestes grammacus)* reached the summits of the Alleghenies soon after 1900 (Brooks, 1938:184). The Dickcissel *(Spiza americana)* bred abundantly from the Middle Atlantic states to New England in the mid-nineteenth century, but Brewster (1906:64) believed they had come to the Eastern seaboard from the open grasslands of the Mississippi Valley only after the forests of the Ohio Valley and Middle Atlantic states had been largely replaced by fields of grass or grain.

The wholesale clearing of forests for agriculture came to an end in nearly all parts of the East during the nineteenth century, if not earlier. Since that time marginal farms have slipped back to forest and the urban population has sprawled into the countryside until the amount of land devoted to farm crops in the East is substantially less than it once was. A few localities may not be as attractive to the cowbird now as in some former time.

Still the cowbird continues to extend its range northeastward and southeastward. In Ontario it has spread northward 200 miles or more in the present century (Snyder, 1957:35). In Quebec the cowbird was already abundant near Montreal at the turn of the century as it is now, but in southeasternmost parts of the province it has progressed from rare to abundant since that time. For example, in Compton County, a hilly timbered district with scattered farms, Lewis Terrill did not see a cowbird in 1899-1902 although he found one parasitized nest; whereas, in the adjacent county of Richmond with similar terrain, in 1953-1963 he found 65 nests parasitized (27 per cent) out of 237 nests of potential hosts, among 23 out of 33 (69 per cent) passerine species (letter, 1964). In Nova Scotia the cowbird was found breeding first in 1933, but it was a rare summer resident until about 1950 (Tufts, 1961:413) and since that time has become regular in some localities. In Prince Edward Island the first breeding record occurred in 1953, and the bird has become notably more common since 1960 (Vass, 1964:60). In Newfoundland the bird was first seen in 1957 (Mills, 1957:25-27).

In the South Atlantic states the cowbird is expanding its breeding range southeastward, with proof of egg-laying in extreme northwestern Florida and in eastern Georgia in 1957 and 1958 (Webb and Wetherbee, 1960:84). By 1960 it had come to breed generally throughout Alabama, whereas ten years earlier its range had been restricted largely to the coastal belt (Thomas A. Imhof *fide* Friedmann, 1963:5).

In this century the cowbird has increased greatly also in California, but I shall not attempt to treat here its expansion westward.

I am not sure we can account for the cowbird's recent penetration northeast and southeast entirely by habitat changes in those areas. Yet changes in land use have occurred. Dairying is on the upgrade in eastern Quebec (Terrill, 1964, letter), and the raising of cattle has increased greatly on the Piedmont during the last 30 years (Charles H. Blake, 1964, letter). New highways with broad berms are being cut through forests where there are no farms, and herbicides make it easy to keep the vegetation low along the right-of-way. Golf courses, airfields, and houses with mowed lawns are appearing on lands that had been wild. It is possible that even such a minor invention as the rotary lawnmower may have helped the cowbird by making it feasible for cottagers and resort operators to extend grass-cutting into the rough.

That some change has occurred in the Northeast favoring birds of the open country is suggested by the recent increases also of the Horned Lark, Bobolink *(Dolichonyx oryzivorus)*, Red-winged Blackbird, and Common Grackle in the Atlantic Provinces (Tufts, 1961:15, and Stanley E. Vass, 1964, letter).

On the other hand, the cowbird's recent expansion into peripheral areas may be the overflow from a population surplus resulting from its exceptional success with tolerant hosts newly available in the forests nearer the center of its range.

The Measure of a Host

We would like to find measures of the effect of the cowbird and its host on one another.

One criterion is the *frequency* of parasitism, which I shall define as the ratio of nests parasitized to the number of nests of the host. Tentatively, I shall regard less than 10 per cent parasitism, light; 10-30 per cent, moderate; and over 30 per cent, heavy.

Yet this measure by itself is not enough. For example, a host might have a high frequency of parasitism, but, if in each instance it abandons the nest and builds again, keeping up this process until it brings off its own brood unmolested, the benefit to the cowbird will be zero and the damage to a single-brooded host negligible.

A supplemental criterion for measuring the effect of the host and cowbird on one another is *tolerance,* which I shall define as the ratio of cowbirds fledged to the number of cowbird eggs laid in the nests of the host. We would really like to know how nearly the host's care of the cowbird eggs and young approximates its care of its own; but since we do not know the rate of fledging from eggs for many hosts, I shall generalize from the fact that nearly all open-nesting passerine birds produce young from at least 20 per cent of their eggs, and I shall regard a fledging rate from cowbird eggs of more than 20 per cent an indication of a tolerant host.

Obviously, the host-parasite relationship is most important to both species when the frequency and tolerance are both high. Of the two measures, tolerance is the more significant indicator of adaptation, since frequency may depend in part on the abundance of the cowbird. Yet the two measures may not be entirely independent, for low tolerance reduces the probability that a human observer will find all the parasitized nests.

It is disappointing to find how few host species have been studied in sufficient depth to yield reliable measurements of these criteria. For many hosts the samples reported are too small to be reliable, and for many others we have nothing better than the impressions of field students. The information available has been summarized comprehensively by Friedmann (1963).

To learn if hosts in some habitats have adapted more successfully to the cowbird than hosts in other habitats, I have considered the hosts in three categories—grasslands, grassland edge, and eastern forest. Presumably the birds of the grasslands of the midcontinent have been exposed to the cowbird throughout nearly their entire ranges for many thousands of years. The birds of the grassland edge have been exposed to the cowbird for a very long time in the midcontinent region where trees and shrubs have come up against the plains; but a great many of them, nesting also wherever brushy openings occurred in the eastern forest, may have had no contact with the cowbird until recently. Finally, the birds of the eastern forest have probably had negligible exposure to the cowbird until the long-grass prairies were plowed and the forests opened.

To avoid bias in my selection of typical species in these three categories, I have taken the listings of dominant and influent species by Shelford (1963).

Birds of the Grasslands

Shelford names 12 species of passerine birds as most characteristic of the northern temperate grasslands east of the Rocky Mountains (1963:333, 336, 346): Horned Lark, Bobolink, Eastern Meadowlark *(Sturnella magna),* Western Meadowlark *(S. neglecta),* Dickcissel, Lark Bunting *(Calamospiza melanocorys),* Grasshopper Sparrow *(Ammodramus savannarum),* Vesper Sparrow *(Pooecetes gramineus),* Lark Sparrow, Brewer's Sparrow *(Spizella breweri),* McCown's Longspur *(Rhynchophanes mccownii),* and Chestnut-collared Longspur *(Calcarius ornatus).*

None of these 12 grassland species seem to have been studied sufficiently to allow me to express their tolerance of the cowbird in numerical terms. However, Friedmann regarded ten of them as infrequent or poorly known hosts, and only two, the Dickcissel and Vesper Sparrow, as fairly frequent hosts. Therefore, I shall concentrate on the two species of the grasslands believed to be most heavily victimized by the cowbird.

Thus, the Dickcissel is frequently parasitized but, producing no cowbird from eggs in 24 nests of this sample, seems not to hold much promise of being a tolerant host.

The Vesper Sparrow in the regions sampled here is not a frequent host. This confirms my own experience in northern Lower Michigan, where the cowbird's use of the Vesper Sparrow is in notable contrast with its use of the Kirtland's Warbler *(Dendroica kirtlandii).* In the special habitat of the warbler, the Vesper Sparrow is perhaps the most abundant bird. Both nest at the same time, on the ground, and they are of similar size. The only obvious difference in their nests is that the Vesper Sparrow's nests are more likely to be in the open, away from overhanging limbs. But, whereas fully half the warbler nests are parasitized, Vesper Sparrow nests are rarely found with cowbird eggs.

TABLE 1

Birds of the Grasslands

Species	*Nests*	*Nests parasitized* *No.*	*%*	*Cowbird eggs*	*Cowbirds fledged* *No.*	*%*	*Location*	*Authority*
Dickcissel	61	19		19+	0		Oklahoma	Overmire, 1962
	15	5		5	0		Oklahoma	Wiens, 1963
	14	1		?	?		Oklahoma	Ely *in* Wiens, 1963
	17	9		?	?		Nebraska	Hergenrader, 1962
	23	6		?	?		Kansas	Johnston *in* Friedmann, 1963:143
	130	40	31	?	?	?		
Vesper Sparrow	112	9		?	?		Ohio	Hicks, 1934
	74	3		?	?		Quebec	Terrill, 1961
	32	1		?	?		Michigan	Kelley *et al.*, 1963
	218	13	6	?	?	?		

So, from the evidence available, I do not find any of the typical birds of the grasslands to be both frequent and tolerant hosts of the cowbird.

The usual defense of small birds against the cowbird is nest desertion; and, since individual females within a species differ widely in tolerance of nest molestation, cowbird pressure would select rapidly against the more tolerant hereditary lines.

Birds of the Grassland Edge

Shelford names 21 species of passerine birds that nest among shrubs and trees in the "marginal contacts of the temperate grassland." In the "grassland-deciduous forest contacts" he lists the following (315, 316): Yellow-billed Cuckoo *(Coccyzus americanus),* Catbird *(Dumetella carolinensis),* Brown Thrasher *(Toxostoma rufum),* Robin *(Turdus migratorius),* Cardinal *(Richmondena cardinalis),* Indigo Bunting *(Passerina cyanea),* American Goldfinch *(Spinus tristis),* and Field Sparrow *(Spizella pusilla)*; northern part only—American Redstart *(Setophaga ruticilla),* Lark Sparrow, and Chipping Sparrow *(Spizella passerina)*; southern part only—Mockingbird *(Mimus polyglottos),* Loggerhead Shrike *(Lanius ludovicianus),* and Bell's Vireo *(Vireo bellii).* In the "aspen forest edge" (321) he lists the Catbird, Brown Thrasher, Robin, Red-eyed Vireo *(Vireo olivaceus),* Yellow Warbler *(Dendroica petechia),* American Goldfinch, and Rufous-sided Towhee *(Pipilo erythrophthalmus)*; and in the "willow community" (323), a subdivision of the aspen forest edge, Yellow Warbler, Yellowthroat *(Geothlypis trichas),* Red-winged Blackbird, Common Grackle, and Song Sparrow *(Melospiza melodia).*

I have taken the liberty of removing the Red-eyed Vireo from this list of birds of the grassland edge and treating it instead as a charateristic bird of the eastern forest. While, like most forest birds, it comes to the edge of grasslands where the forest touches them, it is not known to be dependent in any sense on grass or openings.

TABLE 2

Birds of the Grassland Edge

Species	*Nests*	*Nests parasitized No.*	*Nests parasitized %*	*Cowbird eggs*	*Cowbirds fledged No.*	*Cowbirds fledged %*	*Authority*
Black-capped Vireo	76	38	50	66	4	6	Graber, 1961.
Bell's Vireo	84	57	68	77	5	6	Barlow, 1962; Mumford, 1952; Nice, 1929; Nolan, 1960; Pitelka, 1942; Wiens, unpubl.
Yellow Warbler	373	130	35	163	26	16	Batts, 1958; Berger, 1951; McGeen, unpubl.: Schrantz, 1943.
Prairie Warbler	385	94	24	108	7	6	Nolan, unpubl.
Yellowthroat	88	37	42	67	19	28	Young, 1963.
Field Sparrow	849	212	25	271	34	13	Batts, 1958; Berger, 1951; Norris, 1947; Sutton, 1960:61-65; Walkinshaw, unpubl.
Song Sparrow	329	149	45	223	68	31	Young, 1963.

Of the remaining 20 species, Friedmann says nine are frequent victims of the cowbird: Bell's Vireo, Yellow Warbler, Yellowthroat, American Redstart, Indigo Bunting, Rufous-sided Towhee, Chipping Sparrow, Field Sparrow, and Song Sparrow. Of these nine species, all but the Bell's Vireo have occurred from ancient times in brushy areas and forest edge throughout much of the eastern continent, and, therefore, I believe, they may have had only partial exposure to the cowbird until recently.

Of these nine most frequent victims, data on four are too scanty to permit me to calculate both frequency and tolerance with confidence. Neither can be calculated for the American Redstart. For the Chipping Sparrow, the frequency can be calculated, and data from Michigan and western Pennsylvania show it to be an infrequent victim there—11 parasitized nests (9 per cent) out of 129, and it may prove to be an intolerant host too, but the data are too scanty to establish the fact (Batts, 1958; Berger, 1951; Norris, 1947; Sutton, 1960:150-153; Walkinshaw, 1944). The Indigo Bunting is a frequent host in Illinois, Michigan, Ohio, and Quebec—65 parasitized nests (34 per cent) out of 193, and available fledging data suggest it may be a tolerant host (20 cowbirds fledged from 44 eggs), but the sample is not large enough to permit us to state this with confidence (Hicks, 1934; Kelley *et al.*, 1963:100; Sutton, 1959:96-98; Terrill, 1961; Twomey, 1945:194; Young, 1963). The Rufous-sided Towhee is a frequent host in Michigan and Ohio—54 parasitized nests (27 per cent) out of 197, but here also the data on cowbird fledging are not sufficient to calculate the tolerance (Hicks, 1934; Kelley *et al.*, 1963: 102; Sutton, 1959:133; Young, 1963).

Five species remain with adequate data, and to these I have added two more for which good data happen to be available, the Black-capped Vireo (*Vireo atricapilla*) and Prairie Warbler (*Dendroica discolor*). The two additions are both birds of semi-open, scrubby-tree country. The Black-capped

Vireo, an inhabitant of the forest-grassland ecotone from Kansas to north-central Mexico, has probably been exposed to the cowbird for a very long time. How much contact with the cowbird the Prairie Warbler had in former times is uncertain. Today it is not a regular inhabitant of the margin between the grasslands and deciduous forest but rather is found in dry, shrubby areas—such as abandoned farmlands, dunes, and sandy, scrub-grown plains—within the forested regions; however, its original range seems to have met the western grasslands in the lower Mississippi Valley (Nolan, 1964, letter).

Thus, among 20 species of the margins of the grasslands I can identify positively only two that are both frequent and tolerant hosts, the Yellowthroat and Song Sparrow, and three more that may prove to be good hosts also when more data are available, the American Redstart, Indigo Bunting, and Rufous-sided Towhee. It is noteworthy that all five species were distributed widely throughout the original eastern forest and probably experienced the cowbird only at the peripheries of their ranges until recently. They seem not to have developed very effective defenses.

On the other hand, the two species with highest frequencies but lowest tolerances of parasitism in Table 2, the Black-capped Vireo and Bell's Vireo, are at present and have been for a very long time exposed to the cowbird throughout their entire ranges. These birds with most complete exposure to the cowbird seem to have developed the most effective defenses against the parasite.

The information here tends to confirm the impression of many field workers that the cowbird prefers to lay in nests located in brush rather than in open grasslands. This preference may be an adaptation by the cowbird to the more receptive hosts found among species that have had less exposure to nest parasitism. Thus, the cowbird succeeds best in the ecotone between

TABLE 3

Birds of the Eastern Forest

Species	*Nests*	*Nests parasitized*		*Cowbird eggs*	*Cowbirds fledged*		*Authority*
		No.	*%*		*No.*	*%*	
Red-eyed Vireo	95	64	67	117	26	22	Batts, 1958; Norris, 1947; Southern, 1958.*
Kirtland's Warbler	137	75	55	125	†	41	Mayfield, 1960.
‡Five woodland species	212	71	33	111	39	35	Berger, 1951; Brackbill, 1958; Brandt, 1947; Hann, 1937; Norris, 1947; Twomey, 1945; Walkinshaw, 1961.

*The well-known study of Lawrence (1953) was omitted from this sample because cowbirds were virtually absent from her study area.

†Fledging rate for cowbirds was calculated from mortality data on eggs and nestlings.

‡Acadian Flycatcher, Wood Thrush, Veery, Ovenbird, and Louisiana Waterthrush.

grassland and forest, held to the grassland perhaps by its feeding habits but reproducing more successfully among the more tolerant hosts of the forest edge, stream valleys, and brushlands.

Birds of the Eastern Forest

I have found only two species of eastern forest birds for which there are sufficient data on nests and cowbird eggs to calculate the frequency and tolerance of parasitism—the Red-eyed Vireo and the Kirtland's Warbler. Interested in finding how others also are faring with the cowbird, I have lumped five, all of them indisputably birds of the forest, for which some information is available: Acadian Flycatcher *(Empidonax virescens),* Wood Thrush *(Hylocichla mustelina),* Veery *(H. fuscescens),* Ovenbird *(Seiurus aurocapillus),* and Louisiana Waterthrush *(S. motacilla).*

The birds of the eastern woodland shown in Table 3 are both frequent and tolerant hosts of the cowbird. I believe they have had little, if any, exposure to the cowbird until recently and have developed no effective defenses against the parasite. Of course, these same species will be less frequent hosts in areas where the cowbird is less abundant.

Consequences to the Cowbird and the New Hosts

Since the cowbird is more successful with the new hosts it has found in the eastern woodlands than with older hosts of the grasslands and grassland edges; and since the cowbird was succeeding formerly with the old hosts, it must now be producing a surplus of young in many areas of the East, unless its mortality after fledging is greater there for unknown reasons. This surplus may help account for the continued spread of the cowbird into peripheral areas of borderline suitability.

No one has demonstrated yet that any host has declined in population as a result of the cowbird. However, studies of some hosts reveal a local cowbird pressure that may be intolerable. Two examples of local populations bearing extremely heavy cowbird pressure are the Ovenbirds, described by Hann (1937:198, 202) as accepting tolerantly 52 per cent nest parasitism and producing only 1.6 young per pair per year, and single-brooded Red-eyed Vireos, described by Southern (1958:200) as accepting tolerantly 72 per cent nest parasitism and producing only about one young vireo per nest. Still, Ovenbirds and Red-eyed Vireos are common in most suitable areas. Perhaps deficiencies in production at one locality are amply replenished by production in other areas, near or far, where cowbird pressure is lighter.

There are still large unbroken tracts of woodland in the East where nesting birds are untouched by the cowbird. It would be useful to know how far into a dense woodland the cowbird penetrates for egg-laying, and how the cowbird population varies according to the availability of open space in a region largely wooded.

For most species we will be slow to notice any general effects on their populations as long as the hosts continue to have breeding areas where the cowbird is scarce. But if the cowbird continues to find access to more nests of various woodland species, I believe the effect on some may become appreciable. Particularly vulnerable, I believe, are small species to which even one cowbird in the nest brings the loss of all the host's nestlings. Examples are the *Empidonax* flycatchers and perhaps small warblers such as the American Redstart and small sparrows such as the Clay-colored Sparrow *(Spizella* *pallida*) (Friedmann, 1963:54, 124, 163). I suspect that these populations escape injury now only because the cowbirds often are not numerous where these hosts are nesting.

The Kirtland's Warbler would seem to be a vulnerable species because it has no reservoir of population in any area that escapes the full attention of the cowbird. The sample in my study lost 43 per cent of its potential production as a result of the cowbird and produced only 1.4 young per pair per year (1960:177, 204). Yet censuses of the entire species showed no decline in numbers from 1951 to 1961 (Mayfield, 1962:173). The mortality rate of free-flying birds of this species may be lower than believed usual for small passerines; or, as I consider more likely, my study sample was more heavily parasitized than the whole population.

The cowbird represents a particularly dangerous type of enemy because, unlike most predators, it is not density dependent; that is, cowbird pressure does not relent when a prey species gets scarce. Since the cowbird does not specialize on any one species, it is not therefore dependent on a continued abundance of that host.

Although most species of birds obviously have a reproductive capacity ample to cope with the ordinary hazards of existence and under unusual stresses often reveal unsuspected reserves, it remains to be seen if some of the small birds of the eastern forest can survive in the presence of an abundant population of the cowbird.

Summary

The Brown-headed Cowbird *(Molothrus ater)*, originally a bird of the short-grass plains of the midcontinent of North America, penetrated into eastern regions when the forests were opened and the tall-grass prairies were plowed for agriculture. The small passerine birds of the eastern forest had little previous experience with this social parasite, and, wherever the cowbirds have become abundant, these new hosts are frequently victimized and are tolerant of cowbird eggs and young. In contrast, the birds of the western grasslands, having had long ancestral experience with the cowbird, are much less receptive to it. Intermediate in receptivity are the birds of the grassland edge, which have been only partially exposed to the cowbird over the ages.

The cowbird's success with its new hosts has probably brought a surplus in population that may help account for its continued expansion of range northeastward and southeastward into areas of marginal suitability. The new hosts, having developed no effective defenses against the cowbird, may be vulnerable to injury, at least locally, when the cowbird becomes abundant in an area.

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BLOOD-EATING IN A GALÁPAGOS FINCH

Robert I. Bowman and Stephen L. Billeb

There are few groups of birds whose feeding habits have been scrutinized more thoroughly by biologists than those of the Galápagos finches (subfamily Geospizinae). Previous studies by Darwin (1845), Snodgrass (1902), Gifford (1919), Lack (1945, 1947), Bowman (1961, 1963), Eibl-Eibesfeldt (1961), Eibl-Eibesfeldt and Sielmann (1962), and Curio and Kramer (1964) concern not only the kinds of food taken but also the manifold adaptations in structure and behavior that permit the most efficient exploitation of available food resources. In view of this fund of knowledge it came as a surprise to several ornithologists participating in the University of California's "Galápagos International Scientific Project" to discover previously unreported feeding habits, some of which are novel to the Galápagos finches. In the case of *Geospiza difficilis septentrionalis* (the so-called "Sharp-beaked Ground-finch") on Wenman Island, we are reporting on what appears to be the first example from the bird world of a species in which one of the *primary* objectives in foraging is the procurement of blood.

Discovery of Blood-eating Habit

Discovery of the blood-eating habit was made in late January 1964 by our small party of scientists who landed on Wenman Island in the Galápagos Archipelago (Figure 1). Explorers have visited this remote volcanic island rather infrequently because of its great distance from the inhabited islands to the south, and also because the one or two landing sites are flagrantly dangerous. Twenty-foot swells incessantly scour the sheer basaltic bluffs of this highly eroded volcano (Figure 2). In the past those fleet-footed explorers who dared jump ashore at the most propitious moment were immediately confronted with inhospitable, overhanging ledges and loose talus. Our expedition was most fortunate to have the logistical support of two U. S. Navy helicopters, thus giving us assurance of a safe, dry arrival atop the tableland at the northeast corner of Wenman Island.

The first indication we had of the sanguivorous habits of *Geospiza difficilis* came on the afternoon of 31 January. Our botanist-colleague, Dr. Raymond Fosberg, a well-known authority on Pacific island vegetation, returned to camp remarking about the strange kind of finch that sits on the backs of the boobies, probing at bloody spots on the wings. Hardly had he finished recounting his experiences when we observed a fully black male finch landing on the tail feathers of a Red-footed Booby *(Sula sula websteri)* that was perched on top of a 12-foot *Croton* bush. Turning its head sideways several times to glance at the finch, the booby seemed little concerned with the pres-

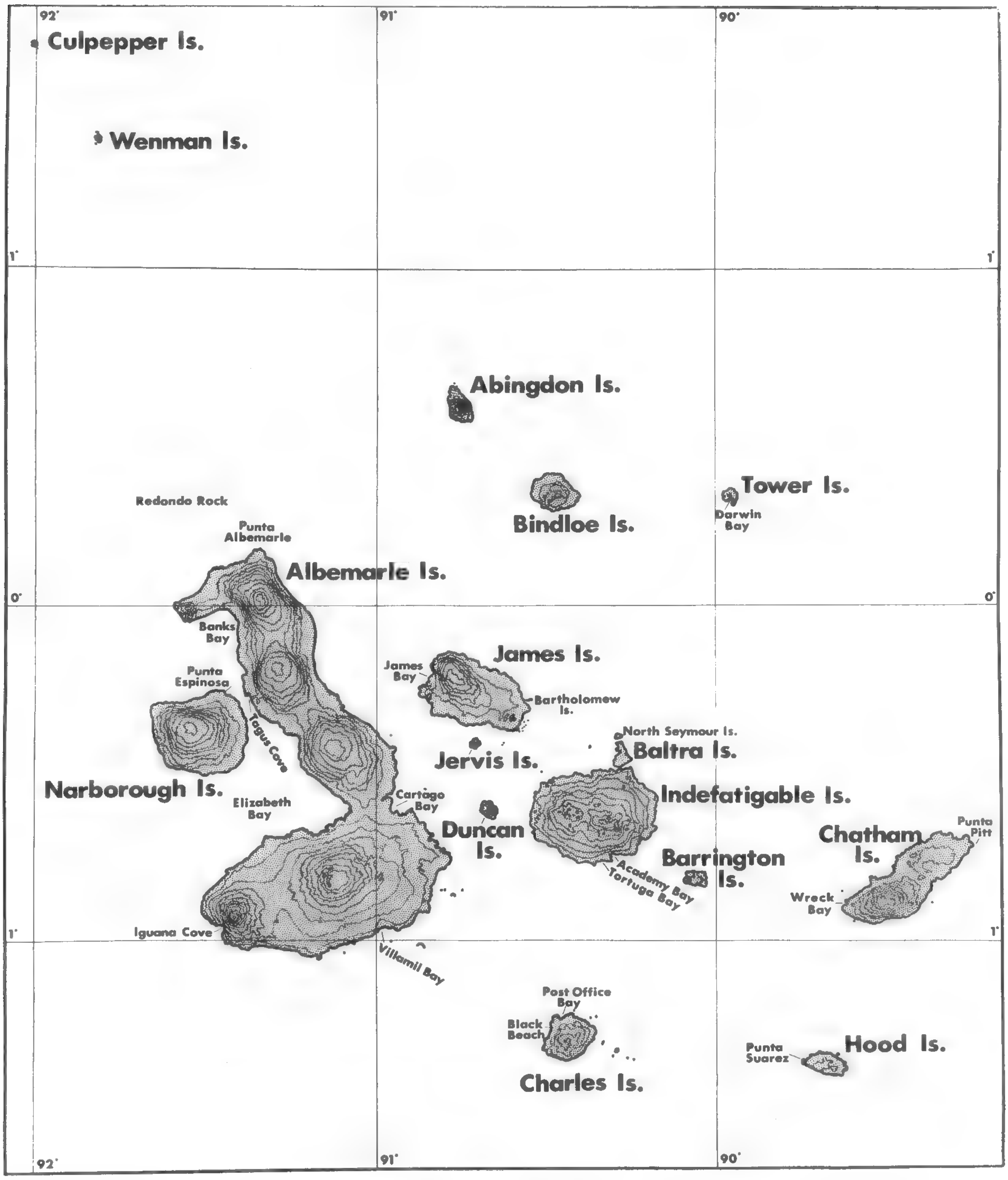

Figure 1. Map of the Galápagos Archipelago showing the location of Wenman Island (upper left).

ence of this 15-gram "freeloader" on its tail, that is, until the finch probed three times with its bill into the booby's uropygeal area. At that moment the Red-footed Booby made a sudden swing of its head, causing the finch to fly away.

Previous to this incident most of our time was occupied with making tape-recordings of finch vocalizations—our primary research activity during the expedition. For this reason we had deliberately avoided the noisy booby colonies. Now, setting aside our recording gear, we wasted little time in systematically investigating the large breeding colony of Masked Boobies (*Sula dactylactra granti*) on the south rim of the large cauldera at the northeast corner of the island (see arrow, Figure 2).

We had walked scarcely twenty yards through the colony when we observed individual finches hopping along the ground between the boobies

Figure 2 *(above)*. Aerial view of the northeast corner of Wenman Island. Arrow indicates the location of observations on blood-eating in *Geospiza difficilis septentrionalis*.

Figure 3 *(below)*. Male *Geospiza difficilis* (indicated by arrow) among nesting Masked Boobies *(Sula dactylactra granti)*.

(Figure 3). The Masked Booby is a ground-nesting species, unlike its close relative, the Red-footed Booby, which prefers to roost and nest in bushes and trees. Most of the Masked Boobies were defending nest-sites, but a few were each sitting on a single egg or a naked young. Within a distance of about 100 yards we observed at least ten instances of blood-feeding by *difficilis* (Figure 4). Many of the Masked Boobies, although not parasitized by the finches during our period of observation, showed signs of earlier attacks by the finches (Figure 5). The innermost (proximal) secondaries, their greater coverts, and also occasionally the adjacent "tertiaries" (on the distal end of the humerus) showed bloodstains. With the coverts matted by blood, the underlying quills of the secondaries were revealed.

Blood-eating Behavior Described

The typical blood-feeding behavior of *difficilis* was as follows. When approaching a Masked Booby sitting on the ground, the finch moved toward the tail region and jumped upon the protruding tips of the primaries (Figures 4 and 9). This perching on its wing feathers usually prompted the booby to turn its head posteriorly, bringing its bill very close to the body of the finch (Figure 7). If the booby's head movement was vigorous, the finch took flight, but generally the booby tolerated the finch on its wing. After a brief peering at the secondary feathers near the bend of the wing (elbow), the finch inserted its bill among the booby's feathers (Figures 4, 8, and 10). During this behavior the finch sometimes buried its head so deeply in the plumage of the booby that the eyes of the finch were almost obscured from veiw. This brought the tip of the bill within reach of the booby's skin surrounding the secondary quills,

Figure 4. *Geospiza difficilis* probing the bases of the secondaries of a Masked Booby where it obtains blood. Photograph retouched.

Figure 5 *(above)*. Close-up view of the left wing of the Masked Booby shown in Figure 4, immediately after a feeding session by *Geospiza difficilis*. Note the exposed secondary quills and the matted secondary coverts that are stained with blood.

Figure 6 *(below)*. Masked Booby adjusting bloodstained flight feathers and dislodging muscid-like flies attracted to the coagulated blood. Same individual as shown in Figures 4 and 5.

Figure 7 *(above)*. *Geospiza difficilis* perched on the primaries of a Masked Booby preparatory to feeding on its blood. As the booby makes a normal backward turn of the head, the bill comes just short of reaching the finch. Photograph retouched.

Figure 8 *(below)*. Close-up view of *Geospiza difficilis* feeding on the blood of a Masked Booby. Photograph retouched and reproduced herewith on its side.

Figure 9 *(above)*. *Geospiza difficilis* perched on the flight feathers of a Masked Booby during blood-eating. The tip of the bill is covered with fresh blood.

Figure 10 *(below)*. Another view of *Geospiza difficilis* clinging to the flight feathers of a standing Masked Booby, and probing for blood.

which it bit, causing bleeding. The blood coursed downward along the quills to its juncture with the vanes, where it was fed upon by the finch. Occasionally blood was smeared on the underlying upper tail coverts, thus giving the impression that a wound had been made at the base of the tail. When a finch made its initial bite, the stimulus caused the booby to turn its head and swing at the finch with its bill. However, the finch was usually alerted by the initial head movement of the booby and merely flew a safe distance away. Normally the finch returned to its perch within a minute, and continued to feed on the accumulating blood on the quills.

We have seen a finch perched on a Masked Booby's back for as long as five minutes, blood-feeding at more or less regular intervals. The bill of an actively feeding finch may become bright red at the tip (as in Figure 9). After such a feeding session there is much wiping of the bill on rocks and twigs in an effort to remove the coagulated blood.

As many as two birds have been seen awaiting their turn to feed on the blood of an "active" booby. Invariably, there was a certain amount of jostling for the best perch on the booby's tail or wing feathers. Never more than one finch was seen at a time on the back of a booby, although F. P. Drowne (*in* Rothschild and Hartert, 1899:110) saw as many as three finches on one booby at one time! The finches awaiting their turn at the booby hopped about on the ground near its tail, keeping a close watch for an opportunity to displace or follow a feeding bird. It seems as though the sight of a finch perched on the back of a booby, or a bloody smear on a booby's wing, serves to attract attention to the booby.

As indicated above, the initial making of a wound, or the re-opening of a previous wound, causes minor irritation to the booby. To judge from the amount of head turning, the boobies were less disturbed by the finches than they were by the muscid-like flies that were attracted to the coagulating blood in the vicinity of the wound.

Extent of Blood-eating

There can be no doubt that the sole purpose of the finch behavior was to obtain the blood of the boobies. Blood-feeding is unknown in other populations of *Geospiza difficilis.* In the field we have studied populations of *G. d. acutirostris* (Tower Island) and *G. d. nigrescens* (Culpepper Island), both of which have Masked and Red-footed Boobies as co-inhabitants; yet this habit was never observed. But on Wenman Island, a large number of Masked Boobies were either seen to be molested by finches or bore tell-tale signs of former victimization. Published reports (summarized in Table 1) indicate that there are breeding or loafing populations of Masked and Red-footed Boobies on Wenman Island at every season; therefore, the blood-feeding habit could be indulged in throughout the year. Although our discovery of blood-feeding was made during the rainy season, the habit seems not to be restricted to this time of year. On 4 August 1897, during the middle of the dry season (June-December), the finch-booby relationship was noted by Drowne (*in* Rothschild and Hartert, 1899:110) who saw *G. difficilis septentrionalis* climbing on a booby's back and pecking in the feathers—a behavior he believed to be directed at finding parasites.

A propensity for feeding on blood was noted by Gifford (1919:242) on 24 September 1906, who discovered that whenever he shot a *difficilis* on Wenman Island, several others would gather about it and peck at the blood.

TABLE 1

Summary of Observations on Boobies, Wenman Island, Galápagos

Date	*Remarks*	*Authority*
30 January-1 February 1964	*Masked:* adults on nesting territory; some nests with eggs; several naked young, 1-2 weeks old.	Field observations of Bowman and Billeb.
	Red-footed: some nests with young; others with eggs.	Same.
"First days of February" 1901	*Masked:* many young and a few eggs; young of all ages and eggs well incubated.	Beck, *in* Rothschild and Hartert, 1902: 407.
	Red-footed: nearly all nests with young in various stages of development, but a few with fresh eggs.	Beck, *in* Rothschild and Hartert, 1902: 406.
22 February 1962	*Masked:* several hundred pairs.	Lévêque, 1964:21.
	Red-footed: all stages; courting adults up to flying young.	Lévêque, 1964:20
4 August 1897	*Species ?:* "noticed some of the finches climbing on a booby's back and pecking in the feathers. . . . "	Harris, *in* Rothschild and Hartert, 1899: 110.
24 September 1906	*Masked:* breeding.	Gifford, 1913:90.
	Red-footed: most birds without nests, but sitting about in trees and bushes; no eggs discovered; young bird just able to fly, taken.	Gifford, 1913:87.
13-21 December 1898	*Masked:* abundant nesting activity; eggs and young.	Snodgrass and Heller, 1904:245.
	Red-footed: nests numerous.	Snodgrass and Heller, 1904:247.

Other Foods of the Wenman Finch

Although blood might, conceivably, be a mainstay in the diet of a few individuals of *difficilis,* it probably constitutes only a minor part of the total food intake of the species. *Difficilis* feeds on a wide variety of items. In January 1964 we saw birds pecking into crevices in the bark of *Croton* bushes where insects are known to occur. More than any other Galápagos finch, *difficilis* on Wenman Island is "earthbound." Hopping about the rocks and ashy soil, this species turns over leaf litter using the bill, and on one occasion, was seen to overturn a small stone (one inch in diameter) using the feet. Grasping the stone to be moved with one foot and anchoring the other foot on a coarse-textured outcrop of lava, the finch was able to dislodge the small stone by pulling strongly with both feet. The bird then searched the exposed ground but was not seen to pick up anything. C. M. Harris (*in* Rothschild and Hartert, 1899:110) observed *difficilis* on Wenman Island eating from a dead seal carcass, and R. H. Beck (*in* Rothschild and Hartert, 1902:399) remarked that most of the cactus blossoms were eaten out by this species in August. We saw one bird examining the feces and cloacal region of a half-grown Masked Booby immediately after the nestling had defecated. By these reports, then, we know the *difficilis* is very resourceful in its search for food.

All our observations indicate that *difficilis* feeds on the blood of only the Masked and Red-footed Boobies. To what extent other large seabirds serve as feeding hosts is unknown, but both the Fork-tailed Gull *(Creagrus furcatus)* and the Frigate-bird *(Fregata minor ridgwayi)* nest in considerable numbers on Wenman Island and could, conceivably, be victimized by *difficilis.*

Advantages of Blood-eating to the Finches

The symbiotic relationship between finch and booby has obvious advantages for the finch, which thereby obtains a liquid proteinaceous meal. Without disrupting its internal water balance, *difficilis* can apparently feed on booby blood (which is approximately isotonic with its own) in the absence of a ready source of fresh drinking water. Bartholomew and Cade (1963:518) point out that most landbirds cannot successfully drink water with a salt concentration of more than about one per cent. However, this is the approximate salt concentration of avian blood and it is possible that *difficilis* can obtain water from this source without any specialized excretory mechanism. Of course, there is also the possibility that *difficilis* drinks sea water and can excrete, via the kidneys, excess salts, as has been demonstrated for the Savannah Sparrow (Cade and Bartholomew, 1959) and for the Zebra Finch (Oksche *et al.,* 1963). Fresh water is occasionally available in small surface puddles during the rainy season (January-May) and, during the dry season (June-December), as large droplets on the spiny vegetation resulting from the condensation of mists *(garúa)* that blow in from the sea. Although we did not observe it in 1964, *difficilis* might obtain moisture from the pulp of the prickly-pear cactus, as is the case in some geospizines on other islands (Bowman, 1961:29). Whether or not blood-eating causes a physiological problem, the fact that this habit is widespread in the population of *difficilis* on Wenman Island would seem to be *prima facie* evidence of its value to the birds as a source of food and possibly water.

Advantages to the Boobies

What the benefits might be for the boobies in their symbiotic relationship with the finches is not so apparent. Disadvantages are obvious. The minor wounds on the elbows of the boobies seem not to hamper their flying ability. However, open wounds are sites for infection, which could lead directly to the death of the booby; or, by inhibiting its ability to fly, the wound could prevent the booby from feeding and indirectly lead to its death. The elbow sore is undoubtedly the cause of some discomfort to the booby, especially when opened repeatedly by finches and molested by flies (Figure 6).

There is some evidence to suggest that the boobies are troubled with ectoparasites, especially hippoboscid or louse-flies. During the heat of the day many such flies can be seen scurrying about the shaded feathers of the head and neck of the Masked Boobies (Figure 11). Such a heavy infestation of these and possibly other parasites surely must be a source of some discomfort for the boobies. Indeed, this is suggested by the interesting observation of Beck (*in* Rothschild and Hartert, 1902:407) who wrote: "A pair of old birds were picking lice from each other's necks seemingly, exactly as a couple of horses will scratch each other." It is not clear whether Beck was referring to true bird lice (Mallophaga) or to louse-flies (Hippoboscidae). We did not observe the finches grooming the boobies for ectoparasites, but there is a distinct possibility that it occurs. Such behavior is implied by the remarks of Drowne (*in* Rothschild and Hartert, 1899:110) who saw *difficilis* standing

Figure 11. Masked Booby with numerous hippoboscid flies (probably *Olfersia fossulata* Macquert) on the shaded portions of head and neck.

on the backs of the boobies pecking into the feathers "... probably in search of parasites." Drowne's field companion, Harris, also observed the Wenman finch "... feeding on vermin on the boobies, standing on the feet and backs of the boobies for that purpose" (*in* Rothschild and Hartert, 1899:91).

Significance of Blood-eating

Blood-eating, as a *primary* method of feeding, is not known to occur in any other species of bird. There are various isolated instances of birds ingesting blood in the course of feeding on other items of food. For example, domestic farm animals such as sheep, hogs, cattle, and horses have been the victims of predatory attacks by Black-billed Magpies *(Pica pica)* in various parts of the United States (Schorger, 1921; Stephens, 1921; Berry, 1922; Kalmbach, 1927; and others). During these attacks the magpies seem to be most interested in flesh and may initially focus their pecking at saddle sores (horses), branding sores (cattle), shearing sores and maggot-infested sores (sheep). In other cases healthy animals, entirely free of sores, have been attacked. The eyes (calves), stomach and rectum (cows), lumbar muscles and underlying kidneys and intestines (sheep) have been involved in these onslaughts, and blood must surely have been consumed, at least casually. Similarly, the African Ox-pecker or Rhinoceros Bird *(Buphagus africanus)* is known to eat large holes in the fleshy parts of the back of wild oxen and domestic cattle (Knowlton, 1909:354-355). The Red-billed Ox-pecker or Tick-bird *(B. erythrorhynchus)* feeds on ticks (primary food) infesting domestic stock and wild game and at times drinks the blood (secondary food) when it oozes from an animal and clots at a spot where several ticks have been attached. It is alleged that the birds deliberately keep these wounds open, even enlarging them, in order to obtain more blood (Van Someren, 1956:426-428). Finally, the Kea Parrot *(Nestor notabilis)*, which lives in the mountainous regions of South Island, New Zealand, is known to eat the meat from deer, goat, and sheep carcasses, and also to pick at the flesh, fat, kidneys, entrails, and blood from the backs of healthy sheep (Marriner, 1909:72 ff.).

Behavioral Similarities in Blood-eating Birds

Several features of predatory behavior are common to most of the forementioned species: (1) The attacks, at least those on domestic stock, occur at times when natural foods are less available. (2) Only some individuals of a local population necessarily participate in predatory feeding. (3) The predatory habit, when it involves domestic stock, is presumably learned, because local control of the offending individuals appears to stop the spread of the habit. (4) Perfectly sound animals, but more often those with sores or wounds, are the object of predatory attacks. (5) Most, if not all, of these "predatory" species are quite omnivorous in their feeding habits. (6) The attacks may be initiated by a single bird or by the mass attack of a group. (7) All the species mentioned show a singular lack of fear of animals (other than man), or are otherwise very curious about their environment and "bold" in their investigation of it.

Possible Origin of Blood-eating Habit

Before proposing an explanation for the origin of the blood-eating habit in *difficilis* on Wenman Island, we need to consider the possible inter-relationship of a variety of facts regarding the boobies, the finches, and the hippoboscid flies.

Both the Red-footed and Masked Boobies are heavily infested with ectoparasites, particularly hippoboscids. These are most obvious on the white plumage that is typical of the adult Masked Booby as well as the white-phase Red-footed Booby. The heavy infestation is probably a source of irritation to the boobies, to judge from the report of mutual grooming for parasites in the Masked species.

Geospiza difficilis septentrionalis is a permanent resident on Wenman Island where it characteristically, but not exclusively, forages at ground level. The omnivorous habit is probably a reflection of critical seasonal shortages of food, thereby necessitating a high degree of adaptability in feeding behavior. The elongate, smallish, conical bill is sufficiently generalized to permit these diverse feeding habits. The use of the feet to hold items of food (Bowman, 1961:25 ff.), to turn over small stones, and to scratch on the ground are examples of the flexibility in behavior in *difficilis.*

To judge from our personal experience on other peripheral islands (e.g., Hood and Tower; see Figure 1), the availability of food is greatly reduced during the dry season (June-December) when fresh water is probably least available.

The absence on Wenman Island of Barn and Short-eared Owls and the Buteo Hawk—the typical avian predators on finches on other islands in the Galápagos—and the complete absence of terrestrial mammals, including man, has promoted a tameness in *difficilis* that is most striking. This species displays an insatiable curiosity about its environment, as do the "tool-using" Galápagos finches, *Cactospiza pallida* and *C. heliobates* (cf. Bowman, 1961; Eibl-Eibesfeldt and Sielmann, 1962; and Curio and Kramer, 1964).

Regarding the ectoparasites of the boobies, relatively few have thus far been collected. Three species of mallophagans of the genus *Lipeurus* have been taken only from the Red-footed Booby on Culpepper Island (Kellogg and Kuwana, 1902:491). The hippoboscid fly, *Olfersia fossulata,* was collected on Wenman Island (Coquillett, 1901:379), presumably from a sulid (either Masked or Red-footed Booby), which, according to Bequaert (1953:250), is the usual breeding host for this parasite.

One of the features of the ectoparasites of the Galápagos is the ". . . unusual eccentricity of the occurrence . . . on the various bird hosts. A species of Mallophaga, obviously normal in such a strictly land bird as *Geospiza* would be found to occur occasionally on such strictly maritime birds as terns . . . . On the rocks of the islands maritime and land birds sit closely huddled, actual contact of the bodies often occurring" (Kellogg and Kuwana, 1902:458).

According to Bequaert (1953:225), a large body size may, in part, account for the heavier hippoboscid infestation on some birds, since it provides greater feeding area, more blood, and more hiding places. The boobies seem to meet these criteria, which accounts for the heavy population of hippoboscids on them. Furthermore, the hippoboscids are most conspicuous on the white plumage of the boobies, and their reluctance to take flight from the host makes them ideal prey for any small finch bold enough to attempt their capture.

The blood-eating habit of *Geospiza difficilis septentrionalis* may have arisen in the following way. In their foraging on the ground, the finches come into close proximity to nesting and loafing Masked Boobies. During the dry season, when free-living insects are less available, the boobies present a concentration of black hippoboscid flies that are very visible on the white plumage (Figure 11). The agile and fearless finches readily pursue the hippoboscids on the boobies, and, as a result of their success, turn regularly to this new and near-constant source of food. The finches acquire a taste for blood, possibly by eating blood-engorged flies, or by overzealous stabbing at flies amidst the plumage, causing an accidental puncture of the booby skin. When the white plumage of the booby becomes accidentally smeared with blood, non-hippoboscid flies are attracted to it, which serves to heighten the interest of the finches in the boobies.

The elbow region appears to be the preferred location for blood-feeding by the finches. It is probably not the best location for hippoboscids because it is readily preened. It is likely, therefore, that the elbow region has been selected by the finch after the blood-eating habit was learned, because not only is it safest from attack by the booby (i.e., allows maximum time to elude the swing of the booby's bill) but also the skin is lightly feathered and is relatively near the surface.

Conclusions

The blood-eating habit appears to have arisen originally as a mutualistic relationship which later changed into a primarily parasitic one. It probably developed first in association with the Masked Booby from which it spread to the Red-footed Booby. The habit is probably learned and is transmitted by tradition from one generation to another. Although not observed by us, it is likely that the finches still feed upon hippoboscid flies, and in this way the boobies receive some benefit from the symbiosis, although the association is biased in favor of the finch.

This discovery, a century and a quarter after Charles Darwin first met with this unusual group of birds, points up the need for greater efforts on the part of biologists to become better acquainted with one of the most remarkable natural laboratories of evolution in the world. The appearance, in recent decades, of several large and seemingly definitive works on the Galápagos finches, has, perhaps, given the erroneous impression to many ornithologists that all the important problems bearing on these birds have been solved. Nothing could be farther from the truth; and we predict that in the years ahead some of the most significant ornithological studies will be based on research carried out in the Galápagos. No one would be more surprised than Darwin himself, were he to know how few biologists have taken up the many challenging problems presented by the Galápagos finches, the birds that inspired many of his views on the origin of species.

Summary

Blood-eating is described for the Wenman Island race of the Galápagos "Sharp-beaked Ground-finch" *(Geospiza difficilis)*. As a primary method of feeding this habit is unknown in any other avian species. Instances of secondary feeding on blood are mentioned and compared with the feeding habit of the finch. The host-parasite relationship between booby and finch and the possible origin of the blood-eating habit are discussed.

Acknowledgment

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BIOTELEMETRY: A NEW TECHNIQUE FOR WILDLIFE RESEARCH

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Biotelemetry, or radio-tracking, may be defined as an electronic technique for obtaining qualitative and quantitative data about an organism and its environment by remote means through space. This paper attempts to familiarize ornithologists with the development and use of the technique.

My interest in radio-tracking devices began in 1958 after I had made an initial inquiry into the navigational ability of nesting Purple Martins *(Progne subis)* by conducting homing trials. Adults were captured at one colony, transported to distant points, and released. The results (see Southern, 1959), while providing some information on speed and accuracy of return from release points, shed no light on the courses taken by the birds in their return and gave no indication of how they responded to environmental conditions prevailing along the courses. Griffin (1963), conducting somewhat similar studies with Herring Gulls *(Larus argentatus)*, followed the birds from release points in an airplane. His results, while suggesting useful clues to navigational ability, still left much to be desired.

Aware that a radio-tracking system would provide a fruitful means of studying the navigational ability of Purple Martins, I started looking into the possibility of devising some types of transistorized radio equipment to track the birds. But the effort was discouraging—the idea seemed hardly feasible. Fortunately I was not alone among field biologists in needing a radio-tracking system, and it was not long before equipment was developed to the point where an interdisciplinary conference was held at the American Museum of Natural History in 1962 to acquaint interested investigators with available equipment and its uses. The symbol of this conference was a Purple Martin wearing a small transmitter. The proceedings (Slater, 1963) provided an introducton to the development of telemetry as a tool in wildlife research.

Thus far radio-tracking techniques have been used most extensively in studies dealing with mammals. While several investigators have attempted to equip birds for field studies, few have done so successfully. This is understandable since birds are flying organisms and consequently present special problems. Besides being more mobile and difficult to track, birds have much less capacity for carrying equipment than mammals because they cannot tolerate equipment that interferes with their streamlining, center of gravity, wing movements, and—if they are nesting—with incubation patches. The difficulties of surmounting both these physical deterrents and special electronic problems have combined to discourage most would-be investigators.

The emphasis of the several papers published on projects that incorporate radio-tracking systems has been primarily on the types of equipment used and the application of different types to particular organisms, with only token reference to the biological data obtained. In other words, the interest has been more in the technique than in the acquisition of information. Now that telemetry systems are available and familiar to many investigators, I am hopeful that their principal aim will be henceforth toward the gathering of quantitative data which have not heretofore been within reach.

In the following pages I will describe briefly my telemetry system and review many published accounts dealing with the application of other such systems to field studies of environmental conditions, mammal movements, avian-activity patterns, fluctuations of egg temperature during incubation, and physiological changes during flight. I will not include the many important papers dealing with the use of telemetry in aero-space biology, in medical research, or in laboratory-conducted behavior studies. Readers interested in these possibilities should refer to the work of Essler and Folk (1961, 1962), Geddes (1962), and Mackay (1963). Many of my comments and examples will necessarily be drawn from my own experiences with the technique.

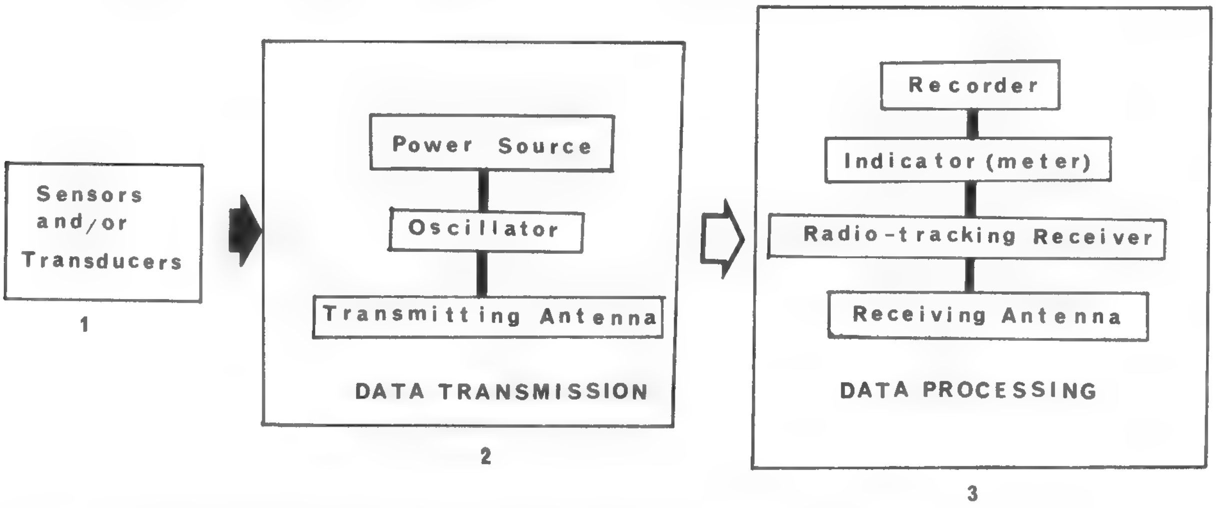


Figure 1. Block diagram showing the major parts of a telemetry system.

The Tracking System

The scope of a biotelemetry system may be divided into three essential parts: (1) Acquisition of biological data by means of various sensors and transducers; (2) data transmission and signal conditioning; and (3) data receiving and processing for interpretation by the investigator. Systems used in physiological or environmental studies usually consist of all three but the ones used solely for tracking or locating animals include only Items 2 and 3 (see Figure 1).

In order to satisfy Items 2 and 3, we must have transmitters for attachment to animals; receivers for picking up transmitted signals; and direction-finding antennas for locating the animal's position. These requirements are met in my tracking system—in part, a modification of the one described by Cochran and Lord (1963) and representing the cooperation of several individuals—as follows:

Transmitters.—These units must be small, lightweight, powerful, long-lived, reliable, and operated on suitable frequencies. My units are crystal-controlled, transistorized, battery-powered oscillators having loop antennas.

I construct my own units and the size and weight correspond somewhat to the size of the bird being studied. For instance, transmitters for Bobwhites *(Colinus virginianus)* weigh about six grams; those for gulls about 40 grams; and those for Bald Eagles *(Haliaeetus leucocephalus)* about 80 grams. The main reasons for increased weights are (1) bigger birds carry larger power supplies thereby increasing transmitter life, and (2) extra encapsulation is usually necessary for protecting units from larger birds. Transmitters are of two types: continuous-signal and pulse-signal models. Mercury cells serve as power sources. Silicon-rubber compounds, epoxies, and fiber glass are used for encapsulating transmitters.

Gull-sized transmitters have aluminum-loop antennas about seven inches in diameter and half an inch wide. The transmitter package is constructed along the antenna base and is about 0.50 x 0.50 x 2 inches (Figure 2). Units are attached to the bird's breast by means of nylon or plastic harnesses (Figure 3). My receivers have a frequency-band width of 100 kilocycles (various frequencies between 26 and 151 megacycles have been used) and transmitters may be spaced about five kilocycles apart thereby permitting 20 units of different frequencies to be operated simultaneously with as many individual animals to be recognized. By using a combination of pulsed- and continuous-signal transmitters (see Southern, 1963a), it would be possible to have at least 40 different signals operating at one time. Various methods could be used to increase this total several times.

Components for each transmitter cost between $8.00 and $10.00 and the average biologist, with experience, can construct one in about an hour. A modest amount of laboratory equipment is required (see Southern, 1963a, or Verts, 1963). Custom-made transmitters cost about $35.00. Figure 4 presents a view of the general set-up required for constructing transmitters.

Transmitter life is a function of the type of battery and the power consumed. The life of a system can be estimated on the basis of the following formula:

$$\text{LIFE IN HOURS} = \frac{\text{MILLIWATT HOURS OF BATTERY}}{(\text{VOLTS}) \times (\text{MILLIAMPS CONSUMED})}$$

My gull-sized units operated for about 60 days, eagle transmitters for about 90 days, and quail units for about seven days. It is possible to have gull-sized transmitters operate for about one year. During navigation studies I designed my units so that transmission would cease after two weeks, thereby freeing that particular frequency for re-use.

Tracking ranges for birds perched near ground level averaged about two miles (0.5 to 3.5 miles). Flying birds have been tracked at distances up to 30 miles from the receiver. Local conditions (power lines, soil types, irregular terrain, etc.) may severely limit tracking ranges. Often the formulas used by engineers for predicting transmitter life and range have proved unreliable when applied under field conditions.

Radio-Tracking Receivers.—I have two types of receivers. One type may be used either as a portable or mobile unit. It is a crystal-controlled double-conversion superheterodyne with a sensitivity that gives good bearings with signals of less than one-tenth microvolt. It weighs about six pounds and is easily carried by means of a shoulder strap. Figure 5 shows this type of receiver.

The second type of receiver is a converted army command unit (BC 453) which is operated only as a mobile unit (Figure 6). It is comparable to the

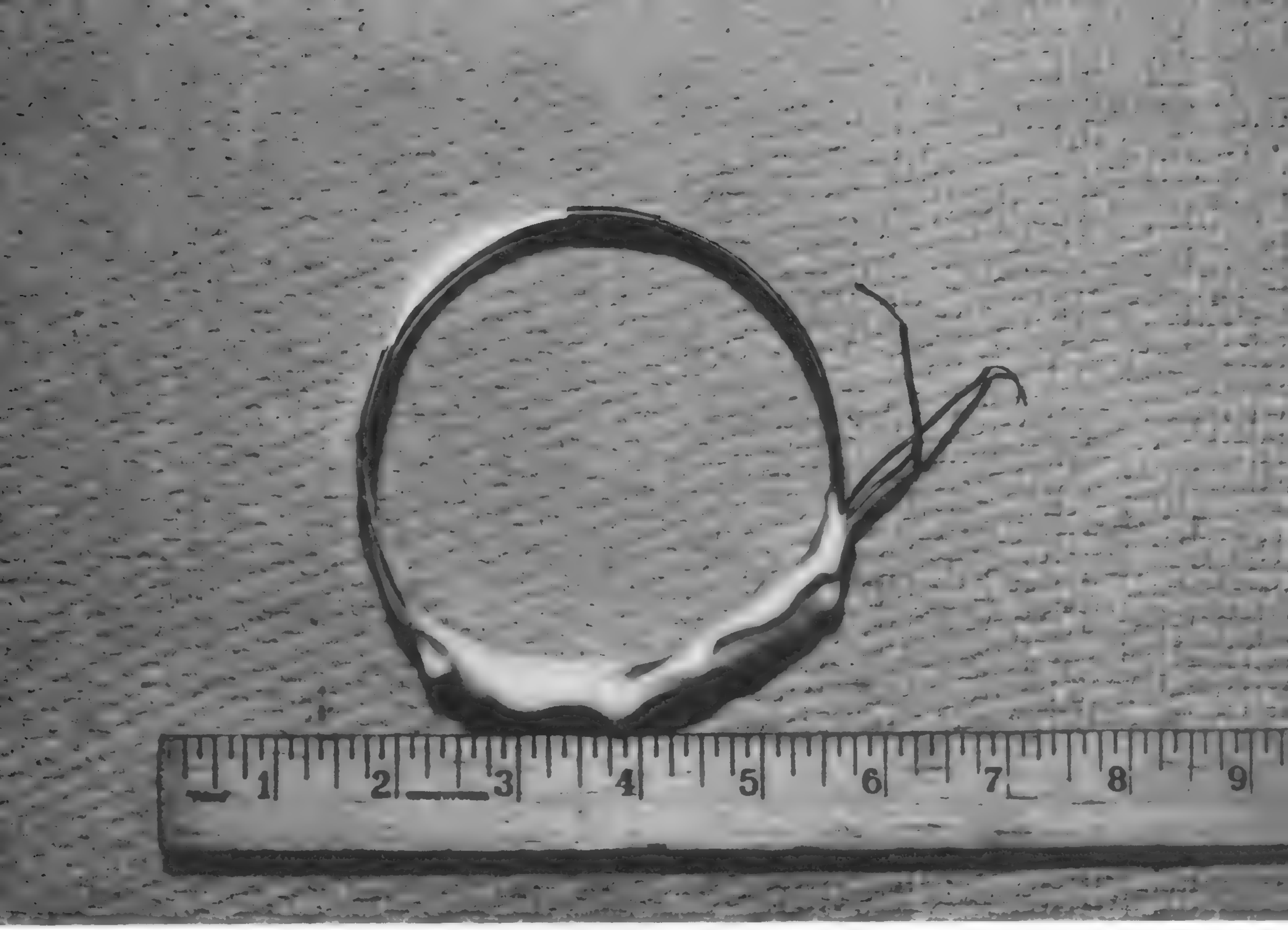
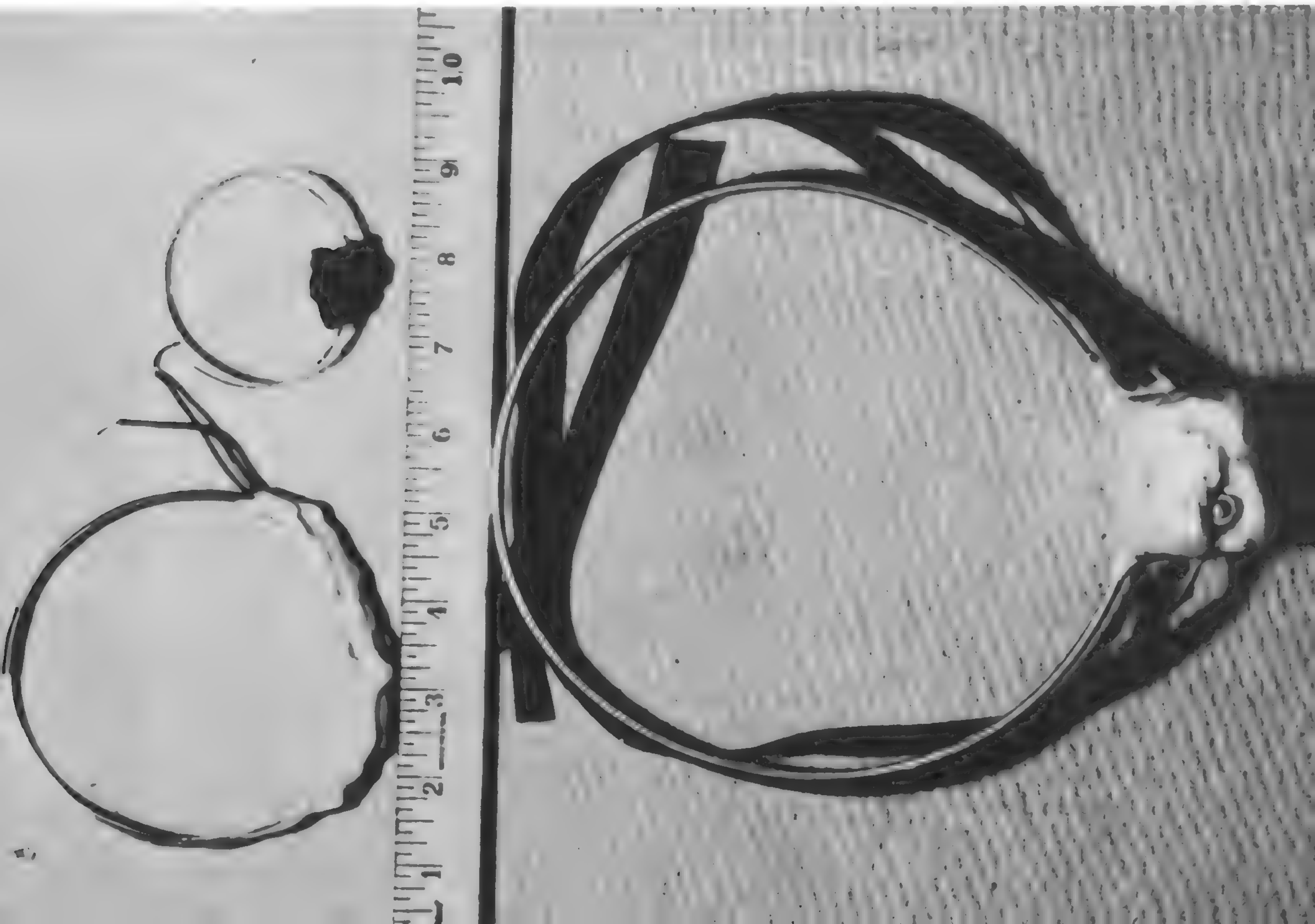


Figure 2 *(above)*. Transmitter for Herring Gulls. Wires are connected just prior to use and encapsulated with a fast-drying, silicon-rubber compound.

Figure 3 *(below)*. Three sizes of transmitters designed for different species of birds. Top left, transmitter for Bobwhites; bottom left, unit for Herring Gulls; right, the device used on Bald Eagles. The ruler is calibrated in inches. Two harness straps (black) are attached to the eagle transmitter.



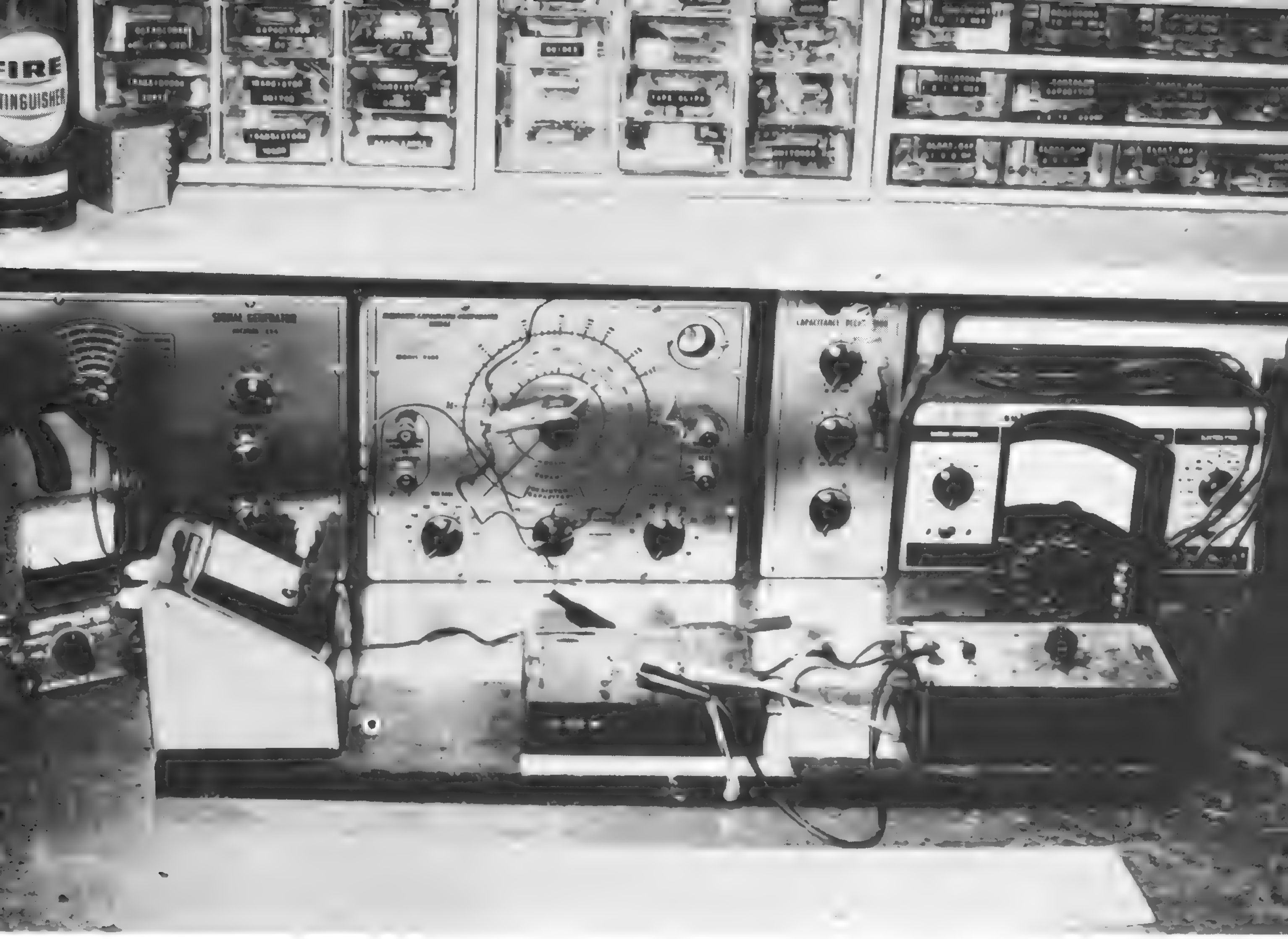


Figure 4 *(above).* Partial view of the author's electronic facility for constructing transmitters. Essential items are in the foreground, from left: the transistorized power-supply, signal-strength (absorption) meter, bread-board circuit for matching components, resistance substitution box, and VOM meter.

Figure 5 *(below).* A transistorized tracking receiver being used as a portable unit. Note the hand-held loop antenna and the headphones.

transistorized model in performance. The former unit costs about $540, the latter about $180. A receiver is the most expensive single item in the telemetry system and the biologist must have it custom made. My units were constructed by Sidney Markusen of Cloquet, Minnesota. James Ashe of Freeville, New York, also provides receivers.

Direction-Finding Antennas.—I have used three types of antennas: (1) hand-held loops; (2) vehicle roof-mounted loops; and (3) permanent station yagis. Each type served a particular purpose. An antenna was mounted in association with a compass rose and had a needle aligned so as to indicate the position of the sharpest antenna null (the point at which the signal strength meter or headphones register a zero, or near-zero reading; generally at right angles to the strongest signal). The null was used to give a bearing on the animal's location in relation to the receiving station. The strong signals were used for general tracking. The antenna was rotated in order to obtain the best reception of these indicators. Triangulation by two units was essential for following rapidly moving birds during navigation studies. One unit was satisfactory for following more sedentary birds. Tracking accuracy was within about one degree. However, I was usually unable to check accuracy during actual homing trials.

Signals may be recorded on magnetic tape recorders or strip chart recorders for later analysis of behavior patterns, etc. Appropriate jacks are built into the receiver for connecting leads from the above and from headphones. A signal strength meter is built into the receiver.

More detailed information on this type of tracking system may be obtained by referring to Cochran and Lord (1963), Lord and Cochran (1963), Southern (1963a), and Verts (1963).

Application of the Technique

To Environmental Data.—A system for telemetering ambient temperature, light intensity, relative humidity, barometric pressure, soil moisture, or other environmental factors for which transducers are available would be of unlimited value to field biologists. Such a system would eliminate much of the necessity of constantly checking thermometers or reading other instruments. Cole (1963) has successfully telemetered ambient temperatures with an accuracy of 0.25° C. Apparently he did not telemeter data for the other parameters listed above, but he indicated that the basic circuitry described in his paper, with a few modifications, would probably suffice. His system is modest in cost and uses a transistorized pocket radio as a receiver. Equipment of this type could be placed in bird nests located in trees, burrows, or cavities and provide a continuous record of, for instance, temperature changes within the nest cup. DeVos and Anderka (1964) have also developed a system for telemetering microclimatic data. While possibly not as versatile as Cole's, their transistorized field equipment can receive and transmit (107 megacycles) data recording up to 24 channels of climatic variables over distances of 20 miles or more. Continuous recorders are used at receiving stations. Approximate cost involved in setting up a transmitting and receiving station is $900.

To Mammal Movements.—Several studies come under this category and at least five different tracking systems are involved. Eight studies will be discussed briefly.

Grizzly Bears. Frank Craighead *et al.* (1963) obtained a prototype tracking system through the Philco Corporation in 1960, and equipped their first captured grizzly bear *(Ursus horribilis)* with it in 1961. The 2- to 2.50-pound

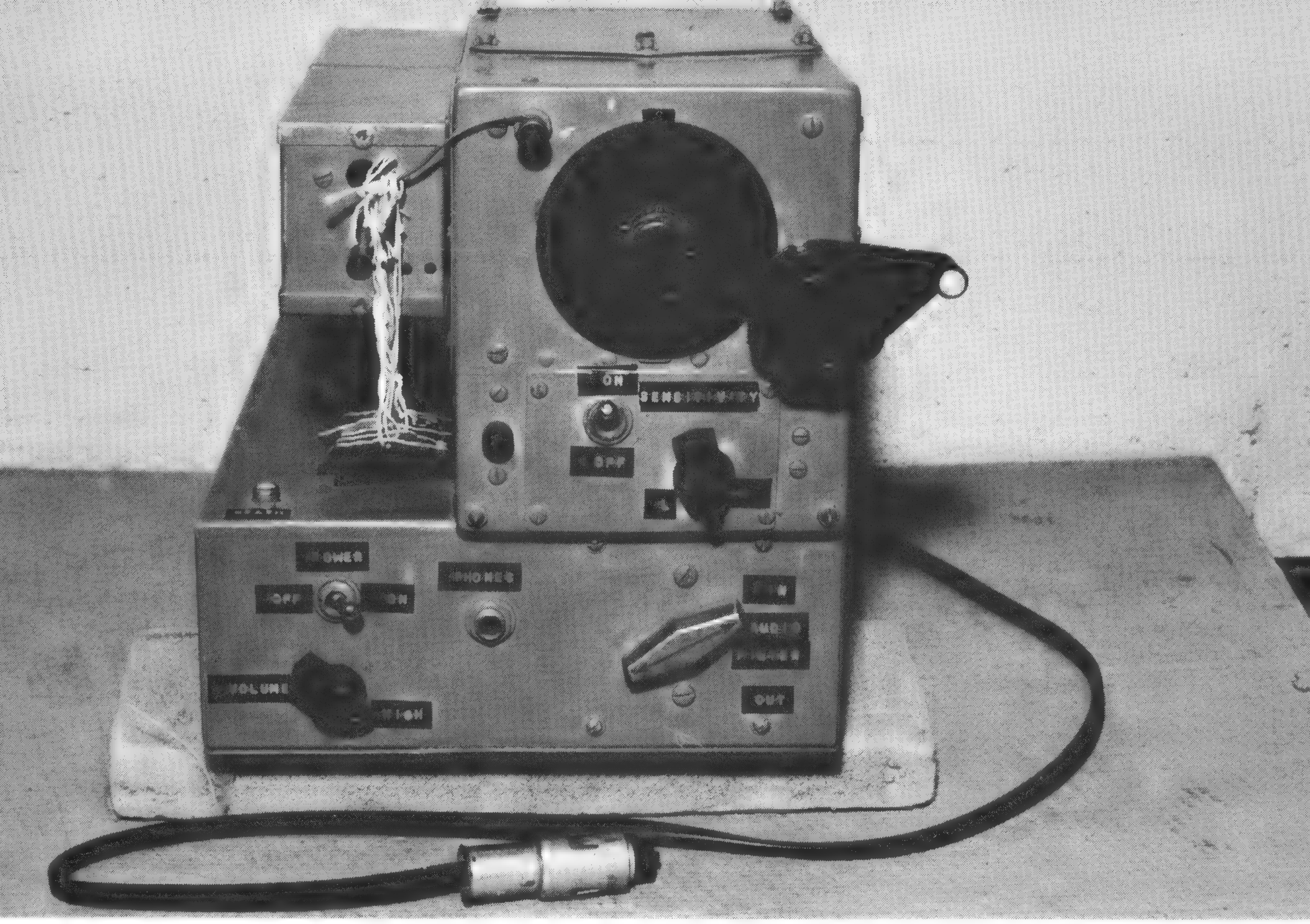


Figure 6. A connected Army Command Tracking Receiver. Power cord is inserted into an automobile cigarette-lighter socket.

transmitter, designed as a collar and operated at 32.02 megacycles, had a life of about one month and a maximum effective tracking range of 0.5 mile in rolling, sparsely wooded country. Tests indicated their accuracy of plotting a bear's position to be within about 50 feet. One bear was tracked for 30 days. Direction-finding receivers were used in vehicles or as portables. This equipment enabled the researchers to obtain information on bear movements, range sizes, feeding habits, activity periods, hibernation, and intraspecific relationships. The results represented a significant improvement over data obtained by previous methods.

Woodchucks. Two investigators, LeMunyan and Merriam, used different telemetry systems to study the habits of this species.

LeMunyan *et al.* (1959) described transmitters suitable for implantation subcutaneously or in the peritoneal cavity of woodchucks *(Marmota monax).* The size of the units probably restricts their use to animals of this size or larger. Terrestrial range was 25 yards but subterraneous range dropped to about 18 yards. Average transmitter life was 161 days. Each transmitter cost about $25.00 before labor. It was believed that physiological (i.e., heart activity) information could also be telemetered by this unit.

Merriam (1963) utilized low frequency (100 to 150 kilocycles) telemetric equipment. During 1961, he implanted transmitters subdermally in 21 woodchucks. The 8- x 2-centimeter transmitters had a life of three to four months, cost about $10.00 (plus 10 hours labor), and weighed approximately 45 grams. Transmission range was short and receiving loops were placed at entrances to burrows. Merriam used an automated receiving-recording system which increased the continuity of movement records for each animal. The receiving system recorded the identity of marked woodchucks in each of 50 burrows every five minutes. During 22 days, marked animals were located 8,921 times.

Success in tracking was about 65 per cent. Seventy-two per cent of the data received were entirely trustworthy. Each discarded datum represented the loss of five minutes, rather than days or weeks as would be the case with some other methods. The technique, as well as the results, approached what he considered to be an ideal situation. There was no comparison between the increased quantity of data received this way and that obtained previously by marking and retrapping.

Striped Skunks. Verts (1963) described techniques and equipment for radio-tracking skunks *(Mephitis mephitis).* His system, also a modification of that described by Cochran and Lord (1963), included collar-type continuous-signal transmitters as well as mobile and portable receivers. Verts outlined in detail the techniques for constructing the types of transmitters he used on skunks. Locations of animals were determined by the triangulation of several bearings. Accuracy of positioning was about ± 25 feet at 0.25 mile and about ± 25 yards at 0.50 mile. In some cases different types of skunk activity could be distinguished by means of variations in the rhythm of the received patterns of signal intensity. Verts tracked skunks for about one year while employed by the Illinois Natural History Survey. Since then the system has been used in a continuation of this project and in a study of red foxes *(Vulpes fulva)* by Gerald Storm (correspondence).

Porcupines. Marshall and others (1962, 1963) attached transmitters by means of modified dog harnesses to three porcupines *(Erethizon dorsatum).* Their locations were determined at dawn, midday, and dusk. Most of the positionings were verified by homing on the radio signals and making sight observations of the animals. Data were obtained on movements, activity, habitat selection, types of shelters, and the behavior of porcupines in relation to mosquito attacks. Marshall's equipment will be discussed below under Ruffed Grouse.

Malayan Rats. During 1963, in connection with leptospiroses studies, Sanderson and Sanderson (1964) used modifications of Cochran's *(loc. cit.)* telemetry equipment to track successfully three species of rats *(Rattus mulleri, R. sabanus,* and *R. jalorensis)* in Malaya. Rats weighing between 106 and 365 grams were equipped with transmitters weighing from 16 to 32 grams. Ground-to-ground tracking range varied from 50 to about 350 yards. Nine wild rats, which remained in heavy cover and/or moved only at night, were tracked for periods of one to 16 days. This preliminary report clearly indicated the value of radio-tracking systems to particular studies. The Sandersons obtained information on home ranges, linearity of ranges, overlapping of individual ranges, overlapping of species ranges, movements, periods of activity, and interspecific variations in habitat preferences. They were also able to collect soil samples from areas of known rat activity and examine them for leptospires.

Raccoons. Ellis (1964) during 1961-62 tracked seven raccoons *(Procyon lotor)* for a total of 33 nights. Transmitters and receivers were of the type designed by Cochran *(loc. cit.)* and discussed by Verts *(loc. cit.).* The resulting home range and population data related the following topics: Diurnal and nocturnal movements; cursorial and arboreal habits; minimum distance traveled per hour; average distance traveled per night; feeding patterns; and movements of individuals in relation to population densities. The maximum error in plotting an animal's position was about 20 yards at 0.25 mile. Fixes were usually taken at two-hour intervals, but occasionally an animal moved a sufficient distance during 15 minutes or so to permit a second accurate bearing. The major difficulty in obtaining fixes was caused by blocking of the signal by topography, heavily foliated woods, or emissions from power lines.

Mice. Rawson and Hartline (1964) used telemetry in homing studies of deer mice *(Peromyscus maniculatus gracilis).* Their miniature transmitter was similar in design to Cochran's *(loc. cit.),* weighed 2.5 to 2.7 grams, emitted pulsed-signals at 27 megacycles, and was implanted subcutaneously. It was not crystal-controlled and transmitter life was probably very short. Signals from two transmitter-equipped mice were detected by portable receivers at distances of about 45 to 60 meters. Transmitters were recognized by the repetition rate of pulses which can be adjusted by the proper selection of components during construction. The temperature sensitive units oscillated at all subcutaneous temperatures but not at or below 25° C. The ratio of transmitter weight to body weight was 1:10. Units were implanted beneath the skin in a mid-dorsal position extending from the lower thoracic through the lumbar region. The transmitter caused no difficulty in locomotion. The mice climbed trees and moved through dense vegetation in much the same way as normal mice. In addition, they kept their fur well groomed. The telemetry techniques used in this study indicated the spatial movements of mice, the periods of activity, the location of nests, and appeared superior to conventional trapping methods for determining homing speeds of small mammals.

To Avian-Activity Patterns.—Only three papers can be cited under this heading. Two of these pertain to the actual applications of telemetry in ornithological research whereas the third simply concerns a tracking system that was developed for birds.

Ruffed Grouse. Marshall (1963) and his students have spent considerable time adapting tracking equipment to birds in attempts to obtain field data on movements. His transmitters weighed between 37 and 45 grams and had a life of about 1,160 hours. Receiving ranges varied from 0.75 mile up to 1.89 miles, depending on the type of antenna (e.g., portable or fixed) being used. The frequency range was 150.815 to 151.085 megacycles.

As has been true in many instances, the battery life proved to be only one-fourth of that predicted. Transmitters were placed on the backs of Ruffed Grouse *(Bonasa umbellus)* by means of yokes. Since Marshall's prototype transmitters upset the balance and/or flight dynamics of grouse, the emphasis was switched to porcupines (see above). However, a new transmitter model weighing 37 grams was later used successfully in grouse studies. With these units the activity of grouse appeared normal and flight was unimpeded. Two recovered birds showed no signs of injury from the harnesses.

Accuracy of the system in locating transmitter-equipped grouse was dependent on the accuracy of azimuth determinations obtained by directional antennas. At seven-eighths of a mile the error in azimuth determinations averaged five to six degrees (99 determinations). When the intersection of two azimuth readings was used to locate a transmitter, the error averaged 184 feet at distances of less than three-eighths of a mile and 301 feet at distances of three-eighths to three-fourths of a mile.

Data were obtained on the location of birds, types of ground cover used, ground conditions in relation to weather, and behavior (resting, walking, flight, and feeding on buds). Many more locations were obtained for grouse by means of this technique than by conventional methods, such as color-marking. In addition, evidence of owl predation was found by plotting the position of "downed" transmitters and locating the units.

Pigeons. Singer (1963) described a system designed to track pigeons *(Columba livia)* during flight. Transmitters weighed 2.5 ounces, measured about 1.5 by 0.75 inches, and had a three-foot-long trailing wire antenna. Singer mentioned that micro-miniaturizing techniques could be applied to this design, thereby reducing its over-all size by 50 to 75 per cent. However, the lack of a power supply of comparably reduced size would remain a major problem. The units operated at 140 megacycles.

A transmitter was attached to the pigeon's back by means of straps and a canvas container which encircled its neck and breast. Two pigeons were tracked for distances up to 25 miles. Apparently considerable time was required for pigeons to become accustomed to carrying these units. Louis C. Graue (correspondence) is currently using similar equipment with this species during avian navigation studies.

Bald Eagles, Gulls, Mallards, and Bobwhites. My first tracking equipment was ready for field tests during the summer of 1962. Although I still lacked models small enough for Purple Martins, I did have units that could be attached to Ring-billed Gulls *(Larus delawarensis)* and Herring Gulls. The results of these tests were satisfactory and confirmed my belief that it was possible to follow the flight paths of birds during homing experiments. I spent most of the summer becoming familiar with operation of the receivers, plotting direction-finding accuracy, determining tracking range, and observing wing-clipped, transmitter-bearing gulls that were released on Douglas Lake (Cheboygan County) in northern Lower Michigan. At the end of the summer it was obvious that further tests were required in order to determine more precisely the limitations of my equipment and to learn the variables affecting its operation. Therefore, during the fall and early winter I attached transmitters to six Bald Eagles (see Southern, 1964), members of a population wintering along the Mississippi River in northwestern Illinois. By means of radio-tracking techniques, I hoped to increase my previous data (Southern, 1963b) on the feeding ranges of adult and immature Bald Eagles, the length of time they remained within my study area, the range of individual birds, the period of seasonal dispersal, and general behavior.

Tracking range for Bald Eagles perched in deciduous trees or standing on the ice was about two miles. The maximum distance obtained between the receiving unit and a flying bird was approximately 28 miles. By taking a series of fixes with a mobile tracking unit, I followed an immature bird for about 38 miles.

Variations in signal patterns were caused by the activity of the transmitter-bearing bird. I found that I could recognize distinctive signals and thereby determine when an eagle was soaring, flapping its wings in flight, preening, pecking at the transmitter, or wading after fish. While these data warrant further examination, it is already obvious that careful correlation between observed bird movements and received signal variations can provide a valuable technique for behavior studies conducted under field conditions.

One immature Bald Eagle was periodically relocated and tracked during a five-week period. Occasionally I tracked one of the birds for an entire day, recording its complete activity pattern from leaving the roost in the morning until returning at night. Since most of my field work was conducted on weekends during this project, considerable data necessarily went unrecorded.

Sometimes hours or days elapsed before I was able to resume tracking a particular bird. On several occasions transmitter-bearing Bald Eagles were added to my census figures solely on the basis of radio contacts.

When compared with color-marking or back-tagging techniques, radio-tracking is clearly superior in studies such as mine. During two winters I recorded only eight sightings of 10 color-marked Bald Eagles, whereas I obtained 118 radio fixes on six eagles during five weeks. In addition there were several periods of continuous tracking for entire days.

Since 1962, I have continued to use this equipment in my studies of orientation and navigation. Transmitters have been attached to 75 gulls and the routes taken by these birds during homing trials have been followed for distances exceeding 100 miles in some instances. Contacts have been maintained with a particular bird for as long as eight hours. Much data of extreme importance toward answering the navigation question have been accumulated and I will publish them at a later date.

I have attached transmitters to Mallards *(Anas platyrhynchos)* and Bobwhites during limited studies of the movements of these species. I experienced great difficulty in developing transmitters small enough to fit quail. Very small mercury cells (RM 312R) were used and transmitter life was shortened to about one week. I encountered further difficulty in attaching the units to birds without interfering with their brood patches.

Egg Temperatures During Incubation. In 1957, Eklund (1963; see also Eklund and Charlton, 1959) used radio thermometers designed by the American Electronics Laboratories to determine internal temperatures of eggs of the Adélie Penguin *(Pygoscelis adeliae)* and the South Polar Skua *(Catharacta skua)* during incubation. Transmitters inserted into the eggs telemetered temperatures, accurate within 1° C., to receivers located 130 to 180 feet from the nests. This study was conducted in the extreme cold of Antarctica.

To Physiological Data During Flight.—One of the leading workers in this area is Einar Eliassen. Eliassen (1960, 1963), who has used telemetry in attempts to determine the claims that flight makes on the energy metabolism of birds, their heat regulation and circulation, attached transmitters weighing about 40 grams and operating at 90 megacycles to domestic ducks and "sea gulls." The units represented two to two and one-half per cent of the birds' weight. The transmitter was placed at the medial line on the bird's back so as not to displace the point of equilibrium. The whole unit was put in a "box" of linen cloth and sutured to the skin. This telemetering system recorded the heart rate and stroke pressure from the right ventricle of flying and/or resting birds. Information on the pulse rate and pressure in the *arteria ascendens* was also obtained. This study suggests the great potential of telemetry equipment in this area of inquiry.

Lord *et al.* (1962) also reported on the telemetering of physiological data. They recorded, somewhat accidentally, the respiration (breathing) rate of Mallards. The telemetry system was designed by Cochran *(loc. cit.)* and used in conjunction with a strip-chart recorder. They found that breathing was synchronized with wing-beats in a ratio of 1 to 2.

Discussion

The contributions that might be made by biotelemetry in a variety of ornithological studies are apparent from the preceding review of projects. Suitable equipment is available, and for about $1000 field investigators can obtain the basic items. While this may appear to be initially expensive, more careful analysis reveals that it is relatively economical when compared with the man-hours normally required to procure similar data in quantity. Such a system could be used with bird species of about dove-size or larger.

I must stress, however, that use of this technique will not result in an armchair approach to research nor will it solve all of the investigator's problems. On the contrary, as much work as ever will be required since more aspects of the animal's activity will come under surveillance. Often new, and sometimes unexpected, problems are encountered when a species is equipped for the first time with transmitters. Particular difficulties are certain to arise during long-range tracking of birds. My telemetry system, as well as the others mentioned in this paper, is not adequate for following birds during migratory flights. Air-borne tracking receivers would serve to overcome some of the problems but, at the same time, tend to introduce new ones. Many advancements in engineering will be necessary before we will be able to track birds from their breeding grounds to the wintering areas.

We are at present experiencing only the initial attempts at using this new technique in wildlife research. Future modifications and developments in electronic systems will undoubtedly provide us with mere capsules which we can place within the body of even the smallest birds and telemeter therefrom various types of data. While this day may not be far away, we should for the present take advantage of the biotelemetry equipment we have, however limited, and use it to the fullest possible extent.

Summary

In the last five years increasing interest has been shown in the use of radio-tracking systems in field investigations. Several workable tracking facilities have been developed and used in various projects. The paper reviews accounts pertaining to the use of telemetry in field studies. In addition, brief mention is made of the author's use of biotelemetry in avian navigation studies. These systems are designed to enable investigators to record data (e.g., spatial position, body temperature, heart rate, etc.) about animals roaming free and under natural conditions without being under direct observation. The several disadvantages (cost, added complications, lack of units for smaller species, inadequate range, etc.) of the existing equipment fail to distract from its realized or potential value in biological research. Any impression that biotelemetry is a means for solving all field problems, and thereby making other techniques obsolete, is erroneous. Biotelemetry is simply another tool that will enable biologists to obtain new data for formulating answers to their many questions.

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THE COLOR PHASES OF THE WESTERN GREBE

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It may come as a surprise to many that there are two color phases in a bird so well known as the Western Grebe *(Aechmophorus occidentalis).* Yet when George N. Lawrence first described the species (*in* Baird, 1858:894-895), he had examples of both phases before him and named each as a separate species, calling the dark-phase birds *Podiceps occidentalis* and the light-phase birds *Podiceps clarkii.* By 1886 the first edition of the American Ornithologists' Union's "Check-List of North American Birds" recognized the two forms as variants of the same species, and since that time, the existence of this variation has been largely forgotten. Recently, Dickerman (1963) described a small subspecies of the Western Grebe from the Mexican Plateau, calling it *Aechmophorus occidentalis clarkii.* (This application of the name *clarkii* was possible because one of Lawrence's cotypes was an example of the new race and could be designated lectotype of the new form.)

Briefly, there are dark-phase birds in which the bill is a rather dull greenish-yellow and the black of the crown extends below the eyes, the lores, and the narrow line of bare skin extending from the eye to the gape; and there are light-phase birds which have orange-yellow bills and light faces—the black of the crown not reaching the lores or the eyes (Figure 1). The culmen is black in both, and in study skins, most of the greenish-yellow of the bill in dark-phase specimens darkens to a dusky color, whereas the brighter color of the bill in light-phase birds is less altered. Other plumage characters which appear to be correlated with the phases are the more extensively white flanks and the paler gray backs in the light-phase birds. The crown and nape are deep black in birds of both phases, but the dark stripe down the back of the neck is narrower in the light-phase birds than in the dark-phase birds.

At the Bear River Migratory Bird Refuge near Brigham City, Utah, I saw only a few birds which I could call intermediate between the two phases, most individuals appearing to be clearly referable to one phase or the other. However, among museum skins, specimens showing intermediacy are rather numerous. Just how much of this intermediacy, if any, can be attributed to age or season remains to be determined.

In the Western Grebe, there appears to be a premium on individual recognition of adjacent birds in a nesting colony, the advantage presumably being that when territories have been settled, recognition of neighbors may reduce aggressive behavior. This recognition, I think, is primarily achieved by the striking individual differences in voice mentioned by Robert W. Nero (*in* Palmer, 1962:96) and is evident to anyone who carefully studies a colony; but plumage pattern may also play a part. Considerable variation can be seen in the flank patterns of a group of birds (Figure 1), and a "pinto" bird which I watched at Bear River represents an extreme example of the latter type of variation.

The color phases of the Western Grebe are comparable to the "normal" and "ringed" phases of the Common Murre (Southern, 1939), and as is the case with that species, the proportion of the phases within populations varies clinally. The Canadian populations of the Western Grebe consist almost entirely of dark individuals. Nero (1962:96) reported five light birds among approximately 500 dark ones at Old Wives' Lake, Saskatchewan. In the Dakotas, I have found a roughly similar ratio of light to dark birds. At the Bear River marshes, light birds comprise approximately 12 per cent of the population; and in Mexico, all or nearly all individuals are of the light phase (Dickerman, 1963).

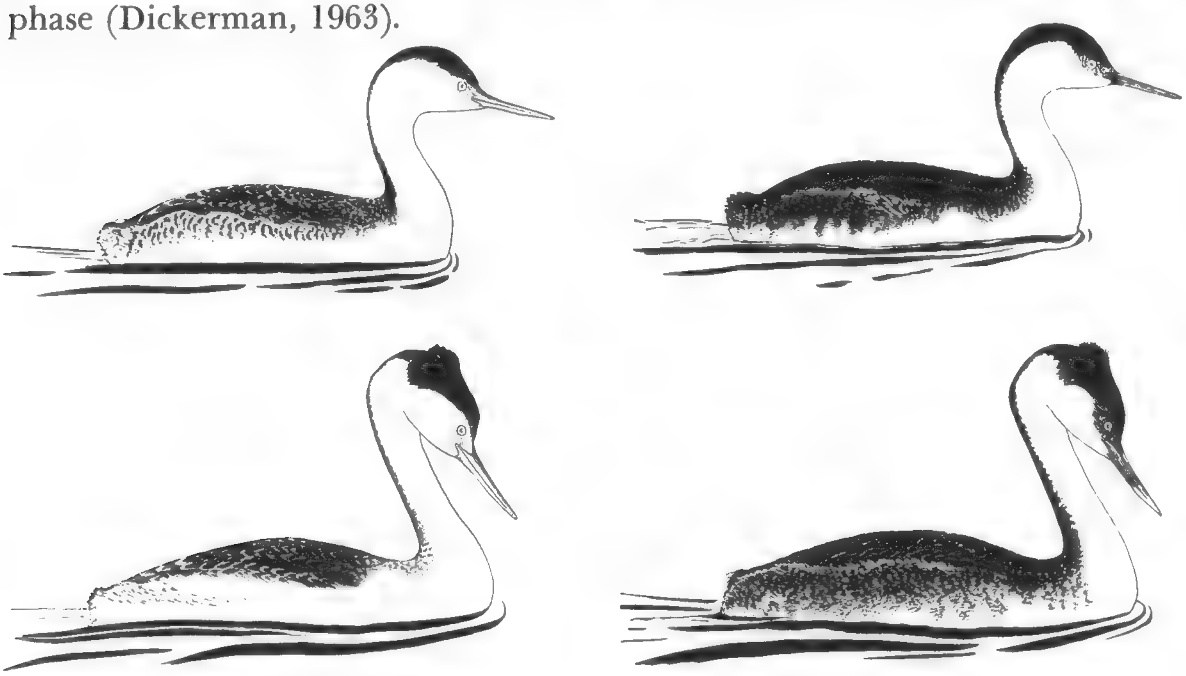

Figure 1. Color phases of the Western Grebe. Left, light-phase birds. Right, dark-phase birds. Females above, males below. The bird, upper left, is somewhat intermediate but nearer to the light phase. Drawings by John Tottenham.

The existence of distinct color phases in a large and conspicuous species suggests lines of study not possible in monomorphic species. One of these is the matter of preferential mating. Do individuals tend to mate with birds of like phase, with birds of the other phase, or is no preference evident? Western Grebes tend to choose a mate of their own phase. Of the five light-phase birds in the colony of 500 studied by Nero at Old Wives' Lake, two were mated to each other. If mating were random as regards phases and the sex ratio of the light-phase birds were two to three, the chance of one of these five birds picking a light-phase mate would be less than one in ten thousand. At the Bear River Refuge in spring, 1963, I made several censuses of the Western Grebe population, recording particularly the numbers of dark-dark, light-light, and dark-light pairs swimming together and presumably mated. The results are shown in Table 1. The over-all proportion of light birds to dark ones was 57 to 422, or nearly 12 per cent. Of 127 pairs recorded, 109 were dark-dark, 14 light-light, and 4 dark-light. If mating were random as regards color phase, the expected pairings would be 95 dark-dark, 2 light-light, and

TABLE 1

Evidence for Preferential Mating in the Western Grebe

Pair type	*Random distribution*	*Distribution found*
Dark: dark	95	109
Dark: light	30	4
Light: light	2	14

30 dark-light. The striking disparity between the number of expected and recorded mixed pairs and between the number of expected and recorded light-light pairs is convincing evidence that individual Western Grebes tend strongly to select mates of their own phase, as is the evidence from Nero's work.

While the existence of preferential mating in this species is in itself of interest, an explanation of the mechanism by which it occurs would be still more interesting. For such a mechanism, I can only offer an hypothesis: selection of a mate of like color phase might be accounted for by imprinting. In the case of grebes, as opposed to that in most ducks, both parents incubate and care for the young. Indeed, the association of young grebes with their parents is especially close; the parents take turns carrying the small young on their backs, the unencumbered parent spending much of its time obtaining food and feeding the young. Under circumstances like these, it would seem unlikely that a young grebe could become imprinted on one parent. One would expect therefore that the young of like parents would select a similar mate, whereas the young of a mixed mating would have a 50:50 chance of tending to select a mate of its own phase. In this way a system of mating preferences like those of the Western Grebe could be maintained with little or no change in the over-all proportion of the phases. In such a system, there would be no need for any bird to know what its own color phase was.

In accounting for how such a system came into being one must again resort to hypothesis. It is possible that the two phases developed in isolated populations, the light phase in the south and the dark phase in the north. These populations then presumably came together after the phases had become differentiated but before the populations had reached the species level.

In the matter of linking the wintering grounds of various populations of a species with their breeding grounds, too many ornithologists work with individual specimens when careful study of the characteristics of populations can usually produce far more precise results. The ratios of dark to light birds in the various populations of the Western Grebe could well be used to match the wintering grounds with the breeding grounds of each population, without the taking of a single specimen. Western Grebes are gregarious not only on the breeding grounds but also on the wintering grounds; and there is evidence (Munro, 1941:48-51) that they migrate in flocks. For the determination of the ratios of light to dark birds in a population, museum specimens are of very limited use because series are small and, especially, because there is probably a bias on the part of collectors to take the brighter, that is the light-phase, birds.

What is needed are counts of dark and light birds in each of the major breeding colonies and in each of the major wintering concentrations. In many instances, a given wintering population might be identified by its size and the ratio of dark to light birds in it.

Our present knowledge suggests that the migration is largely east-west. The sample of wintering birds from British Columbia and Washington which I have examined in museums is small and appears to be strongly biased in favor of light birds (8 dark, 5 light, 1 intermediate). Specimens of breeding birds from Canada and the Dakotas number 36 dark and 1 light, whereas counts in these areas indicate that the ratio is more nearly 99 to 1. It is likely that the ratio of dark to light birds based on counts of birds wintering in the Puget Sound area and northward will be considerably higher than the ratio based on specimens.

The only large sample of wintering birds available in museums is from the California coast. In this sample there appear to be significantly different ratios in the northern and southern parts of the state. Specimens taken north of Point Concepcion are about equally divided between dark and light birds—20 dark to 23 light (plus three intermediates); those taken south of Point Concepcion are predominantly light—3 dark to 16 light. These birds may represent the breeding populations from various parts of California and, possibly, southern Oregon, but to date no counts of the breeding birds of these areas are available.

A related problem which needs attention is the question of color phases in the downy young. In Dawson (1923:2046) there is a photograph of two small downy Western Grebes which appear to differ considerably in the patterns of their heads. Specimens of downy young should be examined to see if such dimorphism actually exists and, if so, to describe it. More important would be the matter of whether or not this dimorphism is related to the color phases of the adults. Collecting small downy young of parents of known phase would be a first step in solving this problem. A program of banding might logically follow.

Summary

Two color phases are found in adults of the Western Grebe, the major differences involving the amount of white on the face and the color of the bill. The grebes show a strong tendency to mate with birds of like phase. There is need to check the evidence for color phases in the downy young and to determine the relationship between the phases of the adults and those of the young. The proportion of light and dark birds may be used to characterize a population and to identify it on both the breeding and the wintering ground.

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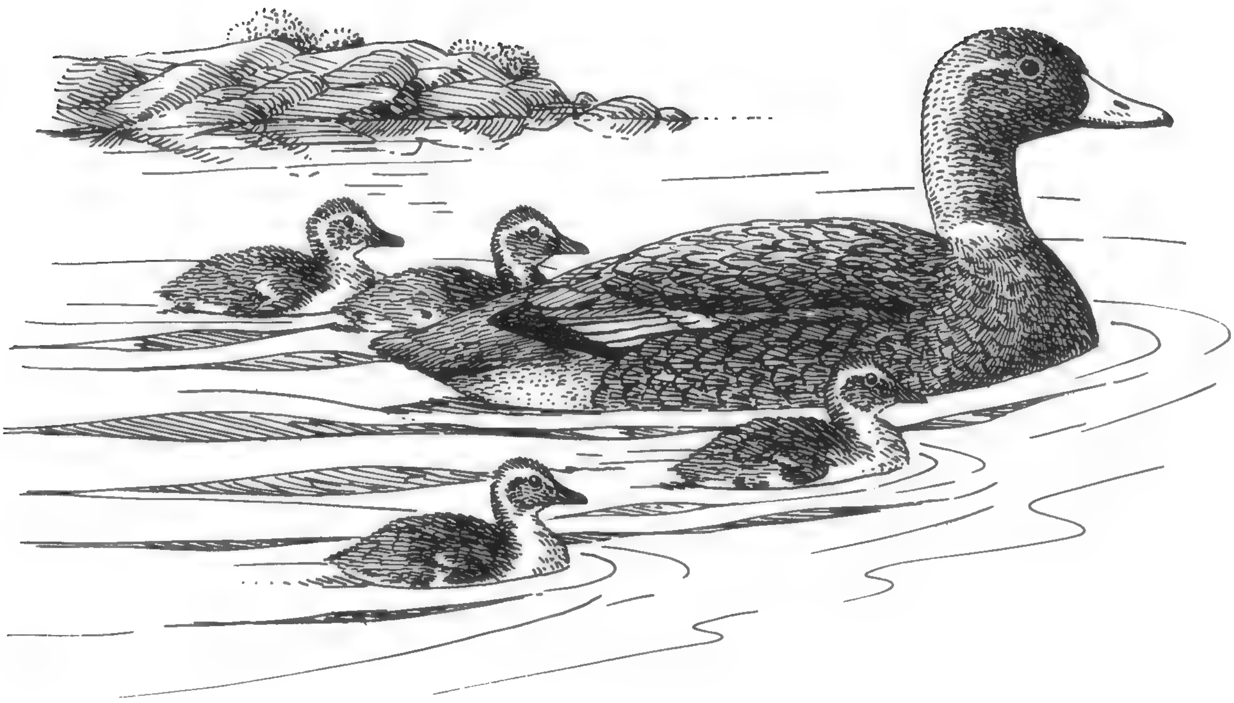

Steamer Duck, *Tachyeres brachypterus*

KELP GEESE AND FLIGHTLESS STEAMER DUCKS IN THE FALKLAND ISLANDS

OLIN SEWALL PETTINGILL, JR.

Photographs by the author, courtesy of Walt Disney Productions, unless otherwise indicated.

Kelp Geese and Flightless Steamer Ducks are peculiar to the coastal regions of southern South America, from southern Chile south to Cape Horn, and the Falkland Islands. Few ornithologists have visited these desolate shores and fewer still have stayed long enough in any one area to make detailed studies of these birds in their natural environment. While in the Falkland Islands from October 1953 to March 1954, Mrs. Pettingill and I observed both Kelp Geese and Flightless Steamer Ducks at several places in the archipelago. My objective here is to summarize our notes and impressions while confirming or adding to information acquired by others.

Kelp Geese

Kelp Geese *(Chloëphaga hybrida)* are moderately sized but nonetheless robust geese with comparatively short tarsi and rather broad feet adapted to maneuvering over slippery ledges and rocks. The sexes are remarkably different (see Figure 1)—the gander pure white with bright yellow tarsi and feet, the goose blackish brown, with white barring on the breast and sides, white eye-ring, white back, tail, and abdomen, and yellow tarsi and feet. Both sexes have a formidable though somewhat blunt spur emerging from the wrists. Young males-of-the-year resemble the females.

Kelp Geese share the genus *Chloëphaga* with four other species, the Andean Goose *(C. melanoptera)* of the high Andes, the Ashy-headed Goose *(C. poliocephala)* of southern South America, and the Ruddy-headed Goose *(C. rubidiceps)* and Upland Goose *(C. picta)* of *extreme* southern South America and the Falkland Islands. In the opinion of Delacour (1954), these species are not true geese but sheldgeese, more closely related to ducks. Although they have goose-like bills and graze like geese, all five show numerous characteristics such as a metallic speculum and scutellated tarsi that are akin to ducks while two species—the Upland and Kelp Geese—exhibit great color difference between the sexes as do most ducks.

Of these five geese, the most aberrant is the Kelp Goose which has forsaken an upland existence to live on the sea coast where it nests not far above the reach of the tides and forages on seaweed. Non-migratory and sedentary, pairs rarely leave their home shore anytime during the year. This acquired contentment to stay in one place accounts for the fact that Kelp Geese in

Figure 1. A pair of Kelp Geese at Kidney Island. The white gander has assumed the vertical stance while protesting the presence of the photographer.

the Falklands and those in extreme southern South America—southern Chile and Tierra del Fuego—have developed, during prolonged isolation from each other, certain distinctions, mainly in size, that warrant their separation into subspecies. The larger form, *C. h. malvinarum,* inhabits the Falklands.

Because there are no land mammals in the Falklands or birds large enough to prey upon geese and because men rarely intrude on their territories, Falkland Kelp Geese rarely take flight for safety's sake. They showed no alarm when we approached them slowly. Only when we were practically beside them did they move away by hopping or walking over the ledges rather than flying. The few times we saw Kelp Geese take to the air on their own initiative were in short flights between their feeding grounds on the very edge of the sea and the high ledges where they loitered or nested. They took off heavily and, once air-borne, flew clumsily, somewhat "down in the stern"; they never sailed and they never flew any higher than was necessary to reach their destination. Obviously the ability of Kelp Geese to fly had deteriorated through general disuse.

We found Kelp Geese common wherever there were rocky shores. The ganders, so conspicuously white against the gray background that we could spot them from a boat even far from shore, impressed us not only by their commonness but by the evenness of their distribution—a gander, it seemed, every 500 yards or so. On a few occasions when the tide was high we saw Kelp Geese grazing on grassy knolls just above the sea, and once I watched a gander plod up a wide beach and drink from a fresh-water stream. Otherwise the Kelp Goose, as we observed it, was wedded to the edge of the sea or to the rocks just above the high-tide mark where it loitered, slept, and nested.

Our familiarity with Kelp Geese stems mainly from a pair we found nesting on Kidney Island on 4 November. The gander, an alert and apprehensive sentinel, standing on a ledge shelf about 25 feet above the high-tide mark, gave me the clue. Since pairs of Kelp Geese are practically inseparable, his mate *had* to be close by. When I reached his lookout, the gander assumed a vertical stance, puffed out his chest, curved his neck back and forward into an S-shape, and, opening his mouth and keeping it open, began a series of soft, protesting *whasp* sounds. (See Figure 1.) I stepped to within five feet of him, but he made no move to retreat. When I discovered the goose motionless on the nest on the edge of the tussock about six feet behind him and walked to it, he made no move toward me. As I parted the blades of tussock and started to touch the goose, she stepped off, giving low sounds—*cronk, cronk, cronk,* etc. Again I started to touch her, again she moved away, keeping the same distance, but never attacking, never feigning to do so. The gander stood his ground. I examined the nest of dead tussock blades broken off and pulled together to form a cup which was lined with down and contained seven eggs. Neither bird flew away. As soon as I withdrew, the goose stepped back on the nest and the gander relaxed from his vertical stance and continued his vigil.

On 29 November, when I visited the nest as I had many times before, there was nothing in the pair's reactions to indicate that five of the seven eggs had hatched. The gander was at his post; the goose sat quietly. But when the goose stepped off the nest with no more than the usual reluctance, there they were—five goslings, just hatched, covered with the fluffiest of white down and not yet ready to leave the nest. As far as the behavior of the parents was concerned, the goslings might as well have been eggs.

The next day, however, brought a change. The goslings were out of the nest on the ledge with the parents, both of which, at the sight of me, gave chest-out, curved-neck displays and uttered the same respective protestations. As I drew close to pick up a gosling, the gander started toward me, wings out slightly, wrist-spurs showing, and put himself between me and his family. This was the extent of his "attack." As I went right ahead to pick up one of the youngsters, he side-stepped, performing threateningly but doing nothing more.

Later that day I watched the family maneuver down to the sea, jumping from one ledge shelf to another, with the gander in the lead and the goose following after the goslings. (See Figure 2.) For the chicks the jumps were considerable, often terminating in rolls and somersaults, but no matter—each chick was well cushioned by a thick coating of down. Once all the goslings had arrived at the water's edge, the gander launched himself, the goslings tumbled in, and the goose followed. The flotilla of seven then set sail toward some adjacent rocks where they paused to feed on the clinging seaweed. (See Figures 3, 4, and 5.)

Being the only Kelp Geese on the east end of Kidney Island, this family had the whole shore to themselves. Although they could have wandered freely in either direction along the shore, they remained within 100 feet of the nest-site. This was the case until we left Kidney Island on 5 December and when we returned on 12 February. By February the five young were nearly full grown and the whole family slightly more wary of us, taking to the water as we drew to within 25 feet of them. On the morning of 22 February, the adults were alone. Later that day I watched the female chase one of the young until it took flight and crossed the small, kelp-strewn harbor. This explained, we thought, why the adults were alone—they had driven away their offspring. But to our surprise, at nightfall all seven birds were together again. Would the adults again drive away the young and continue

Figure 2 *(above)*. A family of Kelp Geese at Kidney Island maneuvering down over the ledges from the nest to the sea.

Figure 3 *(below)*. Now in the sea, the family of Kelp Geese at Kidney Island proceeds to the nearest feeding area. The young stay close to the female.

Figure 4 *(above)*. Two downy young Kelp Geese obtain their first meal of seaweed.

Figure 5 *(below)*. Kelp Geese, young or adult, seldom stay in the sea longer than necessary to reach their feeding areas on rocks exposed by low tide.

to do so until they stayed? Was this the way a family normally breaks up? A vicious storm, from 22 February until we left on 27 February, prevented any further observations of this family.

What we learned about Kelp Geese from the pair at Kidney Island was, in most respects, typical of what we saw of the species while cruising around the Falklands. The sentinel ganders standing high on ledge shelves led us to the conclusion that Kelp Geese most often nest in such places. However, Cobb (1933) mentions that Kelp Geese also nest "just off the beach, sometimes on it" and shows a photograph of a goose on a nest on ground completely surrounded by short grass. Seven eggs seems to be the maximum number; four to six are the rule (Cobb, 1933). The only other nest we examined, on the north side of Kidney Island, contained six eggs. Incubation probably takes 30 days (Delacour, 1954). The nesting period extends over at least two months. We saw two families with very small goslings, certainly not over a week old: one at Carcass Island on 18 December, the other at New Island on 30 December.

Wherever we encountered Kelp Geese, they were consistent in their mild reaction to our intrusion. Pairs feeding on the rocks let us come to within 10 feet of them, sometimes closer, before they moved away, usually walking, seldom flying. With the presence of some 2,300 human beings in the Falklands one might wonder why Kelp Geese, so tame and easy to kill, have not been decimated for food purposes as have many insular birds. The reason is simple: The flesh of the Kelp Goose is unpalatable to anyone no matter how tolerant he is of exotic fare.

The only time we noticed Kelp Geese in the water was at Kidney Island where the family swam across tidal pools, or channels between ledges, as they searched for seaweed. The fact that Kelp Geese do revert now and then to upland grazing was impressed upon us at Lively Island where we saw a family feeding on a knoll high above the sea and within sight, farther inland, of a family of Upland Geese similarly foraging.

Even though Kelp Geese in the Falklands seem to have ample space, strife persists among them. At Carcass Island on 18 December we saw a quarrel between a pair and a stray gander. Both ganders fought with their wings, flailing each other while attempting to grapple with their bills. Occasionally one retreated momentarily, the other pursuing; then, after more flailing, it was the other way around. The goose, far from being indifferent, followed her mate closely, wings outstretched and bill open, sometimes making a threatening lunge toward the intruder but never striking. The quarrel continued for nearly fifteen minutes, with the intruder eventually folding his wings and lumbering away, apparently more from exhaustion than in defeat.

Toward the end of the breeding season ganders show the wear and tear of combat. The primaries and secondaries of one specimen, collected for me on 17 December, were so worn that only the shafts and a few barbs remained—the bird could not possibly have flown—and the spurs protruded from wrists that were virtually bare. The sheep farmers told us that when Kelp Geese wander far enough inland to come in contact with Upland Geese quarrels invariably ensue and that, more often than not, the Kelp Geese are the victors.

With the waning of the breeding season in January and February small flocks of fully-grown young and unpaired adults gather here and there on broad ledges or grassy knolls above the sea, but the mated pairs remain on their territories. We saw pairs in late February, all by themselves, as they had been in October. Just about the last birds we saw as we sailed from the Falklands in early March were a pair of Kelp Geese standing atop a tussock-fringed rock that jutted out of Port William near the entrance to Stanley Harbour.

Flightless Steamer Ducks

Steamer Ducks of the genus *Tachyeres* are strong, heavy, and ungainly with massive, angular bodies, over-sized heads and feet, a lumbering gait, and awkward stance. They are proficient divers and notorious for "steaming" along on the water—that is, propelling themselves with their wings and feet while throwing up spray which, at a distance, is more conspicuous than the birds themselves.

As in Kelp Geese, Steamer Ducks pair for life and the male assists the female in rearing the young but does not incubate the eggs. On the basis of these and other habits in combination with certain morphological characteristics shared with Kelp Geese, Delacour has ventured the opinion that Steamer Ducks represent diving forms that have evolved from the group of sheldgeese, *Chloëphaga,* to which Kelp Geese belong.

For many years controversy prevailed among ornithologists as to the species composition of *Tachyeres.* From the earliest observers in the region of the Strait of Magellan had come reports that some Steamer Ducks were able to fly, others not, although they all looked much alike. Were there two different species, one flying and the other flightless? Phillips (1925) and Peters (1931) considered both of them one species. Chapman (1933), however, suggested that all young Steamer Ducks, until past their first winter, were able to fly and that adults nesting along salt water in which they fed lost their power of flight while those nesting inland along fresh water retained their flying abilities in order to reach their feeding grounds in salt water.

Eventually Murphy (1936) solved the riddle. Studying over 100 specimens of Steamer Ducks from both southern South America and the Falklands, he proved that there were not just two species but three: the Flying Steamer Duck *(Tachyeres patachonicus)* inhabiting both southern South America and the Falklands; the Magellanic Flightless Steamer Duck *(T. pteneres)* in southern South America; and the Falkland Flightless Steamer Duck *(T. brachypterus),* endemic to the Falklands. In the two flightless species, the wings are too short for flight.

All three species of Steamer Ducks are modestly colored, both sexes being primarily dark to light gray, with a brownish wash—especially pronounced on the throat and breast, a white line running back from the eyes, white secondaries, and white lower breast and abdomen. Falkland Flightless Steamer Ducks are more richly colored and feature a deep yellow ring around the neck. The males are conspicuously different from the females by having a whitish head (see Figure 8).

We found Falkland Flightless Steamer Ducks common in all coastal waters—around islands both small and large, at headlands, and in coves and deeply inset bays and harbors. Rarely did we see an individual more than a few hundred feet from shore. They restricted themselves entirely to salt water, never moving inland to breed along fresh-water streams and ponds—the habitat of Flying Steamer Ducks. Nevertheless they drank and even bathed in fresh water. Indeed, on numerous occasions I watched lone birds,

Figure 6 *(above)*. A pair of Flightless Steamer Ducks that lived near and commonly frequented Government Pier in Stanley Harbour. Photograph by S. A. Booth.

Figure 7 *(below)*. Female Flightless Steamer Duck on a nest. Photograph by S. A. Booth.

breeding pairs, and adults with broods deliberately leave the sea and amble up broad beaches to imbibe from streams of fresh water. When such waters were sufficiently deep, the birds immersed themselves, dipping their heads and wings in the water and letting it run over their backs.

Flightless Steamer Ducks, called Loggerheads or Logger Ducks by Falklanders, were tame everywhere, even near the settlements. In the harbor at Stanley, the only town, one pair lived near the Government Pier (see Figure 6), and two or three other pairs held territories on the beach within a stone's throw of the main thoroughfare. Whenever I approached individuals resting on the shore, whether in settlements or in remote parts of the archipelago, they showed no more alarm than domestic ducks, moving casually into the water. Now and then I came upon a lone bird which seemed reluctant to move at all and would launch itself only to avoid being stepped on.

This lack of shyness in Flightless Steamer Ducks is consistent with Kelp Geese and many other island-dwelling birds that have never been preyed upon or seriously molested when on land. Except for a fox, long since extinct, there have been no native land mammals, not even primitive peoples, in the Falklands. The Europeans who settled in the Falklands in recent centuries have practically ignored the species, finding it of no value as a food, its flesh being unpalatable, and no challenge as a target for sport, its indifference to human beings making it as easy to shoot as a barnyard chicken. While there have always been a few people in the Falklands who would kill Steamer Ducks just for the sake of shooting at something, the Government has recently put a stop to this by giving the species full protection.

The indifference of Steamer Ducks toward man does not apply toward other birds. By sheer aggressiveness they literally dominate all coastal birdlife. No penguin, shag, or gull ever comes close to a Steamer Duck without being charged and forced to retreat. Flightless Steamer Ducks are the only waterfowl regularly frequenting the waters just offshore; thus, so far as waterfowl are concerned, they have this area pretty much to themselves. But on the shore and in the shallow water at the sea's edge, they come in contact with Crested Ducks *(Lophonetta specularioides)* and Kelp Geese. Crested Ducks, being much smaller, keep away from Steamer Ducks, rarely letting themselves in for trouble. But this is not the case with Kelp Geese which, being larger and heavier than Steamers, frequently stand their ground and give battle—but not for long. The only conflict I saw between a Kelp gander and a Steamer drake proved to be a mere skirmish with the gander retiring in short order. Several of my Falkland friends reported seeing similar struggles, with the Steamer always the victor. In all duels the birds attack each other head on, whack vigorously with their wings, while grabbing at each other's head and throat.

The Steamer Duck's capabilities for battle are due more to brute strength than skill and to an additional feature—the conspicuous blunt spur, orange-yellow in color, at the bend of the wing, which serves to increase the effectiveness of each blow.

I can personally attest to the fact that Steamer Ducks are as physically tough as they are strong. Anxious to bring back several specimens, I set out to collect one immediately. On my first try, I fired with a 12-gauge shell, Number 10 shot, at point-blank range. I might as well have thrown sand at the bird, for it merely walked away, annoyed. My next try with my heaviest load, Number 7½, was just slightly more annoying. Finally, in desperation, I enlisted the help of a friend who owned a weapon of larger gauge and

Figure 8 *(above)*. A family of Flightless Steamer Ducks at Kidney Island. The young huddle by themselves but characteristically nearer the female.

Figure 9 *(below)*. The same female and her brood. The young are about eight days of age.

used some shells with loads lethal enough for a horse. He obtained three specimens. The two males weighed 9.5 and 9.75 pounds and the female 7.5 pounds. On skinning the birds, I had to use a carpenter's saw for cutting through the crania. The thickness of both the frontal and parietal bones was more like that of a mammal of comparable size.

Steamer Ducks are strongly territorial. The domains of each pair consist of a strip of shore up to and including the edge of vegetation as well as the water lying offshore. At Kidney Island, about every 300 yards of shore was the territory of one pair, except for one short stretch near the west end that was used as a loitering ground or "club" by non-breeding Steamers. Territorial boundaries were the scene of considerable strife, consequently I could easily determine where one territory left off and the other began.

Although Steamer Ducks are by nature belligerent toward all birds which get in their way, combativeness shows up at its best in intraspecific rivalry, especially over territories. Fights are highly dramatic and frequently prolonged. Rival males approach each other very low in the water, with their necks stretched forward, and their heads, middle of the backs, and tail-tips just showing. The closer they approach, the lower they submerge, until one or both disappear to attack from below. The struggle that follows is more underwater than above, and with so much churning and splashing that an observer has difficulty determining just what is taking place. The objective, apparently, is to grasp the opponent's neck and keep his head under water long enough to drown him. I did not see a male killed in this way, but Mr. E. M. Cawkell, an amateur ornithologist residing in the Falklands while we were there, reported seeing a death by drowning result from a struggle. After one long fray of some 20 minutes, I watched the males separate, greatly exhausted, and swim laboriously toward the beaches of their respective territories, using their last vestiges of strength to crawl out of the water and flop on the sand. Their heads were battered and their necks smeared with blood. I rarely saw a fully-mature, white-headed male anywhere whose head did not show scars of battle.

Before actual attack, each male gives a threat-display by rising slightly in the water, throwing his head back and lifting his tail, meanwhile uttering a series of wheezy sounds interspersed with high-pitched, clicking notes. If the male being threatened shows an inclination to retreat, the challenger ceases vocalizations and pursues, "steaming" after him with neck arched and mouth open.

During these squabbles, the females were more often participants than bystanders, "backing up" their spouses with varying degrees of aggressiveness. At Kidney Island, during one encounter between males, the female of one of the pairs continued to circle the scene, sitting high in the water, pumping her head upward, backward, and forward in rapid succession, and giving sounds similar to the male's but distinctly lower pitched and more guttural. At the start of another encounter between males, the females of both pairs followed their mates. As soon as the males submerged to tackle each other, one female, vocalizing strenuously, steamed at the other female which made a hasty departure, first diving to get out of the way. In this instance the more aggressive female temporarily deserted a small brood; the other female was broodless.

[Moynihan (1958) has since published a detailed, illustrated account of the behavior of Flying Steamer Ducks as recorded by him on the east coast of Tierra del Fuego. On reading his observations and comparing them with

Figure 10 *(above)*. Female Flightless Steamer Duck starting to lead her brood to the sea.

Figure 11 *(below)*. Flightless Steamer Duck family on their way to feed in the kelp beds, visible offshore. The female is already in the water; the male is following the brood. Photograph by S. A. Booth.

mine, brief as they are, I find every indication that the behaviors—at least the *aggressive* behaviors—of the two species are practically identical.]

Steamer Ducks usually nest close to shore either in fairly open situations (Figure 7), or in the shelter of a cliff, shrub, or clump of tussock grass, and lay anywhere from four to 10 eggs (Cobb, 1933), rarely more. The female sits closely on the nest and will readily allow a person to touch her. The incubation period has not been determined.

Throughout the nesting season, pairs are inseparable. While the female incubates, the male is invariably nearby between nest and sea, or occasionally in shallow water just offshore. At the appearance of a man, Kelp Goose, or Crested Duck, he shows disturbance by "kee-youing" and may attack the birds but not man.

At Kidney Island on 4 November, perhaps 100 yards from the nest of Kelp Geese we had under observation, was a pair of Steamer Ducks with seven newly-hatched young. Both adults guarded the brood closely. At our approach, they moved slowly into the water, the male keeping himself between us and his family but showing no belligerence. A few half-hearted wheezes and "kee-yous" from him and a croak or two from her were the only protestations.

In the water the youngsters stayed close to the female; on the beach or ledge they huddled either beside or beneath her. After two days of age, we never saw them being brooded even in cold or stormy weather. Instead they simply huddled together, sometimes beside the female, sometimes two or three feet away, but always nearer her than the male. (See Figures 8 and 9.)

On their first day, the female led them nearly fifty feet from shore to kelp beds where they proceeded to dive for food, probably tiny invertebrates. On later days, the female led them to the same place (see Figures 10 and 11) but also paused to forage in shallow water close to shore. Here both she and the young reached down with their long necks, occasionally stirring the bottom with their feet, but never tipping up in the manner of dabbling ducks.

Feeding in the kelp beds frequently subjected the broods to attacks by Kelp Gulls *(Larus dominicanus)*. One day the female and her three-day-old brood were foraging in the kelp bed 100 feet from shore, while the male rested on the beach. Suddenly a Kelp Gull swooped down on the brood. Instantly the female began croaking and circling, meanwhile attempting to reach up and strike the gull with her beak each time the gull came down. Seeing the fracas, the male immediately launched himself and swam full force, wheezing and clicking, to assist in defense. By the time he arrived, the gull had ceased attacking and disappeared. What seemed to have saved the youngsters was their reaction to scatter and dive repeatedly, surfacing just long enough to get air.

Many young Steamer Ducks lose out to predators—not only to Kelp Gulls, but to Skuas *(Catharacta skua)* and Giant Petrels *(Macronectes giganteus)* as well. Our generalization, supported by comments from Mr. Cawkell and other sharp-eyed observers, was that the older the broods, the fewer the young. This was certainly true of broods we saw in December when we made a trip around the Falklands.

The young stay with their parents until practically full grown. On 8 February, we watched a family with six young—an exceptionally large number for the lateness of the season—come ashore on a beach near Charles Point to spend the night. I had to examine the family carefully to distinguish the young from the female. When Gentoo Penguins *(Pygoscelis papua)* ventured too near, they were driven away post haste by the male with all the belligerence of a parent protecting downy young.

At Kidney Island, on 17 February, the same pair we had followed earlier in the season was occupying the same territory, but the young were gone. We saw the pair engage an intruding male in combat and send him on his way back to the club at the west end where 30 or more Steamer Ducks—mainly full grown young-of-the-year—were loitering. It was the same "off-limits" spot that, in October, had attracted half that number of individuals.

As in the case of the Kelp Geese we had watched at Kidney Island, this pair of Steamer Ducks were still on their territory though the breeding season was over. I had no doubt that they would hold it in perpetuity—until something happened to one of them.

Summary

Kelp Geese and Flightless Steamer Ducks in the Falkland Islands were common, sedentary, and strongly territorial, pairs apparently remaining on their sea-shore domains the year round. They were seen to move away from the sea to drink from fresh-water streams and Kelp Geese were noticed occasionally grazing on grassy uplands. Both species, while generally indifferent toward man when compared to most birds, frequently engaged in vigorous encounters with individuals of their own and other species. Pairs among either species were inseparable; the male was nearby while the female incubated and he assisted the female in attending the young.

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RECORDING THE FLIGHT-SPEED OF BIRDS BY DOPPLER RADAR[1]

GARY D. SCHNELL

Over the years many ornithologists have attempted to measure the speed of birds in flight by a variety of methods. Their notes, scattered through the literature, have been summarized from time to time by Meinertzhagen (1921, 1955), Cooke (1933, 1937), and others.

Most of the published flight-speeds were obtained from birds flying parallel to cars or planes while the observer took a reading from a speedometer or air-speed indicator. Many speeds more often than not were recorded incidentally or accidentally by travelers without special regard to the accuracy of the meters or the technique employed. A second method was the timing of flights over a given distance with a stop-watch (see figures assembled by Meinertzhagen, 1955). Where the flights were for very short distances, even a slight error in timing could greatly distort the actual speed recorded. Where the flights were for very long distances, the chances of the birds taking the straight course necessary for accuracy in timing were slight. Meinertzhagen (1921), using theodolites to compute the velocity of migrating birds, succeeded in clocking speeds that are probably more accurate than those recorded by any other method.

In his book on bird migrations, Dorst (1962:324-325) published a table showing flight-speeds for birds used in long-distance homing experiments. Unfortunately many of the speeds in the table that were originally reported in miles per day are given in miles per hour. The table is consequently misleading.

As a tool for determining the flight-speed of birds more precisely, the American Museum of Natural History recently contracted for the construction of a Doppler radar unit (Figure 1). Lanyon (1962) put the unit through some preliminary field tests. I obtained the radar unit on loan from the American Museum during the summers of 1963 and 1964, in order that I might investigate particularly the speeds of bird species used in navigation experiments by William E. Southern at the University of Michigan Biological Station.

The Doppler radar unit made it possible for me to record accurately in miles per hour (with an error of not more than one mile per hour) a large number of speeds, especially those of colonial species. Since the radar unit was portable I could take it to the colonies as well as to areas frequented by non-colonial species.

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[1] Contribution from the University of Michigan Biological Station

Figure 1. Focusing the Doppler radar unit on a Purple Martin. The author sights the unit on the bird while Miss Mary Sue Garner records the indicated speed from the speed-meter on the back of the unit. Photograph by Olin Sewall Pettingill, Jr.

I recorded 1,628 flight-speeds of 17 species of birds. A substantial number of figures were for the following eight colonial species: (1) Herring Gull *(Larus argentatus)* at Rogers City, Presque Isle County, Michigan, 16 and 23 July 1963 and 7 and 9 July 1964; (2) Ring-billed Gull *(L. delawarensis)* at Rogers City, 23 July 1963 and 8 and 10 July 1964; (3) Common Tern *(Sterna hirundo)* at Rogers City, 23 July 1963 and 8 July 1964, and at Lark's Harbor Lodge, 2.5 miles north of Presque Isle, Presque Isle County, Michigan, 31 July 1964; (4) Black Tern *(Chlidonias niger)* at French Lake, Emmet County, Michigan, 11 and 16 July 1964; (5) Bank Swallow *(Riparia riparia)* at Rogers City, 23 July 1963 and 8 and 10 July 1964; (6) Barn Swallow *(Hirundo rustica)* at a colony on the Vanacker Farm, 3.5 miles north of Rosebush, Isabella County, Michigan, 17 July 1964; (7) Cliff Swallow *(Petrochelidon pyrrhonota)* at Lark's Harbor Lodge, 31 July 1964; and (8) Purple Martin *(Progne subis)* at the University of Michigan Biological Station, Cheboygan County, Michigan, 28 July 1963 and 19 July 1964, and at Bowersoc's Landing, Indian River, Cheboygan County, Michigan, 30 July 1963 and 24 July 1964.

The remaining flight-speeds were for the following species: (9) Spotted Sandpiper *(Actitis macularia)* at Bowersoc's Landing, 24 July 1964; (10) Chimney Swift *(Chaetura pelagica)* at French Lake, 16 July 1964; (11) Eastern Kingbird *(Tyrannus tyrannus)* at French Lake, 16 July 1964; (12) Tree Swallow *(Iridoprocne bicolor)* at French Lake, 16 July 1964, the University of Michigan Biological Station, 19 July 1964, and Bowersoc's Landing, 24

July 1964; (13) Cedar Waxwing *(Bombycilla cedrorum)* at French Lake, 16 July 1964; (14) House Sparrow *(Passer domesticus)* at the Vanacker Farm, 17 July 1964; (15) Red-winged Blackbird *(Agelaius phoeniceus)* at French Lake, 16 July 1964, the Vanacker Farm, 17 July 1964, and Bowersoc's Landing, 24 July 1964; (16) Brown-headed Cowbird *(Molothrus ater)* at the Vanacker Farm, 17 July 1964; and (17) American Goldfinch *(Spinus tristis)* at the University of Michigan Biological Station, 28 July 1963, and Bowersoc's Landing, 24 July 1964.

Materials and Methods

The FTB-X(1) Doppler radar, developed by Cardion Electronics, operates on the same principle as the radar used by law enforcement agencies to determine the speed of automobiles. The frequency of radar echoes from moving targets is shifted in a manner that provides a direct measure of the target's speed.

The radar unit consists of five basic elements: (1) A transmitter which provides a source of one-half watt of microwave energy at 9,600 megacycles per second; (2) a transmitting antenna to direct and focus this energy on the bird; (3) a receiving antenna to collect the energy reflected back from the target; (4) a mixer to merge the reflected energy with a small sample of the transmitted energy; and (5) a receiver to amplify and measure the mixer's audible output frequency—the Doppler frequency (Lanyon, 1962). The unit is powered by a 12-volt automobile battery and is coupled with a tape recorder to record the Doppler frequency along with voice commentary. These signals may also be heard through the headphones. Figure 2 is a simplified diagram of the radar unit.

I recorded speeds of birds when they were anywhere from 20 to 50 yards from the unit. Except for 20 hand-released Ring-billed Gulls, all the birds were flying under "natural" conditions. For the greatest degree of accuracy, two people were necessary to operate the unit: one to sight the radar unit on the bird and the other to read the meter and to record data on the transistorized tape recorder.

When I aimed the radar unit at the moving bird (see Figure 1), I could hear the signal in the headphones and a second person could read the bird's

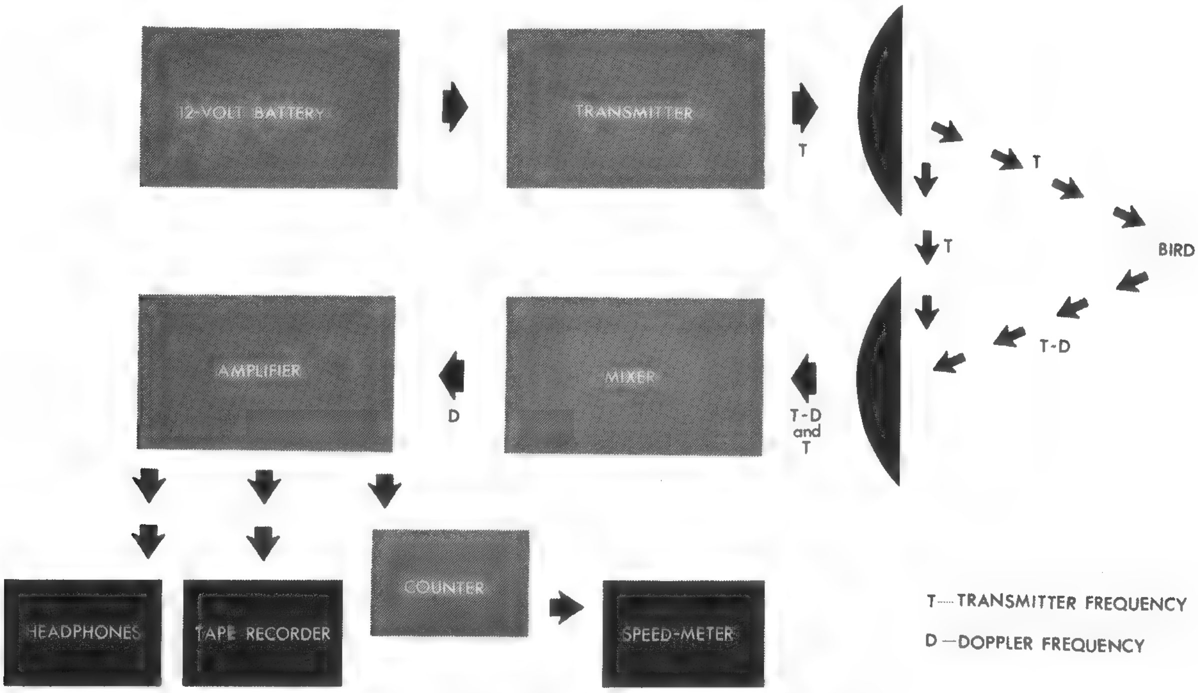

Figure 2. A simplified block diagram of the Doppler radar unit.

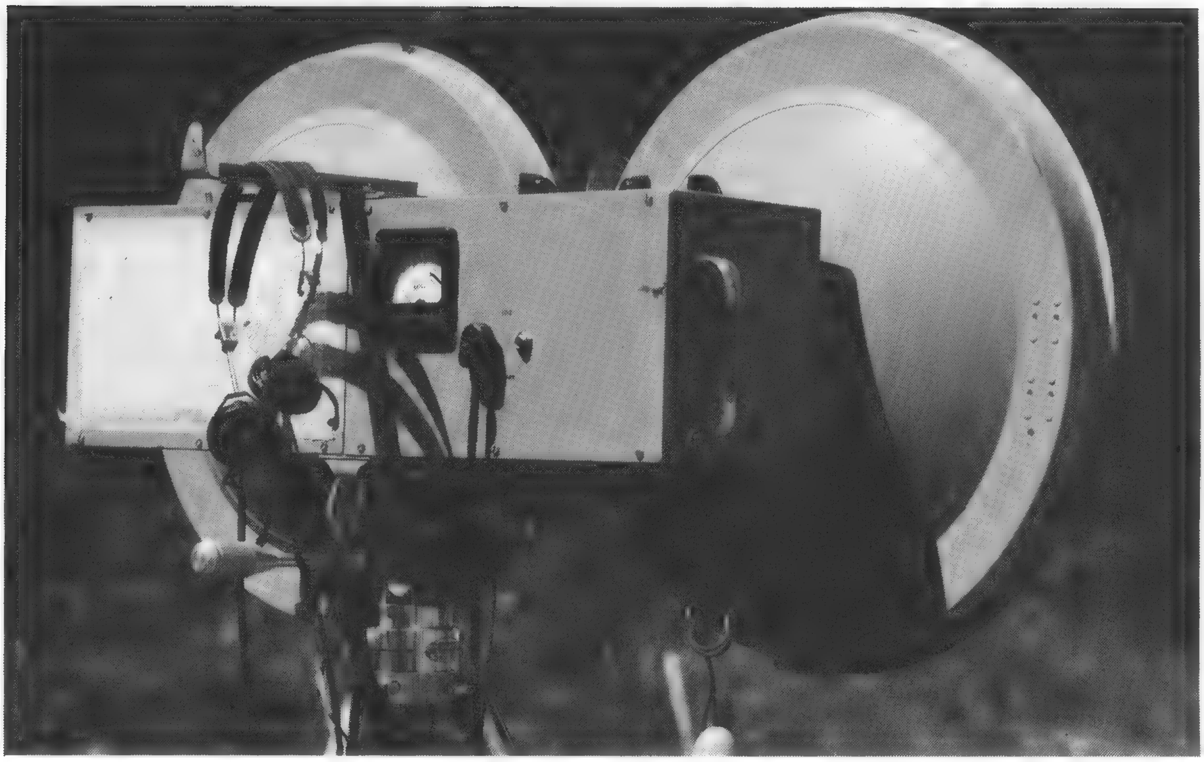

Figure 3. A view of the back of the Doppler radar unit. The left side is the transmitting part of the unit while the right side is the receiving part. The headphones hang from the sight. Just to the right of the center of the unit is the speed-meter. The conversion table covers the left side of the unit. Photograph by Gottfried Hogh.

speed directly from the "speed-meter" (see Figure 2). Slow moving birds produced low frequency signals, while faster moving targets produced higher ones. Each *received* Doppler frequency (determined by the bird's speed) and the speed itself (indicated on the speed-meter) were recorded on the tape recorder.

I saved the tapes of Doppler frequencies for later study by means of an audio-spectrograph. This will provide a pictorial record from which I can analyze flight and wing-beat patterns indicated by slight changes in speed. All of the Doppler frequencies that I recorded will appear on the spectrograms between 30 and 2,000 cycles per second. I recorded an "A" tone of a pitch pipe at the beginning of each field recording to insure against misrepresentation of the Doppler frequencies. This was necessary because the speed of the tape moving across the reproducing head of the recorder can be highly variable and thus may greatly distort results.

The speed-meter, on the back of the unit (see Figure 3), is calibrated at two-miles-per-hour intervals. Early results showed that my observations were biased if I attempted to record speeds to the nearest one mile per hour. Consequently I placed all speeds in proper two-miles-per-hour intervals. For example, all recorded speeds of 20 mph and under 22 mph were placed in one interval and its midpoint (i.e., 21 mph) was considered representative of the interval. If the recorded flight-speed of an individual bird varied (e.g., accelerated from 21 to 29 mph), an average of the extreme values was computed (25 mph) and included in the sample.

If a bird failed to fly exactly parallel to the transmitted radar beam, I had to determine the angle between the beam and the bird's flight and use a correction table to compute the bird's true speed. A scale on the tripod mount of the unit aided me in determining the angles. Since the difference between a bird's indicated speed and its true speed is insignificant when the deviant angle is between 0 and 20 degrees, most of my determinations were made when the angle fell within this range.

I used a hand-held Lafayette wind-velocity indicator to determine wind direction and velocity. Because most birds were flying low and close to the observer, I feel that I obtained a fairly accurate indication of winds that affected the birds. However, updrafts resulting from high rocky piers and buildings caused changes in wind direction and velocity and affected the flight of some birds. I had no way of measuring these effects.

When winds were greater than five mph, I divided my sample into three groups: birds flying across the wind; with the wind; and into the wind. Birds flying directly with the wind, or at an angle of less than 45 degrees to this course, I placed in the "with the wind" category. Similarly, birds flying directly into the wind, or at an angle of less than 45 degrees to such a course, were placed in the "into the wind" category. The remaining birds I listed as flying across the wind.

Results

When possible, I analyzed recorded speeds statistically. I assumed that flight-speeds of birds flying under the described conditions were normally distributed. With the exception of one sample (bimodal) of Barn Swallow speeds, my assumption was supported by my data. A summation of the flight-speeds for each species studied is given below. Information given for larger samples includes: the arithmetic mean; the standard deviation (± SD); the range (in parentheses); and the 95-per-cent-confidence interval for the arithmetic mean. (The confidence interval is stated in full, proper form in the first sample but is thereafter referred to simply as "confidence interval.") The values for Bird Species 1-8, 14, and 16 are summarized in Figure 4.

1. *Herring Gull*—Total: 267 speeds in or near the colony. I recorded 130 speeds in winds of less than 6 mph. The mean speed was 25.0 ± 5.73 mph (range from 15 to 39 mph). Assuming that the speeds I collected represent a random sample, I can state at the 95-per-cent-confidence level that the interval from 24.01 to 25.99 mph straddles the true population mean—i.e., the mean for all Herring Gulls flying under similar conditions. I also recorded speeds for gulls flying in winds of 6 to 15 mph. The mean speed for 84 birds flying *across* the wind was 25.6 ± 7.72 mph (range from 11 to 43 mph) and the confidence interval from 23.93 to 27.27 mph. The mean for 29 birds flying *with* the wind was 34.7 ± 7.15 mph (range from 21 to 49 mph) and the confidence interval from 31.98 to 37.42 mph. The mean of 24 birds flying *into* the wind was 18.8 ± 8.11 mph (range from 7 to 39 mph) and the interval from 15.37 to 22.23 mph.

2. *Ring-billed Gull*—Total: 277 speeds in or near the colony. I took 257 speeds when winds were less than 8 mph. The mean was 22.7 ± 5.86 mph (range from 11 to 43 mph), and the confidence interval from 21.98 to 23.42 mph. In addition, I took the speeds of 20 hand-released gulls (three of which were immature) in winds of 1 to 2 mph. The birds that were released directly in front of the unit and tracked as they accelerated to a constant speed averaged 13.7 ± 1.34 mph immediately after release (range from 11 to 17 mph). The interval from 13.12 to 14.28 mph should straddle the true mean speed if a person were to release an infinite number of birds. The birds accelerated to an average speed of 24.9 ± 2.57 mph (range from 21 to 27 mph)

and the interval from 23.77 to 26.03 mph should straddle the true mean for an infinite number of releases in the colony. I observed no significant difference in the acceleration rate of the two age groups.

3. *Common Tern*—Total: 26 speeds. I recorded 23 speeds in a small colony during a one mph wind. The mean speed was 26.0 ± 2.48 mph (range from 21 to 29 mph), and the confidence interval from 24.93 to 27.07 mph. I also recorded two speeds of individuals flying along the beach into a 3 to 7 mph wind. One bird traveled at 37 mph, while the other varied between 33 and 41 mph. Another bird flew 15 mph into a 20 mph wind.

4. *Black Tern*—Total: 128 speeds with no wind, all over a marshy area where the birds nested. Mean, 17.5 ± 3.29 mph (range from 9 to 31 mph); confidence interval from 16.92 to 18.08 mph.

5. *Bank Swallow*—Total: 126 speeds, divided into two groups: (1) Speeds, 95 in all, near the colony in winds less than 6 mph. Mean, 21.3 ± 2.72 (range from 13 to 31 mph); confidence interval from 20.74 to 21.86 mph. (2) Speeds, 31 in all, of birds feeding over the Ring-billed Gull colony some distance from the swallow colony, with wind at 7 mph. The variable flight patterns in these cases made it very difficult for me to determine the actual effect wind had on the flight. Therefore, since speeds were recorded during moderate winds only, I have not indicated the direction of flight in relation to winds. The mean was 30.7 ± 5.68 mph (range from 23 to 41 mph) and the confidence interval from 28.62 to 32.78 mph.

6. *Barn Swallow*—Total: 243 speeds of birds flying in winds at 9 to 10 mph near a colony in a large barn. Of birds flying *across* the wind, 129 speeds. Mean, 17.0 ± 5.32 mph (range from 5 to 33 mph); confidence interval from 16.08 to 17.92 mph. This sample was bimodal, with modes at 13 and 21 mph. Of birds flying *with* the wind, 35 speeds. Mean, 22.2 ± 5.94 mph (range from 11 to 35 mph); confidence interval from 20.16 to 24.24 mph. Of birds flying *into* wind, 79 speeds. Mean, 16.7 ± 4.27 mph (range from 9 to 33 mph); confidence interval from 15.74 to 17.66 mph.

7. *Cliff Swallow*—Total: 177 speeds, all taken near the colony during winds at 20 mph. Of birds flying *across* the wind, 42 speeds. Mean, 15.3 ± 4.37 (range from 9 to 23 mph); confidence interval from 13.94 to 16.66 mph. Of birds flying *with* the wind, 59 speeds. Mean, 19.4 ± 5.47 mph (range from 9 to 31 mph); confidence interval from 17.97 to 20.83 mph. Of birds flying *into* the wind, 76 flight speeds. Mean, 12.9 ± 4.48 mph (range from 5 to 23 mph); confidence interval from 11.88 to 13.92 mph.

8. *Purple Martin*—Total: 252 speeds taken near the colony. Of birds when there was no wind, 169 speeds. Mean, 21.7 ± 6.05 mph (range from 5 to 41 mph); confidence interval from 20.79 to 22.61 mph. Remaining speeds recorded during a 9 mph wind. When flying *across* wind, 50 speeds. Mean, 19.4 ± 3.64 mph (range from 13 to 27 mph); confidence interval from 18.35 to 20.45 mph. When flying *with* the wind, 17 speeds. Mean, 19.2 ± 2.99 mph (range from 13 to 23 mph); confidence interval from 17.66 to 20.74 mph. When flying *into* the wind, 16 speeds. Mean, 18.8 ± 3.79 mph (range from 11 to 25 mph); confidence interval from 16.78 to 20.82 mph.

9. *Spotted Sandpiper*—Two speeds, both of 25 mph. Birds flying over land with no wind.

10. *Chimney Swift*—One bird flying 15 to 21 mph. No wind.

11. *Eastern Kingbird*—Five speeds from different birds flying over a marsh, four of 21 mph, one of 13 mph. Little or no wind.

12. *Tree Swallow*—Two speeds of 5 and 19 mph with no wind. A third speed of 11 mph into a 9 mph wind.

13. *Cedar Waxwing*—Three speeds of 21, 23, and 29 mph. No wind.

14. *House Sparrow*—Total: 84 speeds of birds flying near a barn in which they nested. (No wind direction indicated since most of the birds were somewhat shielded by the barn from the 9 to 11 mph wind blowing at the time.) Mean, 17.7 ± 5.25 mph (range from 5 to 39 mph); confidence interval from 16.56 to 18.84 mph.

15. *Red-winged Blackbird*—Three speeds, one of 17 mph and two of 23 mph, with no wind. Two speeds during a 9 mph wind, one of 17 mph *into* the wind, the other of 21 mph *across* the wind.

16. *Brown-headed Cowbird*—Total: 26 speeds of birds flying about a farmyard. (No wind direction indicated since most of the birds were shielded by a large barn from a 9 to 11 mph wind.) Mean, 18.4 ± 3.43 mph (range from 13 to 27 mph); confidence interval from 17.01 to 19.79 mph.

17. *American Goldfinch*—Three speeds of birds flying when there was no wind. One speed of 39 mph near the bottom of a dip in undulating flight; the second of from 21 to 33 mph; and the third of 19 mph. The latter two birds were at varied points in their undulating flight.

Discussion

I used the *t*-test (at the five-per-cent-confidence level) to analyze differences in mean flight-speeds of larger samples, except where the mean squares of samples were found to be significantly different. In these cases, Cochran's approximation of this test was employed (see Snedecor, 1956).

Wind velocity affected flight-speeds in varying degrees depending on the species involved. Herring Gulls flying with 6 to 15 mph tail-winds maintained speeds faster than those recorded for gulls flying across the wind or without wind. Also Herring Gulls flying into the wind were slower than birds flying across the wind or without wind (see Figure 4). In 9 to 11 mph winds, Barn Swallows flying with the wind were faster than those flying across or into the wind, but I found no significant difference in speed between Barn Swallows flying into and across the wind. However, my sample of Cliff Swallow flight-speeds across 20 mph winds showed a significant difference from samples of birds flying with or into the wind (see Figure 4). Winds of 9 mph did not affect the flight of the larger Purple Martins.

Increases in speeds of birds flying with the wind were greater than the corresponding decreases for birds flying into the wind (see Figure 4). It thus appears that birds flying into the wind may increase stroke pressure in an attempt to counteract the wind effect. On the other hand, birds flying with the wind do not seem to decrease their stroke pressure to as great a degree to correct for similar wind velocities. Also, because of the streamlined shape of birds—with feathers overlapping in a regular pattern from the anterior portion of its body to the posterior—birds flying with the wind are probably affected more by the wind than are birds flying into the wind.

Speeds of Herring Gulls flying across the wind were nearly the same as those of birds flying when there was little or no wind. Purple Martin speeds across the wind were significantly slower than those of martins flying during no wind. Nevertheless, the mean speeds for this species on windy days were slower than the mean speed of the sample taken when there was no wind (see Figure 4). A variable other than wind velocity probably caused this discrepancy.

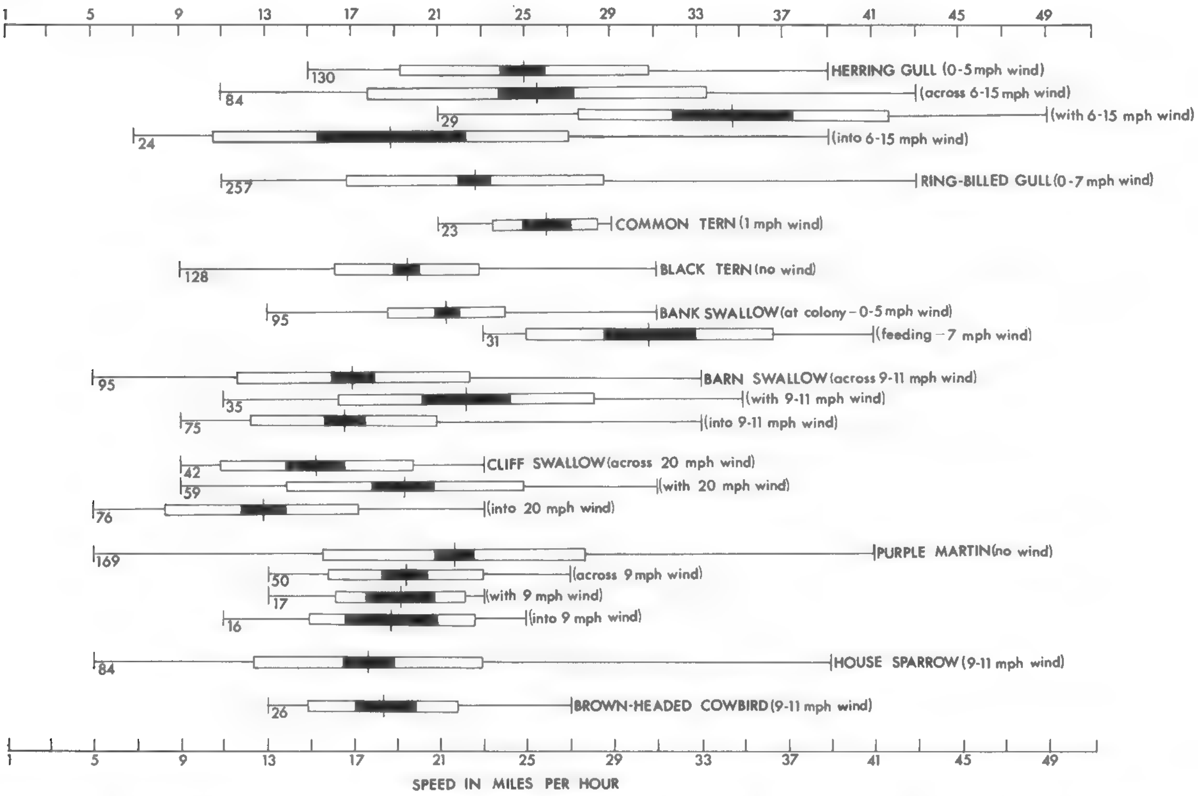

Figure 4. The flight-speeds recorded for 10 bird species. Horizontal lines show observed ranges. Rectangles mark the standard deviations, with the solid black indicating the 95-percent-confidence interval for the mean. Vertical lines through the rectangles indicate the mean speeds. The number of flight-speeds in each sample is given near the left end of each horizontal line.

The mean flight-speed for feeding Bank Swallows was faster than that of swallows flying near the colony (30.7 mph : 21.3 mph). My field observations indicate that birds of other species also fly faster when they are feeding than when they are near the home colony.

Herring Gull speeds were faster than those of the smaller Ring-billed Gull (25.0 mph : 22.7 mph). Mean flight-speeds of Common Terns were faster than those for Black Terns (26.0 mph : 17.5 mph). I found no important difference between the flight-speeds of Bank Swallows and Purple Martins or between Barn Swallows and Cliff Swallows when they were flying across the wind. However, the mean speeds for Bank Swallows and Purple Martins were appreciably faster than those for Barn and Cliff Swallows.

Quantitative data are now needed for comparison of flight-speeds of birds under different conditions (e.g., while feeding, in migration, etc.). Tapes of Doppler frequency signals should be analyzed for wing-beat and flight patterns of different species.

The Doppler radar unit has enabled me to obtain a great number of accurate flight-speeds in a relatively short time. The fact is that I recorded more flight-speeds in two summers of field work than have been reported in the ornithological literature to date. The unit has proved its value as a tool for research. Henceforth it should aid ornithologists not only in obtaining flight-speeds of any or all bird species but in correlating flight-speeds with physiological and behavioral data. Its potential as a research tool is unlimited.

Summary

During the summers of 1963 and 1964, while in northern Michigan, I used a Doppler radar unit to determine flight-speed of birds.

The radar unit is described. I recorded 1,628 speeds of 17 species. The speeds of eight colonial species were analyzed in detail. With the exception of one sample, all speeds were taken of birds flying under "natural" conditions. Flight-direction was recorded with relation to wind. Mean flight-speeds ranged from 12.9 miles per hour for Cliff Swallows flying into winds at 20 miles per hour to 34.7 miles per hour for Herring Gulls flying with winds at 6 to 15 miles per hour.

Wind velocity affected the flight of most birds. The effect was less for birds flying into the wind than for those flying with the wind. Speeds of birds flying across the wind were, for the most part, not significantly different from those of birds flying without wind.

The mean flight-speed for feeding Bank Swallows was faster than that for birds flying near the colony. Herring Gulls were faster than Ring-billed Gulls. Common Terns flew faster than Black Terns. Bank Swallows and Purple Martins were faster than Barn and Cliff Swallows.

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Coucal, *Centropus sinensis*

CHARACTER DISPLACEMENT IN SOME PHILIPPINE CUCKOOS

KENNETH C. PARKES

Brown and Wilson (1956) proposed the term "character displacement" for a "seldom-recognized and poorly known speciation phenomenon that we consider to be of potential major significance in animal systematics." The phenomenon in question is that in which two species whose ranges overlap differ more or less markedly from one another where both occur together, but are similar to one another where each occurs alone. Alerted by the Brown and Wilson paper to watch for such cases, zoologists could, after 1956, no longer refer to character displacement as "seldom-recognized." Although Mayr (1963:83) sought to replace the term character displacement with "sympatric character divergence," Brown (1964) showed that the grounds for such a change were fallacious. "Character displacement" has thus become a widely-accepted and useful addition to the vocabulary of evolutionary studies.

Explanation of Character Displacement

Brown and Wilson express the phenomenon of character displacement in two ways: (a) the two species involved *diverge* in their area of sympatry; (b) the two species *converge* (in presumably adaptive characters) in their respective areas of sole occurrence. The authors several times refer to such divergence and convergence as alternative or complementary descriptions of the same phenomenon. This is true primarily of the end results, the appearance of the animals to the eye of the classifier. As a careful reading of Brown and Wilson's paper reveals, completely different sets of factors operate to influence the convergent and the divergent character displacement.

There is an additional dichotomy, involving factors likely to result in character displacement. The two major kinds of species interactions in areas of overlap are called by Brown and Wilson "ecological displacement" and "reinforcement of the reproductive barriers."

The first of these, ecological displacement, concerns the evolution of adaptations permitting a reduction in competition between two related sympatric species. Typically this involves, in birds, the size of body and of bill or other food-getting apparatus; but Brown and Wilson's concept of character displacement would also cover behavioral alterations, such as a change by one of the species in nest-site preference where nest-sites are at a premium. It is, of course, difficult to know whether such behavioral

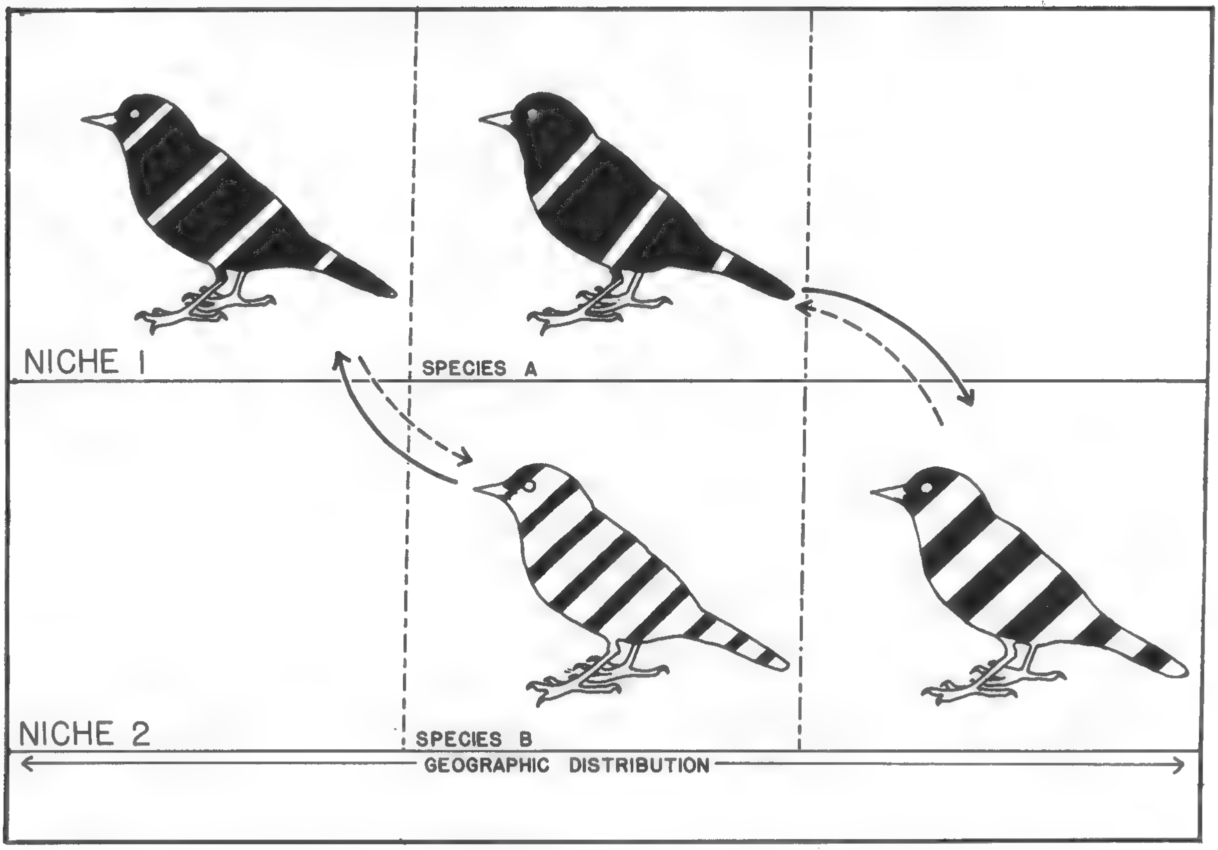

Figure 1. Diagrammatic representation of *ecological character displacement*. As shown here, Species A, when entering a vacant niche usually occupied by Species B, evolves some of the adaptive characters typical of B (and vice versa). This kind of character displacement can involve convergence (unbroken arrow), divergence (broken arrow), or both.

alterations are truly genetically based, and, indeed, the whole controversial concepts of "competition" and "exclusion" are inextricably involved in this ecological type of character displacement (Brown and Wilson, 1956:59-61; Mayr, 1963:66 ff.; Brown, 1964). It is in such cases of ecological displacement that the relative importance of divergence within the zone of overlap and convergence outside it are sometimes difficult to assess (Figure 1).

The other major type of interaction between sympatric species, the reinforcement of the reproductive barriers, which Brown and Wilson think is possibly less important, has received much attention in recent years, especially from students of birds and of batrachians (see Sibley, 1957 and 1961, the bibliographies of both, and the transcript of the discussion after the 1961 paper). Interspecific matings are, from the biological viewpoint, almost always wasteful; wasteful of time, energy, and genetic material, since "either the resulting inseminations are ineffectual, or the hybrids produced are inviable or sterile" (Brown and Wilson, 1956:59). The "species recognition signals," usually both behavioral and morphological, are the characters which tend to be reinforced in areas of sympatry. The morphological characters often involve organs employed in displays.

Needless to say, when two related species are sympatric, *both* the ecological and the signal-reinforcement types of character displacement may well ensue. This seems to be true, for instance, in what Brown and Wilson (1956: 50) call "the classic illustration of character displacement," the case of the rock nuthatches *Sitta tephronota* and *S. neumayer* presented by Vaurie (1950, 1951). In this instance, the modification of bill shape in the area of sympatry clearly indicates a shift in ecological niche at least as far as foraging is concerned. It is difficult, however, to find an ecological explanation for the displacement in facial pattern (reduction in eye-stripe in *S. neumayer* and

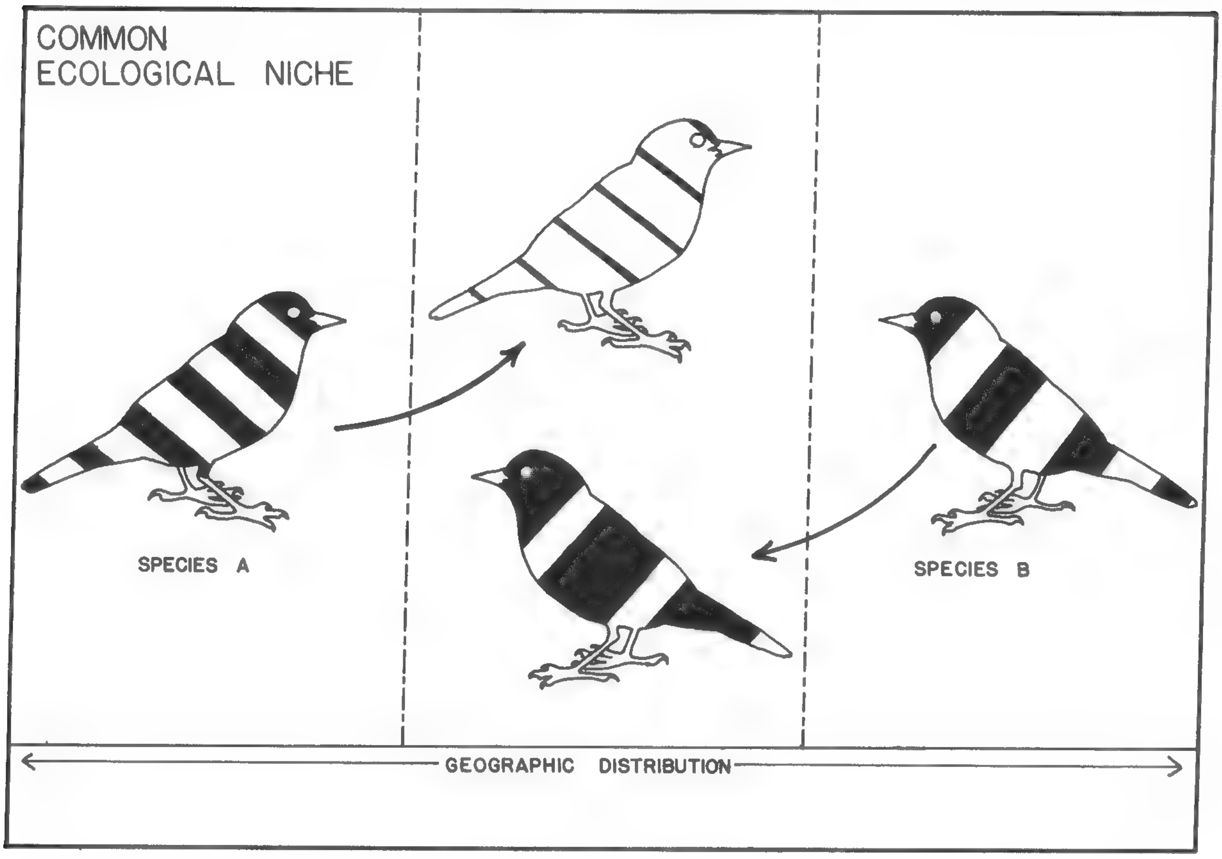

Figure 2. Diagrammatic representation of *reinforcement of species recognition characters* when the two species overlap both geographically and ecologically. Much alike where found alone, Species A and B diverge through interaction in the overlap zone.

enhancement of it in *S. tephronota*) in the overlap zone, and it seems more likely that the facial pattern constitutes a species-recognition signal in this area of sympatry, as briefly mentioned by Vaurie (1951:166). We should note that, as is often the case, the differences between the two species evolved through the alteration of characters already present. In this case, it is an increase and a corresponding decrease in the pigmentation of the eye-stripe, resulting in conspicuously different facial patterns.

Although, as in the *Sitta* case, character displacement in sympatric species may frequently (and perhaps usually) involve both the ecological and signal-reinforcement types, in other instances the two species appear to overlap ecologically as well as geographically. Here the intrinsic reproductive isolating mechanisms appear to be of paramount importance, and the divergent aspect of character displacement prevails (Figure 2). An interesting example, which may be of this sort, occurs in the genus *Centropus*.

Character Displacement in Genus Centropus

Description of the Genus *Centropus*

The genus *Centropus* is a widely distributed, chiefly tropical group of Old World cuckoos collectively known as "coucals." They are largely terrestrial, and when they venture into trees, progress by hopping from branch to branch. They have long tails and relatively short, rounded wings, and rather weak powers of flight. The predominant colors are black (either dull or glossy), white, and various shades of brown. The relationships within the genus are not well understood at present; we need a thorough monograph of *Centropus* of the "distributional history" type.

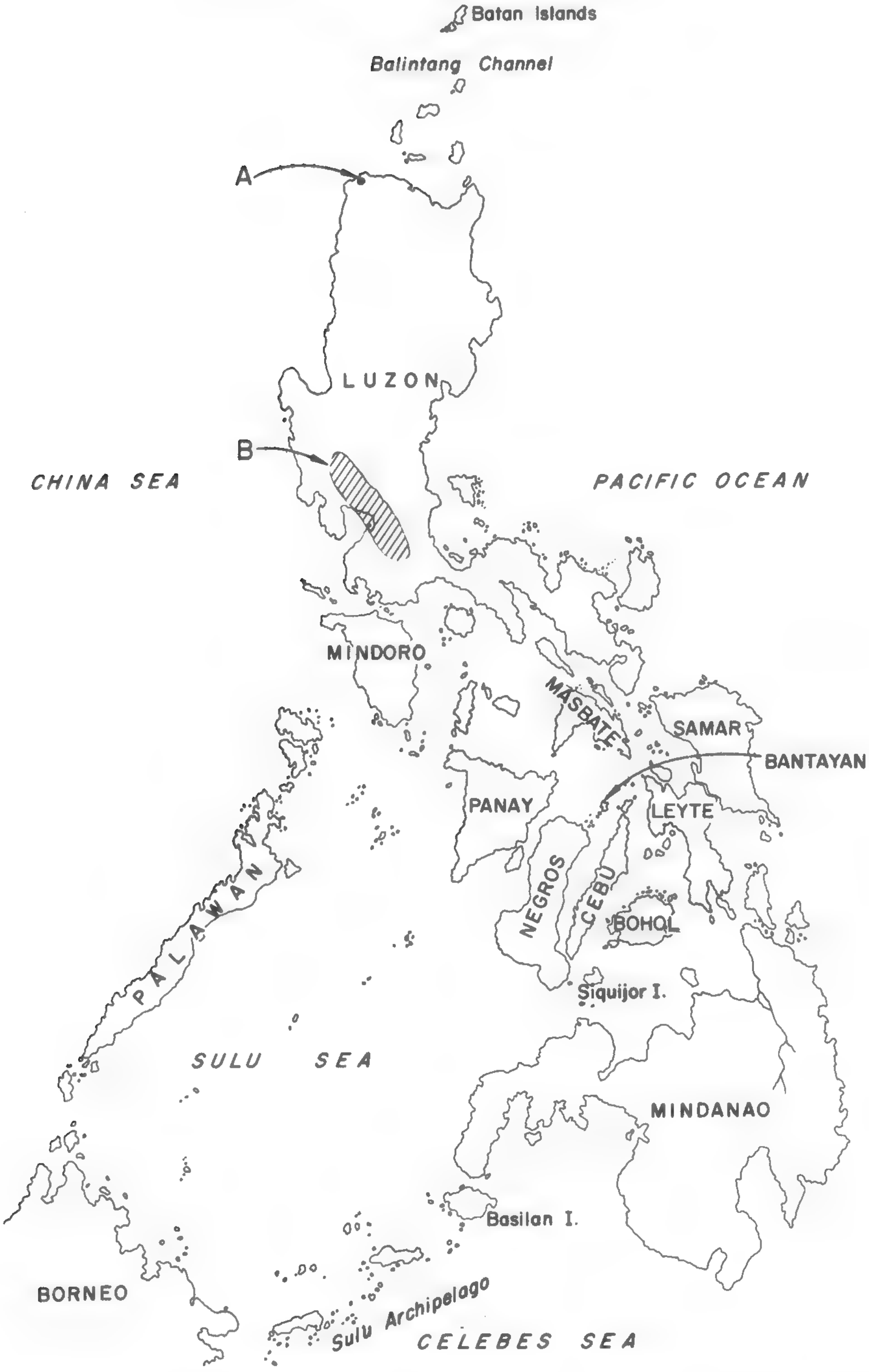

Figure 3. Map of the Philippine archipelago. A. Locality of the hybrid between *Centropus v. viridis* and *Centropus bengalensis molkenboeri*. B. The general area where the author conducted his field work.

Centropus in the Philippine Archipelago

No less than six species of *Centropus* inhabit the Philippine archipelago (Figure 3). Four of these are endemic in the Philippines, and two represent more widely distributed species. One of the latter *(C. bengalensis)* and one of the endemics *(C. viridis)* are the only two species found virtually throughout the archipelago; of the other four, three *(C. sinensis, C. melanops, C. unirufus)* are restricted to a few islands and one *(C. steerei* of Mindoro) to a single island.

The endemic subspecies *Centropus bengalensis molkenboeri* occupies most of the Philippine archipelago although the birds of the outlying Sulu islands are referable to *C. b. javanensis,* the subspecies of the Greater Sunda Islands (Parkes, 1957b). Much of the range of *C. b. molkenboeri* is also occupied by *C. viridis viridis* although melanic races have developed on Mindoro (*C. v. mindorensis*) and on Batan Island, north of Luzon (*C. v. carpenteri*). According to McGregor (1909), both *C. b. molkenboeri* and *C. v. viridis* inhabit the following islands: Bantayan, Bohol, Cebu, Leyte, Luzon, Mindanao, Negros, Panay, Siquijor. Both subspecies have subsequently been recorded from other islands, but this list shows that the two species are extensively sympatric within the Philippines.

Centropus bengalensis and *C. viridis*

There may be some tendency for an ecological separation between *C. bengalensis* and *C. viridis,* but it is certainly not well marked. I collected only two specimens of *C. bengalensis* during two months of field work in central Luzon (Figure 3, B) in 1956; both of these were in scattered shrubs in rather open fields (one in a water-buffalo pasture). I saw or collected *C. viridis* in a wide variety of habitats, from tall grass to fairly dense second-growth woods; I collected one and saw several others in the same pasture from which I took one of the *C. bengalensis.* Habitat descriptions in the literature suggest that *C. bengalensis* may be just as versatile as I found *C. viridis* to be, and therefore we may discount ecological separation between these two species as of little or no importance as an isolating mechanism.

Delacour and Mayr (1946:111-112) describe *C. v. viridis* as "medium" (16 inches) in length, and *C. b. "javanensis"* (=*molkenboeri*) as "small" (15 inches). This is a misleading oversimplification of the size relationship between the two species. As in all *Centropus,* females exceed males in size by a substantial margin. In *C. v. viridis* this difference may be as much as 100 mm (or about 4 inches) in total length, and 37 mm (or about 1.5 inches) in wing length. Although sex for sex *C. bengalensis molkenboeri* averages smaller than *C. viridis,* females of *C. b. molkenboeri* may equal or exceed males of *C. viridis* in size, just as in the North American Sharp-shinned and Cooper's Hawks (*Accipiter striatus velox* and *A. cooperi*). Even in the extremes, however, the contrast in body size is not as great as in the hawks, and we have no evidence that there is any difference in the feeding habits of the two coucals to correlate with the size difference.

Comparision of *Centropus bengalensis* and *C. viridis*

Within the genus *Centropus,* the two species under discussion may not be particularly closely related. The young birds differ quite radically in color and pattern of plumage. *C. bengalensis* has a plumage cycle which includes a so-called "eclipse" (=basic) plumage differing sharply in pattern from the alternate plumage, whereas in *C. viridis* the plumages are the same color the year around (Parkes, 1957a). The breeding season aspect of the two species, however, is generally somewhat similar. Both could be crudely described as black birds with brown wings. When the Philippine endemic *C. v. viridis* is compared with examples of *C. bengalensis* from its entire range, a striking similarity in color pattern will be noted between *viridis* and the geographically distant *C. b. bengalensis* of the Asiatic mainland. Both have the head, underparts, and tail black with a decided iridescent sheen (predominantly green in *viridis,* blue in *bengalensis*); both have the wings and scapulars reddish brown (deeper in *viridis*); and both have blackish tips to the flight feathers of the wings, which are otherwise unmarked. There are a few faintly indicated light shaft-streaks among the lesser wing coverts of *C. b. bengalensis,* but these are inconspicuous and visible only at close range.

The Philippine subspecies *C. bengalensis molkenboeri* is quite different in appearance, but is connected with *C. b. bengalensis* through two transitional subspecies, *C. b. chamnongi* and *C. b. javanensis.* As I have previously indicated (Parkes, 1957b), *C. b. molkenboeri* is rather obviously a derivative of *C. b. javanensis* (and not recognized as different until first shown by Deignan, 1955), but has departed from *javanensis* in such a way that each of the characters used in the taxonomic diagnosis represents an extreme condition for the species *bengalensis* as a whole, combining to make *molkenboeri* the least *viridis*-like subspecies of *Centropus bengalensis.*

The pertinent characters of *molkenboeri* are as follows: the black feathers of head, underparts, and tail exhibit the minimal iridescence within the species; the scapulars and interscapular areas are darkest, contrasting least with the black of the head; back and wing coverts with many strongly contrasting pale shaft-streaks; wing coverts, primaries, and outer secondaries with extensive black markings, tending toward definite barring on the secondaries.

The nature of the distinguishing features of the race *molkenboeri* strongly suggests that we have here an excellent instance of character displacement in an area of overlapping ranges. The significance of the intensified differences between the color pattern of the wing and dorsal areas of the two sympatric species is suggested by the only description I have read of a breeding season "display" in *Centropus.* Gilliard (1950:21) describes an individual of *C. phasianinus nigricans* which he observed "walking slowly across a grass clearing with its head downward and its wings partially open and nearly touching the ground." Such a position would show to best advantage exactly those portions of the plumage in which *C. bengalensis molkenboeri* differs most sharply from *C. v. viridis,* strongly suggesting that these plumage differences have evolved as species-recognition signals.

Hybridization in *Centropus*

When I presented an earlier version of this paper at the 1957 meeting of the American Ornithologists' Union, the concept of the "need" for reinforcement of species-recognition characters in these two species of *Centropus* was purely theoretical. This was deduced from the geographical and ecological coexistence of the two species and the nature of the distinctive characters of *C. b. molkenboeri.* Later, however, I found dramatic evidence for the validity of my theory. Paradoxically, the existence of hybrids is one of the best pieces of evidence that two species interact in a way that would lead to character displacement of the kind discussed above. As Sibley (1961:72) has stated, "hybrids constitute proof that interspecific mating has occurred but the fact that sympatric species of birds differ in visual and/or auditory characters suggests that interspecific interactions are constantly operating to promote and maintain species-specific diversity in the isolating mechanisms of such communities."

In the collection of the Peabody Museum of Natural History, Yale University, is a specimen (no. 48130) which I have identified as a hybrid between *Centropus v. viridis* and *Centropus b. molkenboeri.* It is a male ("T[estes] E[nlarged]") taken at Balaoi, Pagudpud, Province of Ilocos Norte, Luzon (Figure 3, A), by D. S. Rabor and R. B. Gonzales, on 1 May 1959. Its wing length is 150 mm, and its weight, recorded by the collectors, was 117.6 grams. Both of these figures are a good match for males of *C. v. viridis* (see figures for both species published by Rand and Rabor, 1960:334). Although there is overlap, the bill of *molkenboeri* tends to be shorter and proportionately deeper, more strongly arched, than that of *viridis*. The bill of the hybrid is peculiar in being longer than in *molkenboeri*, but even more slender than most *viridis*. Both the rectrices and the primaries of *viridis* are wider than those of *molkenboeri*, and in this character the hybrid is intermediate. The strong green iridescence of the head, tail, and anterior underparts of the hybrid is a *viridis* character, showing possible *molkenboeri* influence only in somewhat of a blackening in the forehead region. The reddish brown of the primaries matches *viridis* in color, but the dark tips are blacker, less brownish. The innermost secondaries are washed with blackish, unlike those of *viridis*. The most conspicuous *molkenboeri*-like feature of the hybrid is the presence of conspicuous pale shaft-streaks on the scapulars and wing coverts, never found in *viridis*. In addition, the specimen is molting out of an "eclipse" basic plumage like that found in *molkenboeri* and never in *viridis*. There is a single old feather of basic plumage on the crown and there are additional remaining basic feathers on the lower breast and most of the flanks and among the tail coverts. These feathers appear similar in pattern to the equivalent feathers of *molkenboeri*, but with the black barring averaging somewhat broader. Thus, as is so frequently the case, this hybrid exhibits some characters of either parent in more-or-less typical form, as well as others in which distinct intermediacy can be seen.

This hybrid appears to be the first reported in the family Cuculidae. Gray (1958) does not even mention cuculids and the *Zoological Record* has no entry for such a hybrid in subsequent issues.

Discussion

Most cases of character displacement of this sort, previously demonstrated, have involved two species not only with overlapping ranges, but also with areas of sole occurrence of each of the species. It may be quite difficult to reconstruct the evolutionary history of such cases and conjecture as to which species "invaded" the range of the other. On the other hand, allopatric populations of both species being available for comparison, we can determine whether one or both species "diverged" in the area of overlap, and what the relative extent of this divergence is.

In the case of the two species of *Centropus*, *bengalensis* and *viridis*, the area of overlap encompasses, for all practical purposes, the *entire* range of one of the species (*viridis*). The fact that we are dealing on the one hand with an endemic Philippine species with several subspecies (*viridis*), and on the other with an endemic Philippine *subspecies* of rather obvious derivation (*molkenboeri*), suggests that *viridis* has been on the scene for a longer period, that *C. bengalensis javanensis*, invading the Philippines, encountered the resident *C. viridis*, and gave rise to the distinctively un-*viridis*-like *molkenboeri*. Other collectors have found, as I did, that *molkenboeri* is less common than *viridis* where the two are sympatric (for example, Ripley and Rabor, 1958:40).

We have additional circumstantial evidence as to the length of time that *Centropus viridis* has been present in the Philippines, fortifying the theory that *C. bengalensis* is the more recent immigrant. The relationships of *C. viridis*, as shown by the plumage sequence and details of color pattern of both adults and young, seem clearly to lie with the widespread *C. sinensis*. I suggest that *viridis*, which is much smaller than *sinensis*, represents an early invasion of the Philippines by *sinensis* stock which evolved a small insular race, the forerunner of the present *C. v. viridis* (Figure 4). This

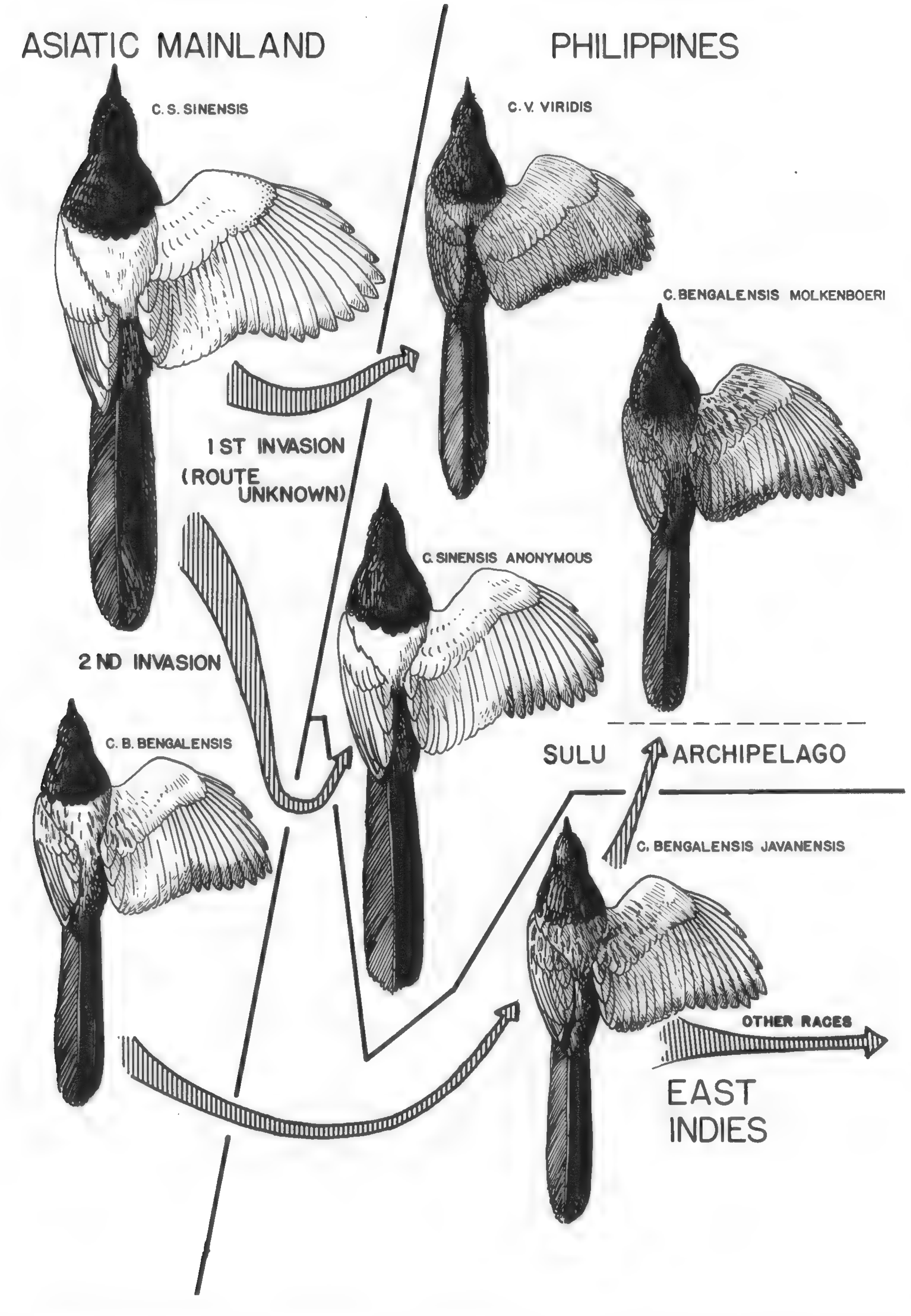

Figure 4. Diagrammatic representation of suggested history of three species of *Centropus* in the Philippines (see text).

small form spread throughout the archipelago, eventually itself giving rise to the two isolated melanic races *C. v. mindorensis* and *C. v. carpenteri.* That this *viridis* offshoot of *sinensis* stock has reached the species level of evolution is shown not only by its obvious morphological differences from modern *sinensis,* but also by the fact that a *second* invasion of *Centropus sinensis* has carried this species as far as the Sulu Archipelago and Basilan in the southern Philippines, where, as the subspecies *C. s. anonymous,* it is now sympatric with *C. v. viridis.*

The substantial difference in size between *C. sinensis* and *C. viridis* probably acts as enough of an isolating mechanism in itself to preclude any strong selective pressure toward character displacement where these two are now sympatric. In addition, there is a suggestion that *C. viridis* itself may be a relatively recent invader of the outlying Sulu Archipelago. F. S. Bourns and D. C. Worcester (quoted in McGregor, 1909:385) comment on the abundance of *C. bengalensis* in the Sulu group as opposed to elsewhere in the Philippines, and, as stated above, the subspecies of *bengalensis* in the Sulus is *javanensis* rather than the Philippine *molkenboeri.* This suggests that when *bengalensis* reached the Sulus, *viridis* was absent, and that both *viridis* and *sinensis* have more recently penetrated the Sulu Archipelago from opposite directions. The first of these two to arrive was probably *sinensis,* as it is represented by the endemic subspecies *C. s. anonymous,* whereas Sulu *viridis* have not been taxonomically separated from those of the rest of the Philippines. There would be little likelihood of interaction leading to character displacement between *C. sinensis* and *C. bengalensis* on the Sulus; they are quite dissimilar, and coexist over a vast range in Asia.

Note: When discussing the relationships of *Centropus bengalensis* in an earlier paper (Parkes, 1957b), I stated that I believed premature the proposal of some authors to "lump" this species with *C. grillii* of Africa and *C. toulou* of Madagascar (the latter being the oldest name for the group as a whole). I still believe that we need a detailed study of the plumage sequence of *C. toulou* before we can determine its affinities, but in all fairness I mention that Mr. H. G. Deignan, who knows *C. bengalensis* well, wrote me as follows (letter of 12 December 1964): "In 1962 I was in Madagascar, and, in some stations, in daily contact with *Centropus toulou toulou*; nothing in voice, habitat, actions, or study of skins could lead me to believe that it was *not* conspecific with '*bengalensis*'." I have not been able to re-examine this case, so continue provisionally to use the specific name *bengalensis* for the Philippine bird pending further study.

Summary

The term "character displacement" was introduced by Brown and Wilson for an evolutionary phenomenon in which two related species with overlapping ranges were unlike one another in the overlap zone, but similar where each occurs alone. Such divergence of characters in the overlap zone may be correlated with ecological competition, with reinforcement of reproductive isolating mechanisms, or both. Two species of the cuckoo genus *Centropus, C. bengalensis* and *C. viridis,* overlap widely in the Philippines with little or no apparent ecological separation. The mainland Asiatic race of *C. bengalensis* looks much like *C. viridis,* which is a Philippine endemic species. The Philippine race of *bengalensis, C. b. molkenboeri,* has diverged in several morphological characters, possibly connected with courtship displays, making it the least *viridis*-like subspecies of its species. That the "need" for such reproductive isolating mechanisms exists is shown by a hybrid between the two species, the first hybrid cuckoo specimen ever reported. It is postulated that an offshoot of the widely distributed Asiatic *C. sinensis* reached the Philippines first and gave rise to *viridis;* the latter has clearly

reached the species level as it is sympatric with a later invasion of *sinensis* on a few islands. Arriving later, *C. bengalensis* responded to the presence of *viridis* by evolving the un-*viridis*-like subspecies *molkenboeri*.

Acknowledgments

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CARNEGIE MUSEUM, PITTSBURGH, PENNSYLVANIA

SOUND PRODUCTION IN TWO SPECIES OF GEESE

Charles A. Sutherland and Donald S. McChesney

With the development of the audio-spectrograph we now have a device for analyzing avian sounds objectively. The subjective terms—pitch, loudness, and quality—do not apply to the audio-spectrograms, which are in a sense the visual interpretations of sounds. Instead we use frequency, intensity, and pattern, respectively; a sound becomes a signal; and any errors, due to a personal reaction to a signal, vanish.

The spectrograph gives us the opportunity to re-evaluate the physics and mechanics governing what we shall refer to as the avian syringeo-tracheal system of sound production. The theoretical material presented here is based specifically on an analysis of the spectrographic patterns of vocalizations of the Ross' Goose *(Chen rossii)* and the Lesser Snow Goose *(Chen hyperborea hyperborea)* and the relation of these vocalizations to the syringeo-tracheal systems of these birds.

In an extensive paper dealing with the vocal apparatus in birds, Rüppell (1933) reviewed the early literature, considered many aspects of the syringeal structure in general, and discussed in particular the role of the syrinx and trachea. According to a translation of his paper, he described the process of sound production in the bird as "Corresponding to the phenomena in a reed pipe," in that "increased tracheal length lowers the pitch of the sound produced in the syrinx." This seems to agree with Myers (1917) who, working with hens, found that shortening the trachea tended to raise the pitch of the hen's calls. Miller (1934), although he questioned some of Rüppell's conclusions, wrote: "The mechanism is to be compared with an organ pipe (reed type)."

The statements of Rüppell and Miller infer that the length of the tracheal air column somehow controls the vibration rate of the tympaniform membranes in the syrinx. Nevertheless, Miller (1934) suggested that, on the basis of his work with owls, this might not be the case.

All three of these investigators assumed that pitch was an accurate measure of the rate of vibration of the tympaniform membranes. However, Fletcher (1934) pointed out that pitch is subjective while Stevens (1935) and Snow (1936) showed that pitch, loudness, and quality are mutually interdependent. Wood (1946:471) demonstrated that the loudness of a sound may be greatly augmented by increasing its overtones or harmonic content, and that, for some people, changes in the intensity of a sound may cause the perceived pitch to vary as much as 35 per cent.

Materials and Methods Used in the Study

Using the audio-spectrograph in the Laboratory of Ornithology we analyzed vocalizations of the Ross' and Snow Geese that had been recorded in the field and deposited in the Library of Natural Sounds. We paid particular attention to the frequency content and the relative amplitudes of the frequencies.

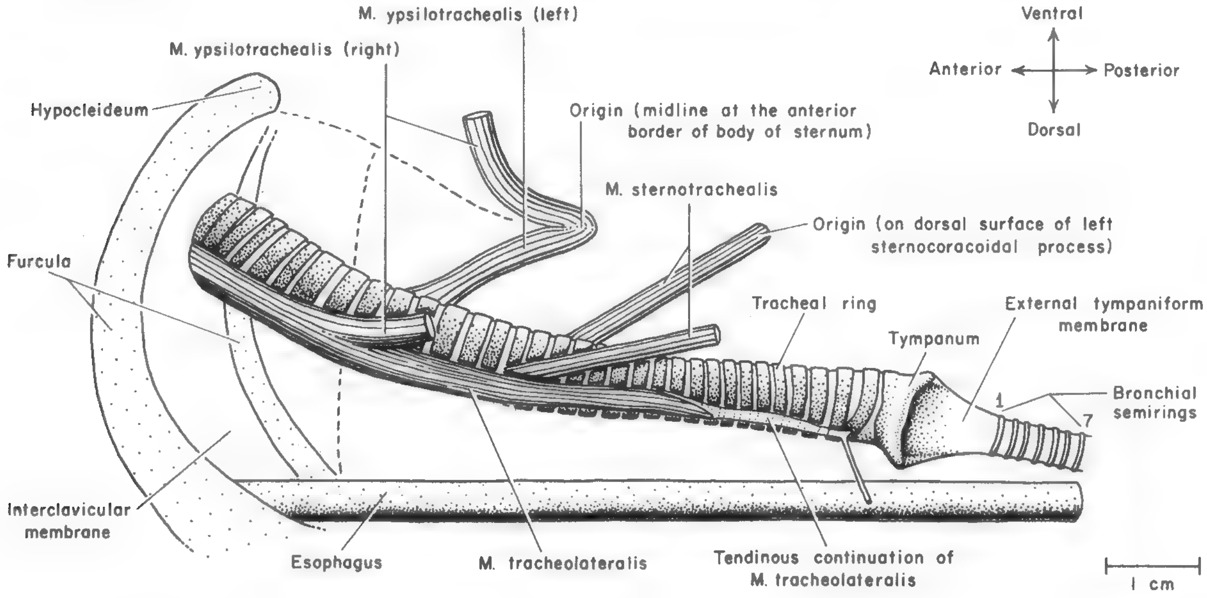

Figure 1. Lateral view of the syringeo-tracheal system in the Hawaiian Goose *(Branta sandvicensis)*. Note particularly: the tympanum which comprises part of the bony wall of the syrinx; the external tympaniform membrane which connects the tympanum with the first bronchial rings; and two muscles, *M. tracheolateralis* (pair) inserted on the trachea and *M. sternotrachealis* (one of pair shown) on the lateral surface of the trachea. (Drawing from *The Condor,* 1958, volume 60, page 304; reproduced with the permission of the editor and Philip S. Humphrey.)

Also in the laboratory we studied in detail the anatomy of the syrinx and trachea of many species of waterfowl, including geese, either *in situ* with the ventral aspect of the bird open to expose the vocal apparatus or from specimens of the syrinx and trachea that, together with the muscles and bronchi, had been removed from the bird and preserved in 70 per cent alcohol. (For an illustration of the syringeo-tracheal apparatus in a goose, see Figure 1.) Frequently we relaxed a preserved specimen in water and attempted to pass a recorded signal through the syrinx and to re-record the resulting signal in order to study the modifications in its frequency content.

After studying the literature describing the action of sound waves in various types of pipes, including open and closed pipes, we measured the length of the tracheae of preserved specimens from the two geese and calculated their hypothetical resonant frequencies. We compared these hypothetical resonant frequencies with the frequencies in the flight calls of the geese recorded in the field.

Results of Study

The spectrographic analysis (Figure 2) showed that the flight calls of the two geese were alike in that each contained at least the first six harmonically-related membrane frequencies. However, the emphasis in each call was different—the lowest harmonic (fundamental) was emphasized in the call of the Ross' Goose while the second harmonic (first overtone) was emphasized in the call of the Snow Goose. Figure 3, A and D, shows graphically how the two calls are alike yet different in emphasis.

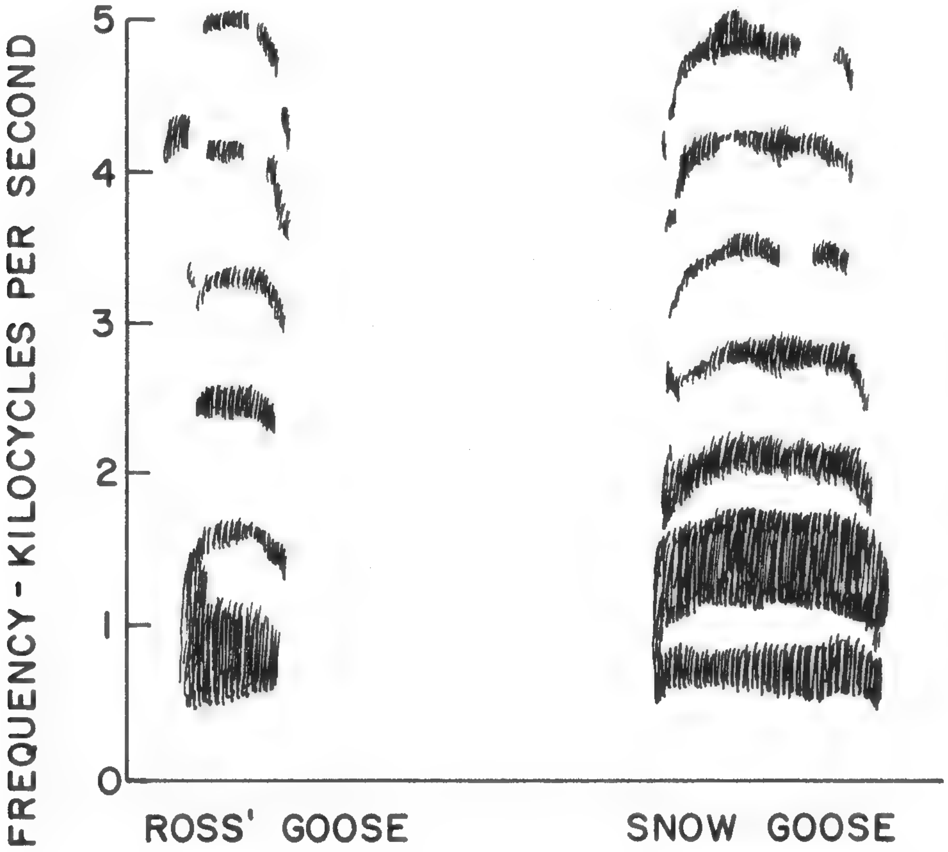

Figure 2. A drawing showing the spectrogram patterns of flight calls of Ross' and Snow Geese. The calls are alike in that each contains the first six harmonically-related membrane frequencies.

A study of the anatomy revealed that the Snow Goose had the longer trachea. Although this result agreed with Myers (1917)—that a shortened trachea raised the pitch of a hen's calls—it seemed to be incompatible with the physical fact that the longer the pipe, the lower will be the frequencies it emphasizes or resonates.

Assuming that the trachea functioned as an open pipe, we then calculated the theoretical resonant frequencies of the tracheae of the two species on the basis of their dimensions, and compared these figures with the frequencies in the flight calls of the wild birds. Figure 3, B and E, shows that these frequencies closely approached the dominant membrane frequencies, A and D, established for the wild birds. This finding cleared up the question of tracheal length as we shall explain presently.

We further substantiated our theory of the open pipe by testing it on other species of waterfowl. When we tried to pass recorded signals through the relaxed trachea of a female Mallard *(Anas platyrhynchos),* this trachea passed some signals, yet would not pass others of roughly equivalent amplitude. The spectrographic patterns of the sounds it did pass showed emphasis and loss of intensity (damping) at the same frequencies that appeared in the spectrographic patterns of the calls of a female Mallard recorded in the wild.

Exactly what is the relationship between the syrinx and the trachea in the production of avian sound? And what causes the emphasis of some frequencies and the damping of others? Our attempt to answer this question follows.

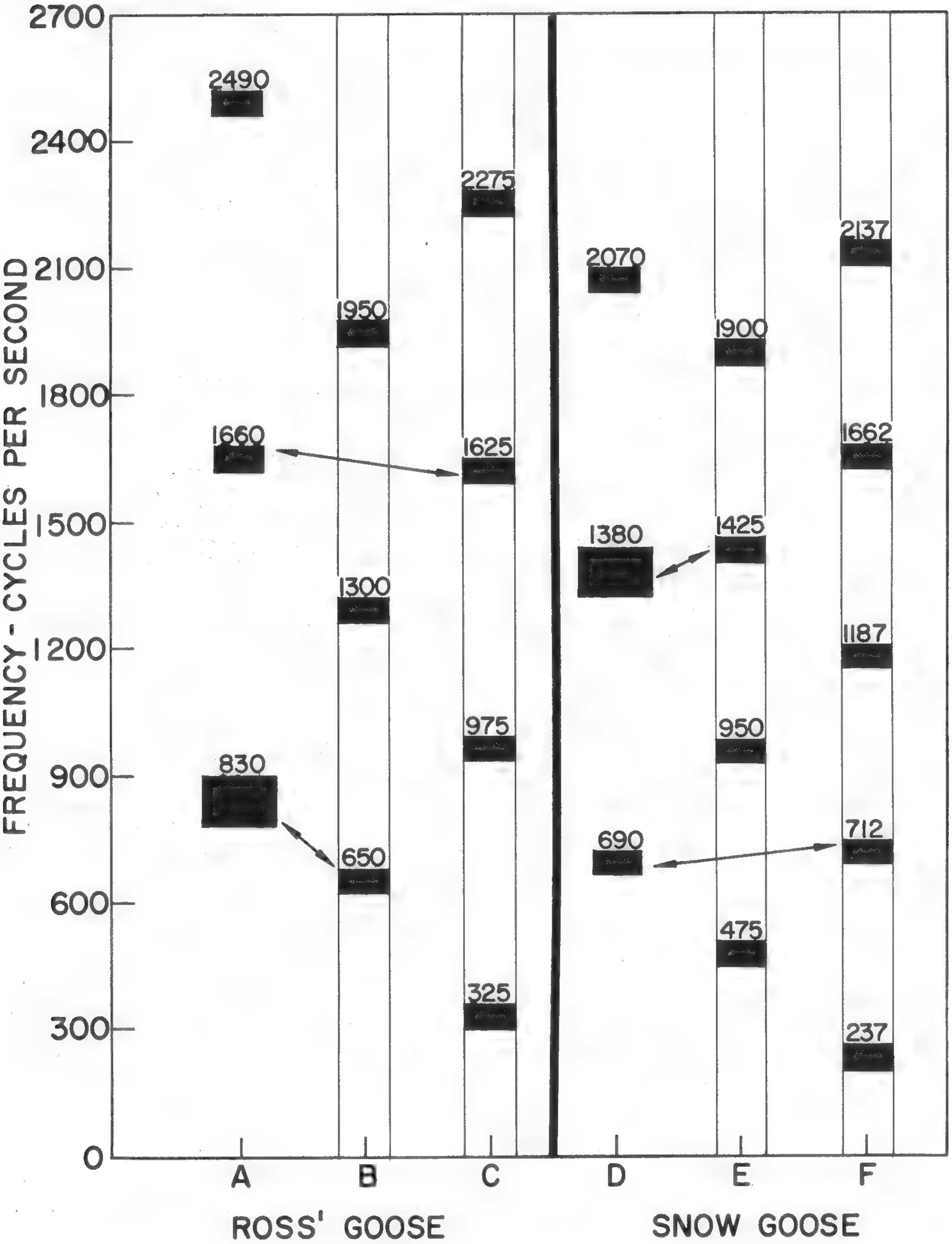

Figure 3. A comparison of the membrane harmonics of Ross' and Snow Geese, showing how the harmonics are different in emphasis. A and D, membrane harmonics of geese recorded in the field. B and E, resonant harmonics of trachea as open pipe. C and F, resonant harmonics of tracheae as closed pipe.

Discussion

Two Categories of Variables Affecting Sound Production

The first set of variables affecting sound production include physical characteristics controlling the actual generation of sound waves. These variables center around the tympaniform membranes of the syrinx (Figure 4). The second set of variables include physical characteristics modifying the sound waves after they have been generated in the syrinx. These variables are mainly associated with the trachea. We will consider the factors in both categories following a brief discussion of the mechanical operation of the vocal apparatus of geese.

Two pairs of muscles, *M. tracheolateralis* and *M. sternotrachealis,* control the syringes of Ross' and Snow Geese. (See Figure 1 for illustration of these muscles.) The first pair shortens the trachea by drawing the tracheal drum cranially. The second pair lengthens the trachea by drawing the tracheal drum caudally. Together these muscles control the cranio-caudal tension of the tympaniform membranes (Figure 4).

The tympaniform membranes are also under continual dorso-ventral tension due to the manner in which they are suspended from the tracheal drum and subjected to changes in air pressure both internally and externally. While the cranio-caudal tension tends to enlarge or widen the lumen (passageway) in each bronchus, the dorso-ventral tension tends to constrict or narrow it. When the trachea is drawn caudally, the cranio-caudal membrane tension is reduced and the tympaniform membranes move toward one another giving each lumen the form of a slit. Air rushing through these slits sets the membranes in motion and generates sound waves. A similar slit is formed when the neck of a toy balloon is stretched laterally.

The equilibrium positions about which the membranes vibrate in each bronchus are determined by the interaction of four forces: (1) The expanding force of the bronchial airstream. (2) The cranio-caudal membrane tension. (3) The compressing forces of the dorso-ventral membrane tension. (4) The positive air pressure within the interclavicular air sac surrounding the entire syrinx.

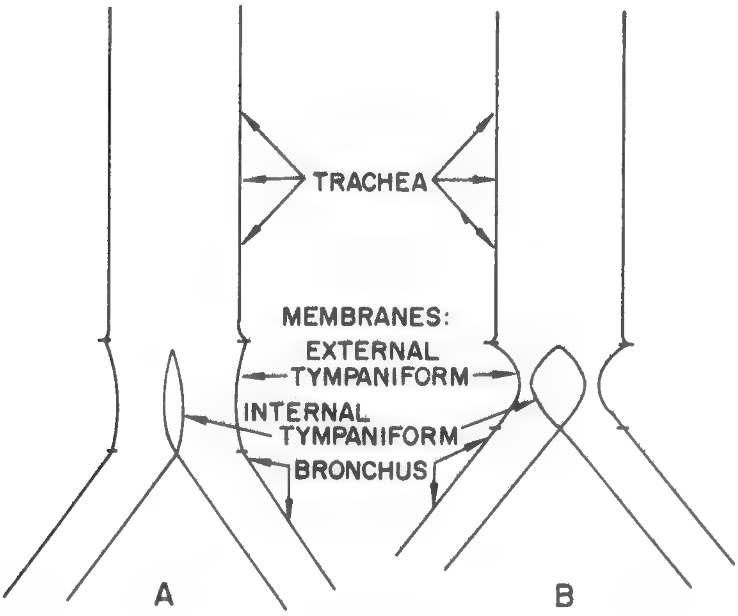

Figure 4. Diagrammatic illustration showing position of tympaniform membranes when under tension (A) and when relaxed (B). In A, the tympaniform membranes are under tension due to the relaxation of the sternotracheal muscles and contraction of the tracheolateral muscles. In B, the membranes—owing to the contraction of the sternotracheals and the reduction of forward tension—have relaxed and bowed into the lumen, creating slits through which the airstream passes.

The air pressure within the air sac impinges directly upon the outer surfaces of the tympaniform membranes. When the bird is exhaling, the area of greatest air pressure is within the bird's air sac and lungs—else the air would not flow out the bronchi and trachea. Therefore, during expiration the pressure within the interclavicular air sac is greater than the pressure within the bronchi. Because the greater pressure within the air sac must tend to force the tympaniform membranes into the bronchial lumen—thereby automatically helping to form a slit (Figure 4)—it is natural to expect sound production to occur when the bird is expelling air. Having performed the simple experiment of blowing air into a bird and then drawing it out, Miskimen (1951) also concluded that sound production occurred during expiration.

Variables Affecting Generation of Sound Waves

The tympaniform membranes do not vibrate at random, producing a jumble of unrelated frequencies. Instead, they vibrate regularly and produce a series of harmonically related frequencies, the lowest of which, for each membrane, is called the fundamental frequency. (Figure 3—830 cps for Ross' Goose; 690 cps for Snow Goose). The higher freqencies, or harmonics, are exact integer multiples of the fundamental. Although Haliday and Resnick (1961:433) state that the frequencies of the membranes do not form such a perfect series, spectrogram patterns indicate that these frequencies may be treated as if they were harmonically related (Figure 2).

The *thickness* and *width* of the tympaniform membranes are two additional factors that must influence the rate of vibration of the membranes. The thickness of the membranes appears, by eye, to be the same in the syringes of the Ross' and Snow Geese. The total membrane area was the same in both species. This similarity, however, may have been coincidental since the membranes were of different lengths and widths.

The Snow Goose had the wider membrane. It also had the lower membrane fundamental frequency. This implies that width may be more important in determining the rate of vibration of the membrane than either the length or total area. Miller (1934), working with the syringes of owls, also concluded this.

Variables Affecting the Resonance in the Trachea

As in all pipes, three major factors share in determining the resonant frequencies of the trachea—length, diameter, and hardness. The formula for approximating the frequency of any resonant harmonic is $F=V/n$, where F equals frequency being calculated, V equals the speed of sound in the tube, and n equals the wave length of the harmonic in question. Such calculations must be corrected—upward when the tube diameter is large compared to the length, and downward when the tube walls are soft and yielding.

Just as a membrane generates a harmonic series of frequencies, so the trachea resonates such a harmonic series. These two sets of frequencies, the membrane-generated frequencies and the trachea-resonated frequencies, are independent of each other. The resonant frequencies of the trachea are those that may be imposed on the tracheal air column with the minimum expenditure of energy. Additional energy would be required to impose other frequencies on this air column.

Thus we can conclude that, when the membrane-generated frequencies are close to the trachea-resonated frequencies, they are emphasized while those that are relatively farther away tend to lose correspondingly more of their energy as they pass through the trachea. This effect of the loss of energy in a signal is known as damping. For birds it means that some of the frequencies in their complex, membrane-generated calls will be damped or filtered out upon passage through the trachea—as happened in the case of the female Mallard.

This implies that the air in the trachea is forced to vibrate at the frequencies imposed upon it by the vibrating membranes (Wood, 1946:76). The tracheal air column does not control the rate of vibration of the tympaniform membranes. And changing the length of the trachea merely causes the trachea to damp or filter out a different set of frequencies which, as mentioned above, serves to modify, for some people, the pitch of the original signal.

Types of Resonating Pipes

There are two types of sound-resonating pipes, the closed pipe and the open pipe. Rüppell's (1933) reed pipe is an example of a closed pipe. At the open end of a closed pipe the air is free to oscillate, hence there are no pressure changes there. Since the air is not free to oscillate at its closed, or reed, end, the pressure must change there (Haliday and Resnick, 1961:430). The vibrating reed pipe promotes these changes periodically by cutting off the airstream entering the pipe. Air draws the reed down over the passage entering the organ pipe in the same way that air blowing through a doorway slams a door shut.

The wave length of the lowest frequency which a closed pipe can resonate or pass with minimum energy loss is equal to *four* times the length of the pipe. This is the pipe's fundamental frequency. In addition to its fundamental frequency, a closed pipe can resonate only its odd harmonics (Haliday and Resnick, 1961:430). The frequencies under C and F in Figure 3 represent the odd harmonics of the tracheae of the geese.

In an open pipe, the air is free to oscillate at both ends, which means that no pressure changes occur at either end (Haliday and Resnick, 1961:430). The wave length of the fundamental resonant frequency of an open pipe is equal to *twice* the length of the pipe. As a result, an open pipe can resonate both the even and the odd harmonics of its fundamental. The frequencies of B and E in Figure 3 represent the resonant harmonics of the tracheae of the geese. A trumpet player and his instrument represent an open pipe system.

Regardless of whether the pipe is open or closed the resonant frequencies are closer together in a long pipe than a short pipe.

Is the Trachea a Closed Pipe or an Open Pipe?

Consider columns C and F in relation to columns A and D in Figure 3. If the trachea functions as a closed pipe, the membrane second harmonic, 1660 cps, in the call of the wild bird, is closest to a tracheal resonant frequency of 1625 cps and would be expected to be dominant in the call. In the call of the Snow Goose, the membrane fundamental, 690 cps, would be expected to be dominant since it most nearly approaches an odd tracheal resonant frequency, 712 cps. Neither is the case.

If the trachea functions as an open pipe, the fundamental, 830 cps, of the Ross' Goose call would be expected to be emphasized in the spectrogram since it most nearly approaches a tracheal resonant frequency, 650 cps. Correspondingly, the second harmonic, 1380 cps, of the Snow Goose's call would be expected to be emphasized since it most nearly approaches a tracheal resonant frequency, 1425 cps. The spectrogram patterns in Figure 2 fit those of tracheae acting as open pipes and seem to confirm our suggestion that the trachea functions as an open pipe. The action of the avian syringeo-tracheal system is therefore analogous to the trumpet player system and not to the reed pipe system.

Conclusions

Three variables contribute to a determination of the frequencies produced by tympaniform membranes: (a) tension, (b) thickness, and (c) width. The rate of vibration of the tympaniform membranes is essentially independent of the length or volume of the tracheal air column. Three factors contribute to determination of the resonant frequencies of the trachea: (a) length, (b) diameter, and (c) tissue hardness. The trachael air column functions as a filter by damping out non-resonant frequencies produced by the membranes. The dominant frequencies in a bird's call are those membrane frequencies which most nearly approach its tracheal resonant frequencies. The action of the avian syringeo-tracheal system is analogous to the action of an open (trumpet) pipe rather than to that of a closed (reed) pipe.

Acknowledgments

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RELATIONSHIPS BETWEEN TWO FORMS OF THE RED-WINGED BLACKBIRD IN MEXICO

John William Hardy and Robert W. Dickerman

The integration of systematics, genetics, and ecology, including ethology, within the last twenty-five years has gradually resulted in a keener understanding of the dynamics of evolution. The systematist working at the specific and intraspecific levels has by necessity become a more sophisticated biologist, realizing that populations in nature are evolving at various rates through mutation and adaptation. The evolutionist continually seeks natural living models to illustrate these dynamic processes and each example he finds poses new problems and further refines his concept of the evolutionary process. This study of the Red-winged Blackbird shows how two races, or subspecies, of one bird species, nesting within sight of each other, remain ecologically distinct and do not interbreed.

Two races of the Red-winged Blackbird, *Agelaius phoeniceus gubernator* and *A. p. grandis,* inhabit the marshes at the headwaters of the Rio Lerma near the village of San Pedro Techuchulco in the State of Mexico. We shall refer to the area as the Lerma Marshes.

Until the autumn of 1963, when Dickerman collected molting young and adults of both *gubernator* and *grandis* from mixed flocks there, *gubernator* was the only race of the Red-wing known to occur in the Lerma Valley. Although post-breeding dispersal of Red-wings could have been responsible for the mixing of the two races, Dickerman considered this unlikely because the valley is mostly surrounded by high mountains. Thus he predicted correctly that both forms bred there and questioned their ecological relationship.

Our work grew out of Dickerman's general interest in marsh-dwelling birds in Mexico and his continuing investigation of the systematics of the Red-winged Blackbird in that country. Even the most superficial examination of the distribution of races of the Red-wing in Mexico as described in the "Distributional Check-list of the Birds of Mexico" (Herbert Friedmann *in* Miller *et al.,* 1957:291-293) will reveal difficulties in understanding the geographic relationships among the named populations. Consider, for example, *A. p. grandis* and *gubernator.* According to the Check-list (pages 292-293), *gubernator* is found in the highlands from Jalisco, Durango, and Zacatecas south to Chiapas. Yet, in the same highlands, *grandis* is said to inhabit Morelos, Hidalgo, and Puebla, thus splitting the range of *gubernator* into two parts.

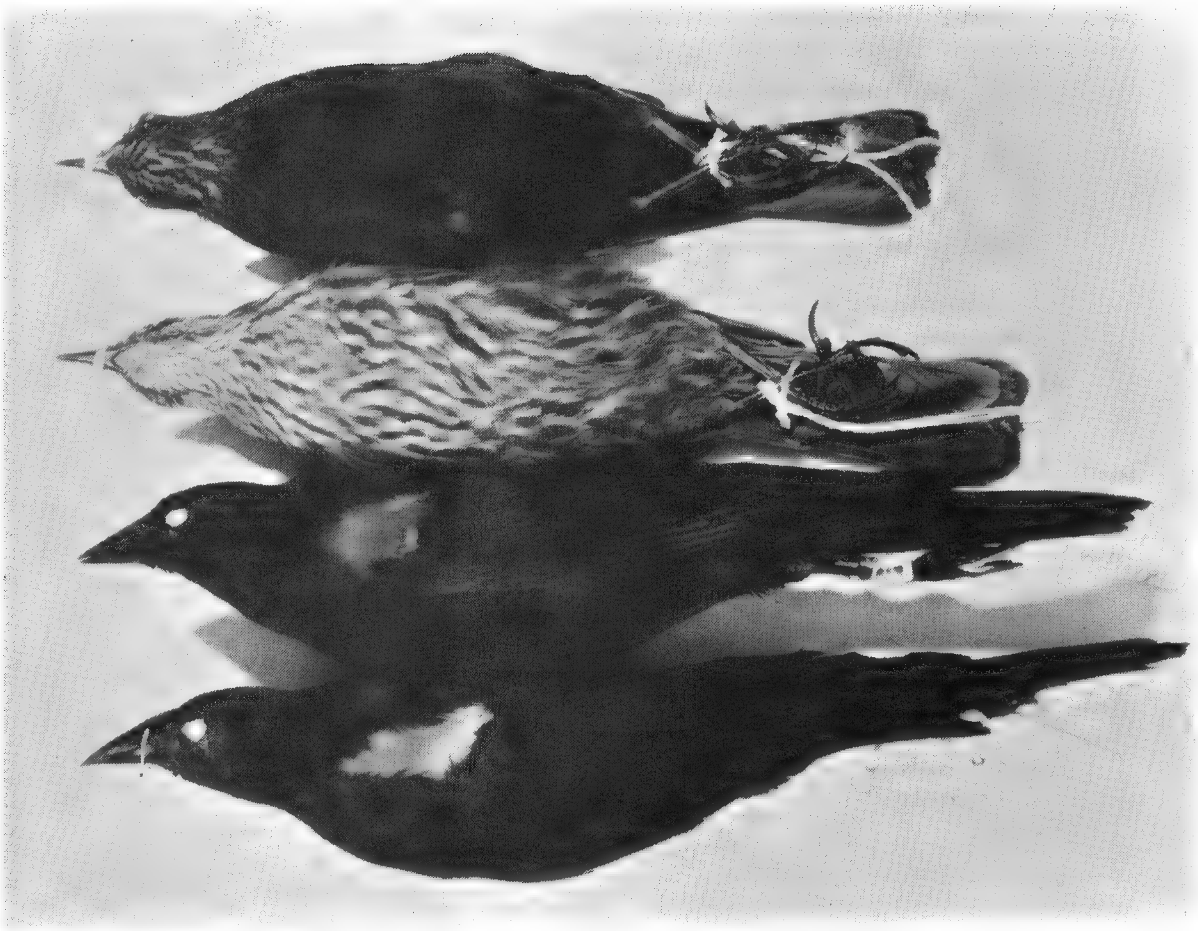

Figure 1. Adult males and females of two forms of the Red-wing, *A. p. grandis* and *gubernator*. From the top down: female *gubernator*, female *grandis*, male *gubernator*, male *grandis*.

Familiarity with the rapidly diminishing marshes of Mexico (see Dickerman, 1963) is basic to any understanding of geographic distribution and subspecific relationships in birds which prefer this breeding habitat. These marshes, scattered through a largely semi-arid land, are widely dispersed and further isolated from each other by numerous high mountain ranges. And populations of aquatic birds living in these wet lands often exhibit extensive geographic variation. To date, eight subspecies of the Red-wing have been described from, or breed in, mainland Mexico.

In the summer of 1964, both of us studied the relationships of *gubernator* and *grandis*. While we worked mostly in the Lerma Marshes, we also investigated populations of Red-wings near Cuernavaca in Morelos (where only *grandis* occurs), in the vicinity of Tlaxcala and Apizaco in the state of Tlaxcala (where the two forms meet and freely hybridize), and near El Carmen, Tlaxcala (Laguna del Carmen, in Puebla, where only *gubernator* occurs).

Plumage Differences

We found adult *grandis* and *gubernator* to be almost completely separable in the field by the long-known differences in their plumage. See Figure 1. Males of *grandis* have red epaulets broadly bordered with a pale yellow; males of *gubernator* have the epaulets either without a yellow border or with a few orange-buff feathers, usually not visible in the field. Females of *grandis* are pale and brown-striped with some individuals showing reddish in the epaulets; females of *gubernator* are almost solid sooty brown, with a small, variable amount of whitish on the chin and a variable amount of reddish in the epaulets.

Description of Juvenal Plumages

The juvenal plumages of these two Red-wings had never been described. We found the color differences between them obvious from the earliest stages of feather growth. Since the juvenal plumage of *grandis* is essentially like that of *A. p. phoeniceus* (see Dwight, 1900:160), it need not be described here. The juvenal plumage of *gubernator* is as follows: dorsal surface nearly solid, dark sooty brown like that of adult females, with buffy borders on a variable number of feathers of the back and tertials. Underparts are duller sooty brown with variable degrees of buff edgings to the feathers. In older juveniles, the edgings sometimes form a faint striped pattern on the breast and abdomen.

Behavorial and Ecological Differences

In the Lerma Marshes we found *grandis* and *gubernator* to be ecologically distinct—nesting within sight of each other but in different habitats. We also noted that the two forms exhibited differences in song and territorial behavior. These differences, particularly the ecological, serve to isolate the two races and prevent interbreeding. In Tlaxcala, on the other hand, the two forms nest together and interbreed freely, forming a hybrid swarm. Figure 2 diagrammatically depicts the results of our study.

Methods of Study

In 1964 we drew rough maps of our study areas where, from mid-June through most of August, we or our assistants made direct observations. We took specimens of birds and plants, all of which are now in either the Moore Laboratory of Zoology, Occidental College (birds and plants), or the University of Minnesota Museum of Natural History (birds only). We collected

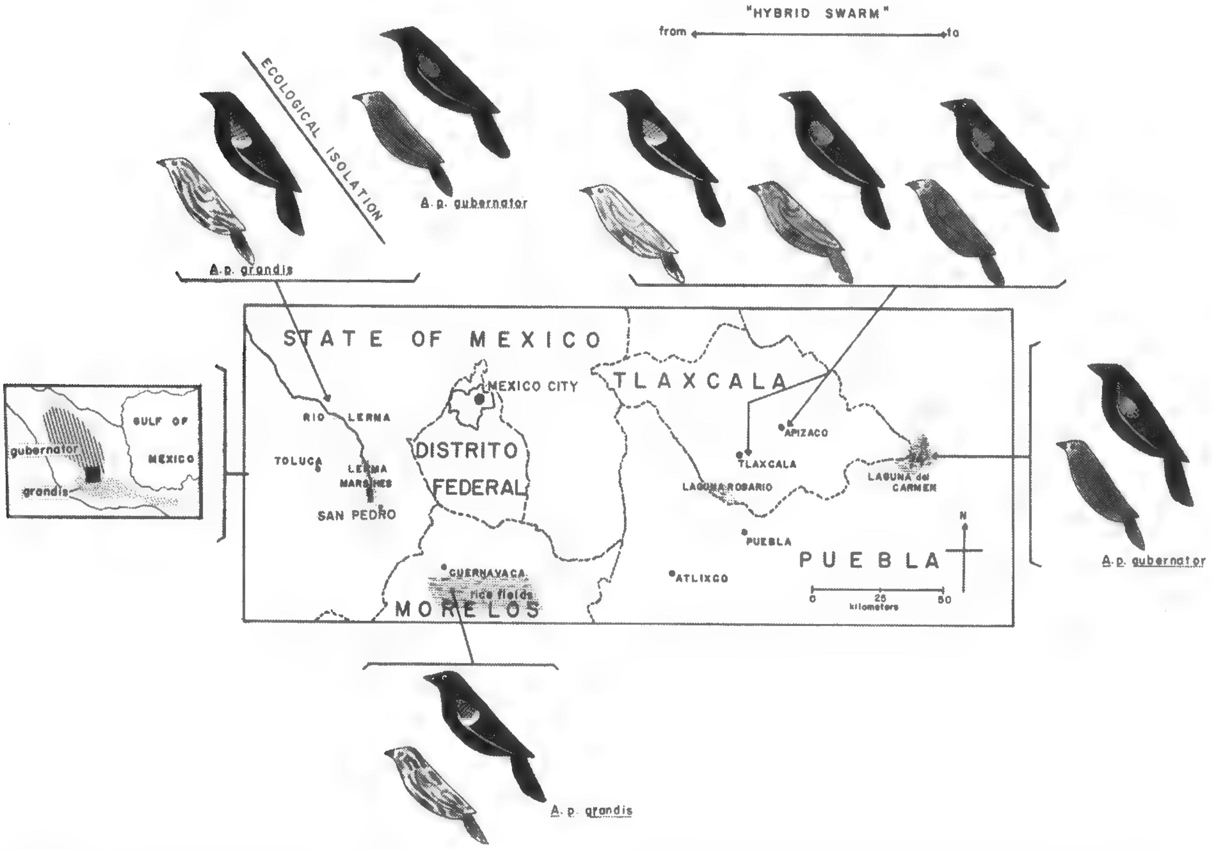

Figure 2. Map summarizing the distribution and relationships of the two Red-wings, *A. p. grandis* and *gubernator*, in central Mexico.

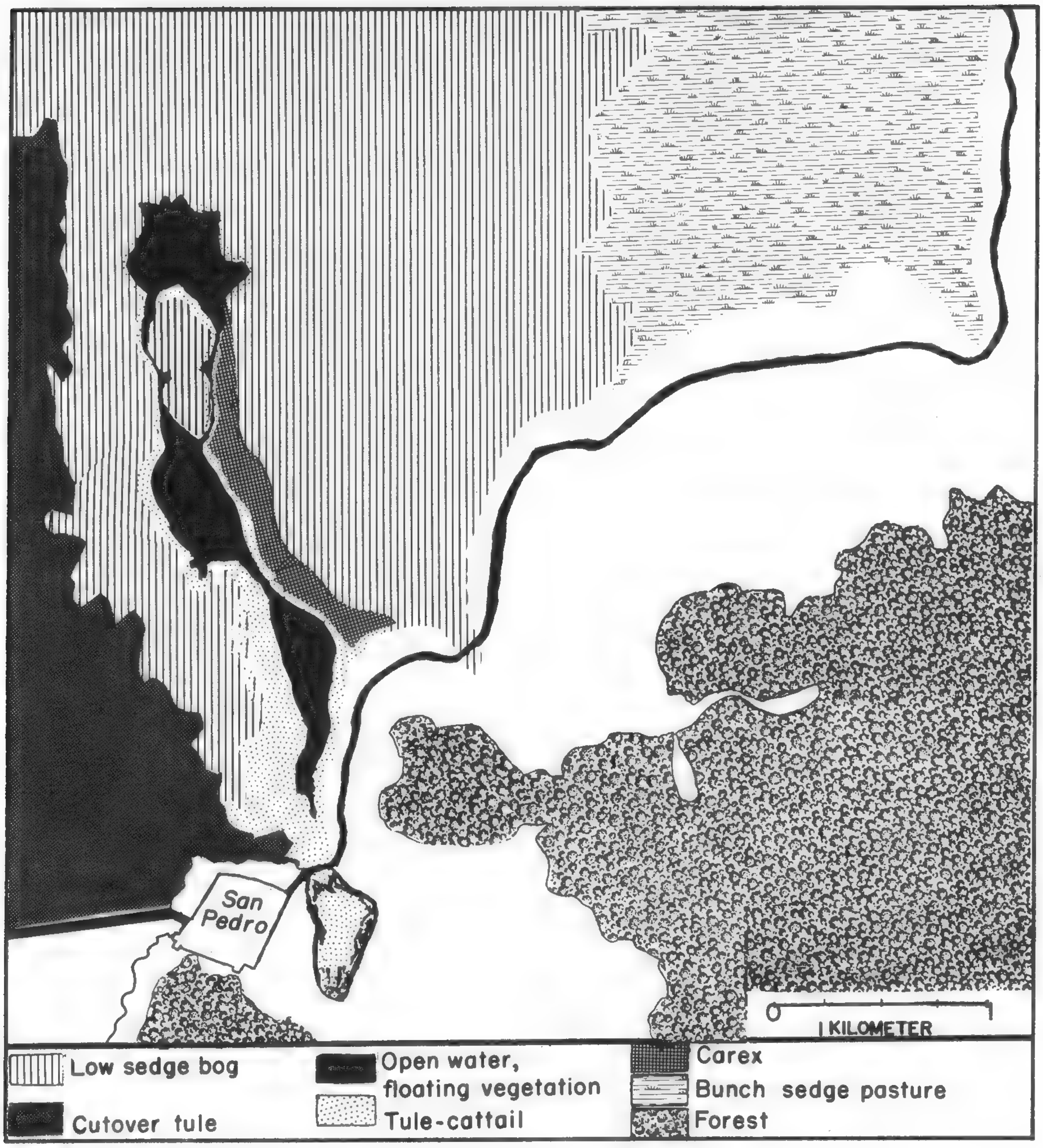

Figure 3. Map based on an aerial photograph showing the major vegetational communities in, and adjacent to, the relatively undisturbed portions of the Lerma Marshes.

insects with sweep nets and preserved stomach contents of all bird specimens for projected food-habits studies. We recorded Red-wing songs on a portable Uher, 4000-report tape-recorder at 7.5 inches per second, using an Altec 684-A microphone mounted with the sound pickup directed outward in a plastic parabolic reflector 24 inches in diameter with a 5.75-inch focal length. We played our Master tapes on an Ampex 960 tape-recorder at 7.5 ips and analyzed them on a Sona-graph 662-A Model recorder, with a frequency range of 85 to 12,000 cycles per second at the above tape-speed input. All our sonagrams were made by using the narrow band selector and the fL-1 position on the shaping switch and were photographed on high contrast copy film to create white backgrounds for the sound patterns.

The Lerma Marshes

Nelson (1897) and Goldman (1951) were among the first biologists to visit the area and describe several of the unusual aspects of its avifauna. They collected there in November 1892 and July 1904 when, according to their description, the area must have been at least ten times its present size, extending east to the village of Lerma at the base of the Sierra de las Cruces. At the present time the relatively undisturbed and undrained part of the marshes is restricted to about 24 square kilometers immediately north of San Pedro Techuchulco. Although some ditching and draining have been done even here, the chief disturbance is from the grazing of livestock and the cutting of the tules by natives for commercial purposes. The large area that is now almost totally devoid of marsh has been ditched and placed under intensive agriculture (mostly corn) and pasture, while aqueducts providing Mexico City with water from the springs of the marsh seem inevitably to ensure complete destruction of the undisturbed area.

Two recent biological surveys of the Lerma Marshes, one limnological (Rioja and Herrera, 1951) and the other broadly ecological (Cantu and Herrera, 1954), give a comprehensive picture of the vegetational and ecological complex. Our map, Figure 3, shows the vegetational communities mentioned in the present paper.

The three principal plant communities significant to the ecology of breeding Red-wings are the Low Sedge Bog-Marsh Community, the Bunch Sedge Pasture *Disturbed* Community, and the Tule-Cattail Marsh Community. Two other communities used by the birds as forage areas are the Open Water-Floating Vegetation Community and the *Carex* Bog-Marsh Community.

Low Sedge Bog-Marsh Community

The low sedge bog-marsh community (see Figure 4), a compact mat, largely composed of sedges overlaying water and forming a quaking "bog," occupies the greatest area within the marsh. Except where natives have dug ditches for dugout canoes and where cattle have worn pathways traversing the bog to and from grazing areas, little open surface water is present. The dominant plants—two sedges, *Eleocharis nodulosa* and *E. dombeyana*—are rather evenly distributed throughout the community and not only form most of the mat but also most of the above-ground cover which is seldom more than one-half meter in height. Other common, but unevenly distributed, plants are *Carex densa, Juncus trinervis, Cyperus* sp., and *Scirpus lacustris,* commonly called hard-stemmed bulrush or tule. All except the tule are low, sparse plants. Tule is an abundant dominant of another community to be described later; in the bog it occurs in scattered, sparse patches, where the bog mat is thin, and reaches a height of two to three meters. (The dark patches just below the horizon in Figure 4 represent this species.) In June and July 1964, there were several common to abundant flowering herbs, *Ranunculus dichostomus, Sium erectum, Sisyrinchium convolutum, Arenaria bourgaea, Castilleja arvensis,* and an abundant and evenly distributed orchid, *Spiranthes graminea.*

In addition to *A. p. gubernator,* widespread nesting birds in this community included the Short-billed Marsh Wren *(Cistothorus platensis),* Eastern Meadowlark *(Sturnella magna),* Song Sparrow *(Melospiza melodia),* Savannah Sparrow *(Passerculus sandwichensis),* Hooded Yellowthroat *(Geothlypis nelsoni),* Yellow Rail *(Coturnicops noveboracensis),* and Mexican Duck *(Anas diazi).* Garter snakes *(Thamnophis* sp.) were abundant and rattlesnakes *(Crotalus triseriatus)* rare (three recorded). Hardy saw one Peregrine Falcon *(Falco peregrinus)*—it was stooping on a Red-wing; Turkey Vultures *(Cathartes aura)* and Barn Swallows *(Hirundo rustica)* flew over the community almost constantly during the daylight hours.

Figure 4 *(above)*. The low sedge bog-marsh community in the Lerma Marshes.

Figure 5 *(below)*. The bunch sedge pasture *disturbed* community in the Lerma Marshes.

Bunch Sedge Pasture *Disturbed* Community

The bog just discussed gradually gave way to the pasture over a broad ecotone (see Figure 3), eastwardly from the open water. The pasture resulted from the lowering of the water table in the bog and the grazing of cattle. The quaking nature of the ground here is greatly reduced and the ground cover much less mat-like with a surface covering of trampled and grazed grass and sedge. Rather evenly distributed are hillocks of earth, out of which grow taller bunches of sedge (Figure 5). The sparse ground cover leaves considerable areas of nearly bare soil which is saturated with water. A false step may send a man up to his hips in dark oozing mud. In the rainy season much surface water accumulates here and numerous interconnecting ponds dot the landscape. Plants present in the bog are found here also, but all are less abundant. The bunches of sedge are primarily *Eleocharis dombeyana* and *E. nodulosa,* while *Scirpus lacustris* is very sparse.

Although *A. p. gubernator* was as common in this pasture community as in the bog, several species of birds, including Short-billed Marsh Wrens, Yellow Rails, and Mexican Ducks, were not seen in the heavily grazed areas. Savannah Sparrows were abundant where some heavier cover offered protected flyways. Striped Sparrows *(Oriturus superciliosus)* and Song Sparrows were uncommon along ditches, and Eastern Meadowlarks were fairly common and evenly distributed. Probably only an additional slight reduction in vegetational substrate would be necessary to eliminate the Red-wing as a breeding bird in this community. Much of this pasture area will undoubtedly be under cultivation within a few years, thus eliminating all breeding birds typical of the sedge bog.

Tule-Cattail Marsh Community

This community represents what most observers would classify as optimal Red-winged Blackbird breeding habitat (Figure 6). It consists of two dominants, tule and cattail *(Typha latifolia),* approximately equal in abundance and ranging from one to four meters in height. As can be seen in Figure 3, these grow in dense, narrow stands (four to ten meters wide) fringing the open water, and in two broad patches on either side of the road at the southeast corner of the marsh. Across the road from the main body of the marsh one of these patches of tules and cattails is approximately 18,750 square meters, surrounded by and interspersed with open water and floating vegetation. This was one of our principal study areas (Figure 7). Although the tule-cattail community is now comparatively limited in extent, there is evidence that it was recently far more extensive. The area immediately northwest of the village is one of cutover, grazed tules (see Figure 3). The disturbance has left a zone of water 10 to 50 centimeters deep with sparsely growing sedge and some floating vegetation. We believe this area may once have been a fairly extensive and dense stand of the tall sedge. The entire tule-cattail community is characterized by surface water 10 centimeters to a meter in depth, and the subsurface vegetational mat, when it exists, is never stable as in the bog.

This tule-cattail community is the breeding habitat of *A. p. grandis.* Other species that breed here are the Song Sparrow, Hooded Yellowthroat, Long-billed Marsh Wren *(Telmatodytes palustris),* King Rail *(Rallus elegans),* Virginia Rail *(R. limicola),* Common Gallinule *(Gallinula chloropus),* and Least Bittern *(Ixobrychus exilis).* The long-tailed weasel *(Mustela fre-*

Figure 6. The tule-cattail marsh community in the Lerma Marshes.

nata) was seen three times. Garter snakes were abundant. Turkey Vultures and Barn Swallows foraged over the area.

Open Water-Floating Vegetation Community

The black area of Figure 3 represents this community. It ranges from open water to a densely matted amalgam of *Limnobium stoloniferum, Lemna trisulca, L. gibba,* and *L. valdiviana, Utricularia vulgaris, Azolla mexicana, Myriophyllum heterophyllum,* and *Marsilea* sp. Red-wings forage in the more densely vegetated parts, perching and walking around on the mat. Song Sparrows and rails also feed and Pied-billed Grebes *(Podilymbus podiceps)* breed here.

Carex Bog-Marsh Community

This community exists as a 250-meter-wide strip between the low sedge bog and the tule-cattail marsh bordering open water. It differs from the low sedge bog in being dominated by a sedge, *Carex hystricina,* with a wide, sharp-edged leaf. The bog mat here seems thinner, and there is more surface water than in the low sedge bog. The predominance of *Carex* reduces the relative prevalence of plants typical of the low sedge bog, but total species composition appears to be the same. Red-wings apparently do not use this zone for any purpose. Both Long-billed and Short-billed Marsh Wrens are present, the former being more abundant but possibly not actually nesting in the community. Savannah Sparrows and Eastern Meadowlarks also frequent this area.

Agricultural Areas

Although there were some truck gardens, most drained marshland and adjacent upland were planted to corn. Both forms of the Red-wing fed frequently in these fields. We estimated that about 50 per cent of their foraging occurred here.

Other Ecological Characteristics

The Lerma Marshes, at approximately 2,500 meters elevation, are surrounded by mountains with pine and fir forest reaching to elevations of

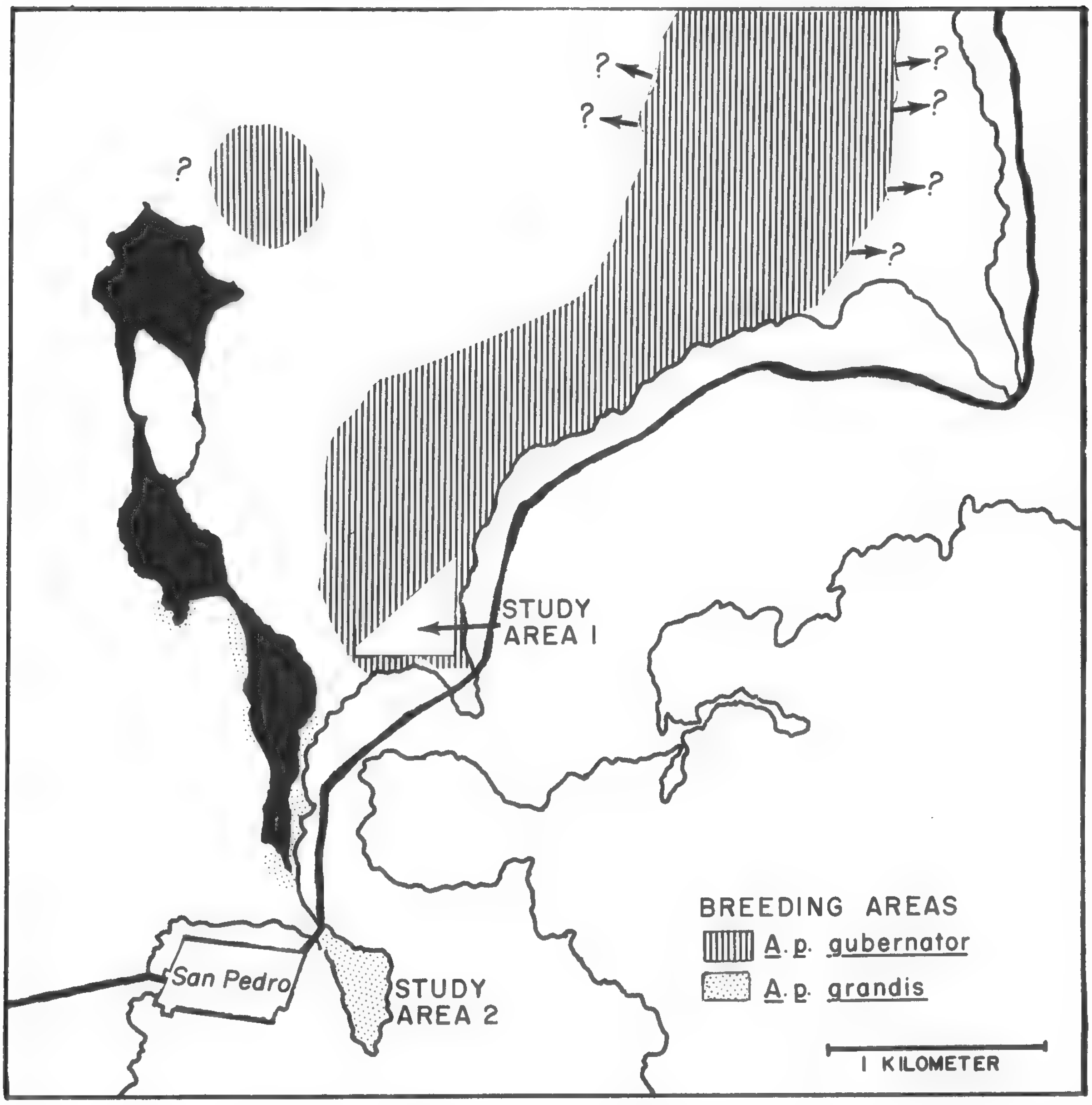

Figure 7. Map showing general distribution of breeding Red-wings and the principal study areas in the Lerma Marshes.

over 3,000 meters. The climate is temperate with a rainy season beginning in June and persisting until late September. The almost daily showers, principally in afternoon hours, are frequently accompanied by heavy hail storms. The remainder of the year is largely dry. Summer temperatures, ranging typically from 15 to 25° C, seldom exceed 25. In winter, sharp frosts occur almost nightly in nearby uplands and occasionally in the valley. Snow, rare even in the mountains, is usually in the form of flurries.

The breeding season of most birds seems to begin in May, probably when the first rains commence. In June and July, we found evidence of breeding (eggs, young, and/or nest-building) for Red-wings, Song Sparrows, Virginia and King Rails, Common Gallinules, both marsh wrens, meadowlarks, Hooded Yellowthroats, and Mexican Ducks.

Most species of birds found in the Lerma Marshes in summer are probably year-round residents. The area is a favorite wintering ground for migrant waterfowl.

Ecology of A. P. GRANDIS

Figure 7 shows the general distribution of the breeding Red-wings and the principal study areas in the Lerma Marshes. Six or seven males of *A. p.*

grandis held territories in Study Area 2. In addition, there were an estimated six males holding territories at scattered places within the remainder of the tule-cattail community. Most of these territories were in the main marsh on the opposite side of the road from Area 2. We feel certain that there were fewer than 20 territorial males of *grandis* in the region of the Lerma Marshes that we studied.

Breeding evidence gathered by us included the following: a female was seen carrying nesting material on 16 June; another was noted with nesting material and one carrying a fecal sac on 2 July; two juveniles were collected on 10 July, all in Area 2. In addition, singing males holding territories were in evidence from mid-June through mid-July in Area 2, and we observed both males and females daily leaving and entering the marsh from the cornfields. Local villagers informed us that this subspecies nests more abundantly in May and June, but we have no direct evidence of this. No grown juveniles or non-breeding adults were in the area during the time of our study.

No *grandis* inhabited the cutover tule areas and, so far as could be determined by our careful search using dugout canoes, none inhabited the dense but narrow tule-cattail strip along the edge of the open water adjacent to the *Carex* sedge bog.

The density of the *grandis* population was so low that it was doubtless responsible for the fact that we observed no overt territorial conflict between males. However, since the singing birds were present in the same places from day to day, they presumably held territories. The area of tule-cattail marsh within Area 2, seemingly optimal habitat, was approximately 12,500 square meters in area. Birds were active over all this area; thus, assuming seven territorial males in Area 2, we can obtain a maximum average territory size of 1,786 square meters. Because the water was deep and the bottom unstable, we had to use dugout canoes and traversed this community on the narrow canals cut by natives for harvesting the tules. We found only one active nest of *grandis* and collected only one fledgling in Area 2.

Interestingly, one nest of *grandis,* empty on 5 August, was discovered in the adjacent cornfield, approximately 250 meters from Area 2. More than a dozen old nests of *grandis* were found in Area 2, however, indicating that nesting had occurred here in the previous year. Nests of *grandis,* lashed to stems and leaves of tules and cattails, are typical for the species.

Why was the population of *grandis* so small in Area 2 when there is obvious abundance of appropriate nesting sites and plentiful food? We believe the explanation in part to be that the *grandis* population has recently invaded this marsh over mountain barriers from its range to the south.

Ecology of A. P. GUBERNATOR

The population of *gubernator* in the Lerma Marshes was many times larger than that of *grandis,* although density of the two populations was similar. Our study area for *gubernator* (Area 1 in Figure 7) was approximately the same size as Area 2, the *grandis* study area. Eight territorial males occupied Area 1, giving a maximum average territory size of 1,563 square meters. The low density of birds again was probably responsible, as it was for *grandis,* for the few territorial skirmishes noted among the males.

Area 1 was in the low sedge bog-marsh, but as mentioned, *gubernator* also inhabited the bunch sedge pasture, showing no preference for one over the other.

Most of the population in the bog-marsh was concentrated in a strip of vegetation approximately 750 meters wide running parallel to the road.

Beyond this zone, we found few birds. We believe that proximity to cornfields was the significant factor in this concentration. In the pasture breeding area, no such concentration occurred, and this was probably due to the fact that cornfields almost completely surrounded the pasture.

As mentioned, there are scattered patches of tules in the bog habitat. Although Red-wing males used these tules as song perches, nests of *gubernator* were placed in the dense *Eleocharis* sedge near the ground and hardly concealed.

Nesting of *gubernator* began in the third week of June. The first completed nest was discovered in the territory of one of the study area males on 22 June and contained one egg on 24 June. On 25 June, the nest was empty and abandoned. On 2 July, Territory 5 contained a nest with two eggs, and on 4 July, four nests were discovered in the bog outside the study area. Two of these contained two eggs, and two contained three eggs. Juveniles ready to leave the nest or just out of the nest were first taken on 7 July and continued to appear through 13 August.

Significance of Unoccupied Areas

Several factors may be responsible for the absence of breeding Red-wings in the *Carex* bog-marsh: (1) Small size of the total Red-wing population, allowing birds to ignore only slightly suboptimal habitat; (2) unsuitability of the vegetational substrate; and (3) competitive exclusion operating between the two Red-wing forms. These possibilities will be discussed below in the same sequence.

We judged that the bunch sedge pasture offered less desirable characteristics of substrate than the *Carex* bog-marsh. In the pasture, disturbance from cattle and human beings must have been greater, nest-sites more limited in number, surface water and the chances of flooding of nests greater, and food supply less. Yet Red-wings were as common in the pasture as in the low sedge bog-marsh.

Examination of the physical characteristics of the vegetation in the *Carex* bog reveals only two factors that might be related to the absence of Red-wings. The leaf blade of the abundant *Carex hystricina* is broad and abrasively edged; this sedge grows so densely that foraging birds as large as the Red-wings might have difficulty reaching the mat surface and plant bases. The abrasiveness of the leaves might have an adverse physical effect on adults and young and thus ultimately reduce breeding success. The fact that the birds of the *gubernator* population obtained much of their food from the substrate within their nesting habitat indicates the importance of foraging opportunity there.

We believe, however, that the principle of "competitive exclusion," or Gause's Principle (Gause, 1934), provides the most logical explanation for the lack of Red-wings in the *Carex* bog-marsh. Our reasoning is simple: (1) The tule-cattail marsh adjacent to the *Carex* bog-marsh appears to be identical to the *grandis*-occupied strip across the open water but is *not* occupied by Red-wings; (2) there appears to be no logical reason for the absence of *grandis* in this optimal habitat except the proximity of *gubernator* in the low sedge bog-marsh to the east; (3) the *Carex* bog-marsh lies between the unoccupied tule-cattail marsh and the *gubernator* habitat. Although, as mentioned above, vegetation may be less than optimal for *gubernator,* it appears probable to us that the unoccupied tule-cattail strip (optimal for *grandis)* and the unoccupied *Carex* bog-marsh together constitute a "neutral zone" from which each form excludes the other.

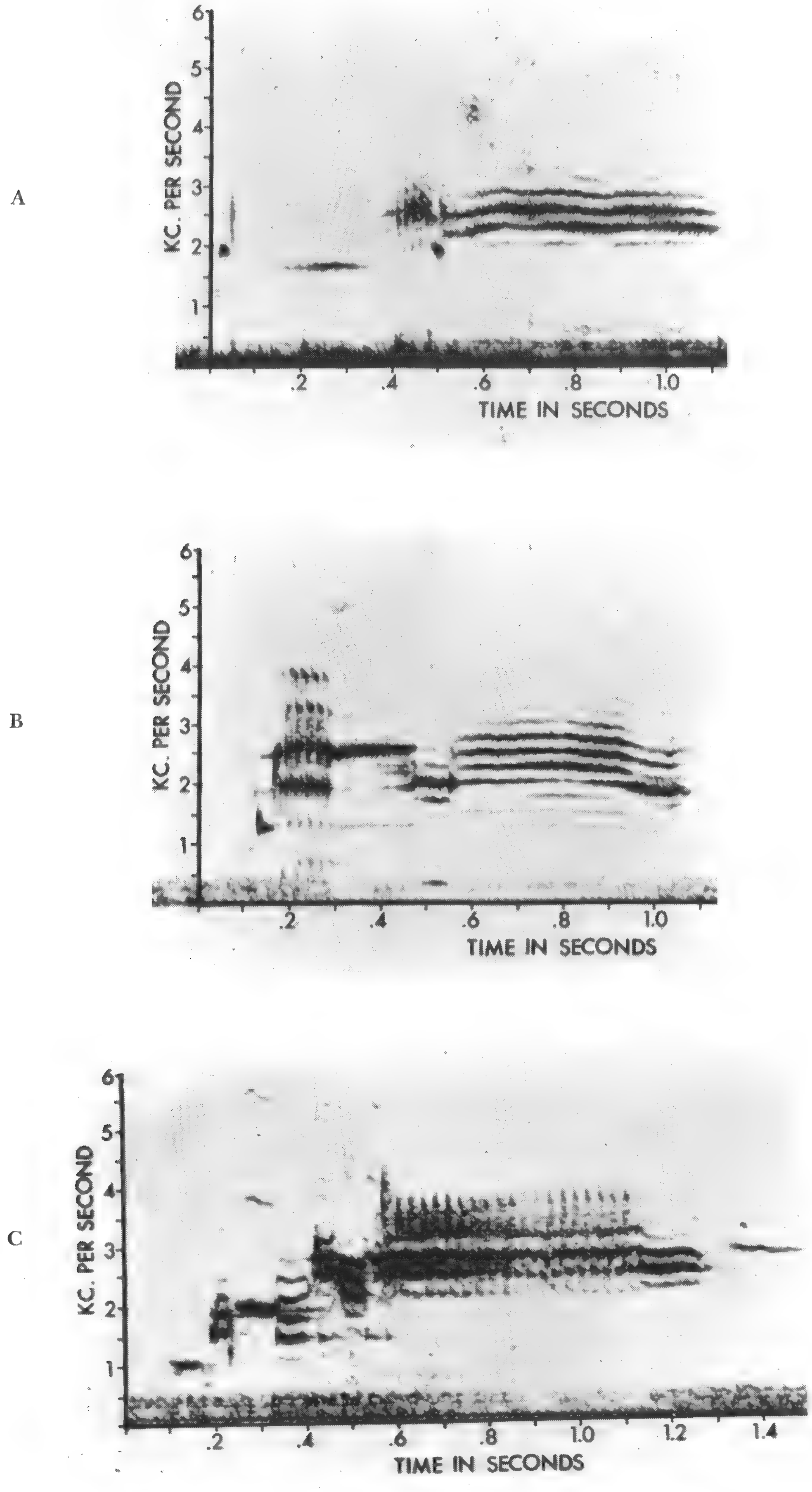

Figure 8. Sound spectrograms of Red-wing songs. A and B, two variations of *gubernator* songs; C, example of *grandis* song.

We also believe that competitive exclusion was responsible for the absence of *gubernator* north of the village in the low sedge bog-marsh designated on Figure 3 just south of the open water. We made a careful examination of this area and found it to be vegetationally indistinguishable from the *gubernator*-inhabited Area 1 and to contain most of the other typical breeding species found in Area 1. Note that *grandis* was present (one territorial male, two females, one first-year male) in the tule-cattail marsh adjacent to the uninhabited low sedge bog-marsh where we never saw individuals of *grandis* forage.

Comparative Behavior

Song Structure

The male songs of *gubernator* and *grandis* were immediately distinguishable to the ear. Sonagraphic analysis reveals that the songs are physically quite different as well. Figure 8A-B shows two variations in the song of *gubernator*. Note that following an opening syllable which may be either extremely simple or fairly complex, a long phrase is marked by horizontal linear structure of three to five parallel tones narrowly arranged between about two and three kilocycles per second. The long phrase is delivered at almost uniform pitch and is sustained for about 0.5 second. The long phrase is not rich but almost piercing in quality, whining at times, especially when it drops in pitch at the close as in Figure 8B. The song is thus simple in syllabification and conservative in harmonic richness. It has great carrying power compared to the song of *grandis*.

The song of *grandis* sounds much like the songs of *A. p. phoeniceus* of the eastern United States. It is characterized throughout by comparatively great harmonic richness and depth; the long syllable, rather than showing distinct linearly arranged tones, is marked by vertical segmentation superimposed upon a faint linear pattern. This produces to the ear the typical tremulous warble that has a pleasing melodic quality. Figure 8C represents a typical *grandis* song.

We noted no differences between *gubernator* and *grandis* in other vocalizations and judged them to be similar to those of the species as a whole.

Singing Behavior

Like many other birds of grasslands or other habitats with few elevated and exposed perches, *gubernator* males gave about half their territorial songs in flight. We observed males singing from perches more than in flight only in midday hours when winds were strong. Singing from perches took place from the tops of the scattered tules. We noted no consistent differences between song from perches and song in flight. In a flight-song, the male usually flew up from the low sedge, mounted slowly in the air at about a 30 degree angle to a height of three to 10 meters, sang at the crest of the climb or just following it, and then sailed and floated down again in another part of the territory, usually 50 to 100 meters away.

Typically, *grandis* males, in the tule-cattail marsh, gave their territorial song while perched at the top of a cattail or tule. Song in flight was rare and never occurred at the crest of a display flight but only just before, or toward the end of, a short level flight from one place to another within the territory.

Table 1 summarizes some data on flight- and perched-song for the two forms. Although we believe that the differences in singing behavior of the two forms are functions of habitat preferences, it should be pointed out that

TABLE 1

Singing Frequency of Individuals in Two Forms of the Red-wing

Form	*Time*	*From perches*	*At flight termination*	*In flight*
A. p. gubernator				
	12:00- 1:00 PM	22	0	7
	8:00- 9:00 AM	3	0	7
	8:00- 9:00 AM	5	0	8
	8:00- 9:00 AM	8	0	1
	8:00- 9:00 AM	2	0	3
	8:00- 9:00 AM	4	0	5
	8:00- 9:00 AM	0	0	4
	8:00- 9:00 AM	0	0	1
A. p. grandis				
	9:00-10:00 AM	21	4	0
	9:00-10:00 AM	4	4	0
	9:00-10:00 AM	2	2	0
	9:00-10:00 AM	3	1	0
	9:00-10:00 AM	0	1	0

song perches of *grandis* often did not effectively expose the singers above the level of the tops of the tule-cattail vegetation. We thus tentatively conclude that the attainment of a visually observed height above ground level vegetation or water surface is the critical stimulus for territorial singing by these male Red-wings.

Attempts at Experimental Behavior Studies

Experimental procedures were inconclusive. Males of both forms showed almost no interest in stuffed dummies of females of either form in the solicitation posture. Such dummies placed in territories usually were ignored, but occasionally the male would fly to a perch nearby for a few seconds. On 2 June, we presented a stuffed dummy of a *gubernator* male in a song-spread posture to each of two territorial *gubernator* males in Area 2 for 15-minute periods. The dummy was stationed near a favorite perch of a male, which reacted by perching and singing near the dummy for a few seconds and then flying away to sing in another part of the territory. Another male showed no reaction under similar circumstances. On 22 June, a third male was presented with the dummy twice at a favorite perch and at a nest-site, but gave no reaction. On 23 June, the dummy was altered. Its bill was closed and wings folded, producing a normal alert perching posture. To this mount, Male 1 gave a strong flight-display of his epaulets as he flew slowly by; then he continued away and gave no further reaction. When the dummy was placed in the territory of a fourth male, the latter was high in the air harassing a

Turkey Vulture. The male quickly returned to his territory and, while still in flight, attacked the dummy but did not touch it. He perched about four meters away, faced the dummy head on, gave the typical icterid head-up display three times, and then retreated without further attack.

In four 15-minute periods, the *gubernator* dummy disguised as a *grandis* male (by the addition of yellow feathers glued along the edge of the red epaulets) was presented to four different territorial males of *gubernator*. There were no responses.

No experiments with the dummy were performed in the *grandis* study area, because of the difficulty in stationing and retrieving the dummy while simultaneously leaving the area relatively undisturbed. However, on solid ground near Area 1, one male *grandis* failed to react to female dummies of either race in the solicitation posture or to the dummy of a stuffed *gubernator* male.

In playbacks of songs, only one male *grandis* showed a positive response. Male 6 responded to playbacks of its own songs by approaching the recorder to within 15 meters, singing with greater frequency, and then flying over the playback unit toward adjacent cornfields.

We attribute the relative lack of responses to the dummies in these experiments to low population densities, which result in fewer normal instances of territorial strife and fewer encounters having to do with mate selection.

Competition and Interaction

We observed no instances of active competition or interaction between individuals of the two forms of Red-wings. We have previously noted our one observation of several individuals of *grandis* feeding in low sedge, but this was in an area of the community not used by *gubernator*. Both Red-wings also fed in the same cornfields which were so extensive that it is unlikely that individuals often encountered each other, at least on a competitive basis. Individuals of each form frequently flew over areas populated by the other form in going to and from adjacent fields. In the approximately twenty-five over-flights we recorded, we did not observe any individual pausing in the habitat of the other race. Several times we saw individuals of *grandis* fly from the edge of the open water opposite Area 2, across Area 2, and into the cornfields beyond the road (Figure 3). Birds in Area 2 several times flew directly across the open water to fields west of San Pedro Techuchulco. We never saw birds stop in the inter-populational hiatus. On two occasions *grandis* females flew low over Area 2 and within three to four meters of perched *gubernator* males without eliciting chase. Females of *gubernator* flying near males of their own form usually elicited chase or a following response, depending on the behavior of the female.

We interpret these anecdotal observations to indicate that a combination of different ecological preferences and behavioral and morphological distinctions are operating to enforce the spatial separation of these two forms of the Red-wing. Moreover, although our observations are certainly limited, we believe our failure to observe individuals of one form in the occupied habitat of the other bespeaks the existence of active competitive exclusion in operation by each form toward the other.

Food Habits

We are unable at this time to make a meaningful comparison of the food habits of the two Red-wings, because our collection of *grandis* is too small and because many of our samples, especially those from gizzards of adult birds, were too finely broken up to permit detailed identification of food types present. Dr. Gordon Orians and his staff, who kindly surveyed the material at his University of Washington laboratory, report that there is only enough information available from the samples to demonstrate the importance of beetles and larval diptera in the diets.

Differences in Structure of Bills

The different ecological preferences of *grandis* and *gubernator* in the Lerma Marshes are reflected in, and perhaps significantly correlated with, differences in bill structure in both sexes of the two forms. Measurements of nostril to bill tip of 19 *gubernator* females ranged from 11.1 to 13.6 millimeters with a mean of 12.3, while the bills of 22 *grandis* females ranged from 12.8 to 15.2 mm with a mean of 13.8. The difference is significant but not of an order of magnitude that would indicate exclusive foraging methods. In bill depth at nostril, the same *grandis* females range from 7.8 to 9.8 mm (mean 9.0) and the *gubernator* females from 8.1 to 9.3 mm (mean 8.5). Comparing over-all bill shape of the females, that of *gubernator* is stouter, more conical, almost like the shape of the bill in Brown-headed Cowbirds *(Molothrus ater)*, while that of *grandis* is slenderer and tapered to a finer point. Similar differences exist in males of the two forms. The bill in male *grandis* is slightly keeled at the proximal end of the culmen, and the bill is long, tapered, and sometimes slightly decurved. Males of *gubernator* have stouter and more conical bills that present a strong, wedge-shaped appearance, with no suggestion of a keeled culmen or a decurved condition. In measurement from nostril to bill tip, 17 *gubernator* males ranged from 13.7 to 15.7 mm (mean 14.6). The bill depth at nostril ranged from 9.2 to 10.5 mm (mean 9.9). Our sample of *grandis* males was too small to allow a comparable statement of bill measurements.

Further analysis of bill differences and possible related ecological differences is outside the scope of this paper and awaits accumulation of more data on food habits and measurements from within and without geographic areas of overlap of ranges of *gubernator* and *grandis*.

Evidence of Introgression

One 13-day-old-juvenile (JNS 176), just out of the nest on 3 August 1964, taken three kilometers north of San Pedro Techuchulco in the bunch sedge pasture, is a perfect intermediate in plumage between *grandis* and *gubernator* juveniles. Its underparts are broadly striped with sooty brown whereas comparable juveniles of *gubernator* are unstriped and those of *grandis* are yellowish buff, diffusely marked with brown. The assumed male parent (JNS 175) of this young bird is *gubernator* in all characteristics except for a narrow margin of pale yellow to the epaulets. This margin is not, however, as prominent as we saw on all *grandis* males in the tule-cattail marsh. Note that the bunch sedge pasture is at least two kilometers from the nearest occupied *grandis* habitat. These two individuals provide the only morphological evidence of previous introgression of *grandis* characters in this *gubernator* population. That such introgression continues is suggested by another male (JNS 129) from the same place which conforms in all morphological characters to *grandis* but sang a typical *gubernator* song and was mated to a typical *gubernator* female in *gubernator* habitat.

Other Red-wing Populations

Laguna Rosario and Apizaco, Tlaxcala

Based solely upon our observations of the relationships of *gubernator* and *grandis* in the Lerma Marshes, one might conclude that they were separate species. But the two forms meet in several other localities where their interaction indicates that the problem is not only more complex but far more instructive to the student of evolution than would be the case if the birds behaved simply as separate species wherever they met.

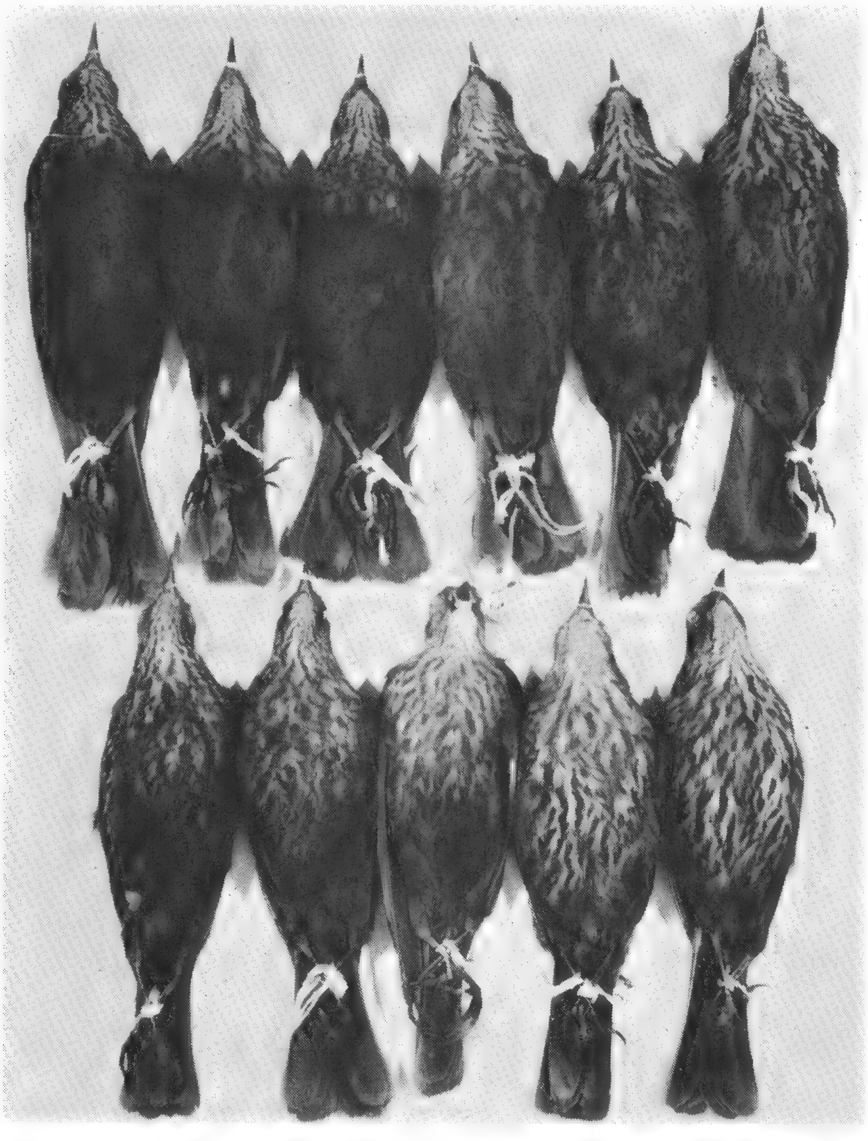

Figure 9. A series of female Red-wings from the areas of Laguna Rosario and Apizaco, Tlaxcala, showing the range of hybrid variation from "pure" *gubernator* (upper left) to "pure" *grandis* (lower right).

The Laguna Rosario is eight kilometers west of the city of Tlaxcala in the state of Tlaxcala. We visited this area on 27 and 28 June. Its marshes are perhaps as extensive as those of the Rio Lerma but far more homogeneous in their tall, emergent vegetation which consists almost wholly of *Scirpus lacustris* in stands similar to those of the tule-cattail marsh in the Lerma Marshes. There is no community comparable to the low sedge bog or the bunch sedge pasture. The tule stands are broad and lush, and, perhaps as a consequence, the Red-wing population is large and dense.

The meeting of *grandis* and *gubernator* here has resulted in a population of birds that may be described as a "hybrid swarm." This hybrid character is expressed in plumage and song and in the fact that no two individuals

Figure 10. Five breeding male Red-wings (plus the mate of the second male from the left) from the Laguna Rosario, Tlaxcala, showing range of hybrid variation in epaulet coloration.

show exactly the same combination of characters derived from the parental types. Some individuals exhibit virtually "pure" plumage traits of either parental form. Some males of *grandis* plumage type had mates of almost perfect *gubernator* type; and the reverse plus many intermediate mating combinations were also present. Songs of males were variably intermediate between the song types of *gubernator* and *grandis.*

The character of the Red-wing population near Apizaco, Tlaxcala, 15 kilometers northeast of Tlaxcala, is similar to that at Laguna Rosario in its hybrid character, but the birds inhabit short grass and sedge pasture instead of tall dense stands of *Scirpus lacustris.*

Figure 9, showing a series of adult breeding females from Laguna Rosario, Apizaco, and intermediate points, dramatically illustrates the hybrid nature of the plumage in these Red-wings. Figures 10 and 11 should be examined simultaneously. We recorded the song of each of the males pictured, and then collected the birds. In Figure 10 the second and third specimens from the left were a mated pair. The sonagrams correspond to the males in Figure 10. All five males were recorded and collected within 300 meters of one another. Note the character of the epaulets in these birds. Male 5 shows a narrow border of yellow, Males 3 and 4 have one or two yellow feathers, Male 2 (whose mate is of the *gubernator* type) is almost pure *grandis* type with a broad yellow band, and Male 1 is totally without any yellow margin to the epaulet. The songs, variously intermediate also, show moderate complexity of the opening syllables and exhibit in the long phrases some linearity of tones and variable suggestions of vertical segmentation. Note that all the songs are intermediate, even those of males exhibiting no intermediacy of epaulet coloration.

We saw no flight-singing by males, and this is probably correlated with the uniform height and abundance of song perches.

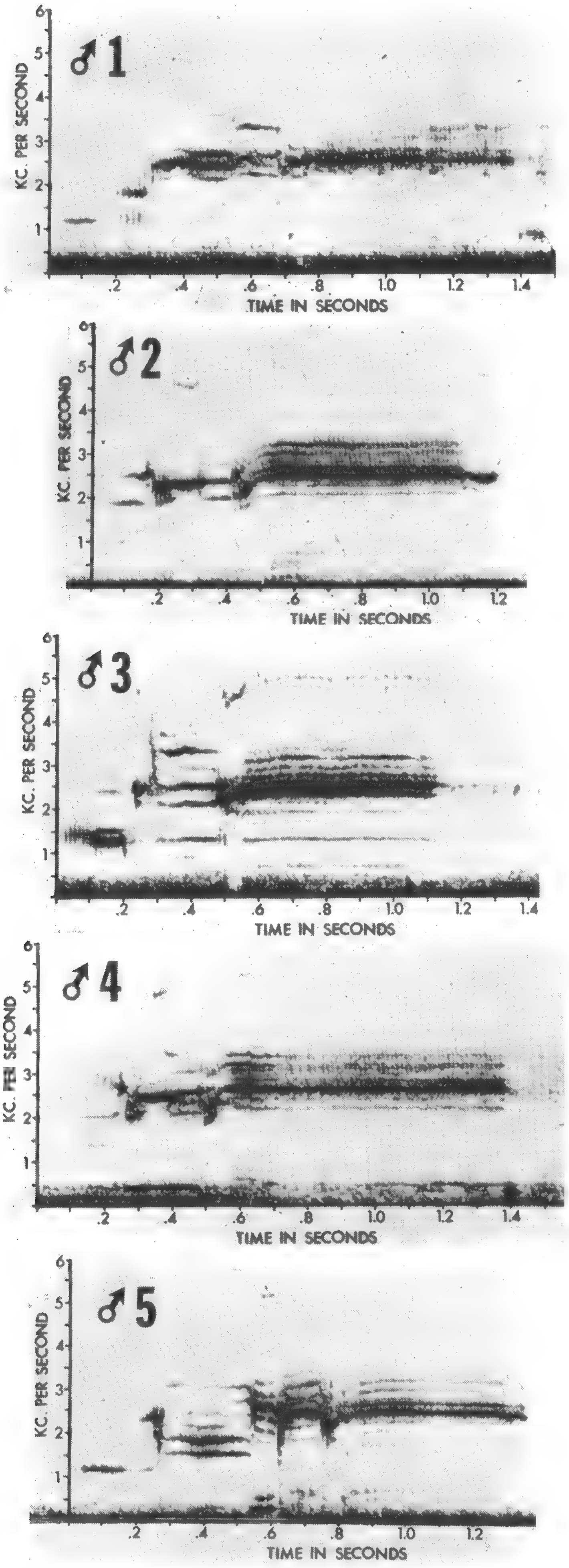

Figure 11. Sound spectrograms of the songs of the same five male Red-wings shown in Figure 10.

Laguna del Carmen, Puebla

This huge marsh, just across the Tlaxcala-Puebla border from El Carmen, Tlaxcala, is about 65 kilometers southeast of Apizaco. We visited it on 28 and 29 June. The vegetation here consists of broad patches of a short sedge (*Eleocharis* sp.) interspersed with extensive white clay mud flats that are sparsely vegetated with dense patches of a tule (possibly *Scirpus pungens*) growing to a height of between one and two meters.

The Red-wing population is virtually pure *gubernator;* in three hours of searching, we discovered and collected two males of the *grandis* plumage type (prominent but dark yellow margins to the epaulets). Each of these birds had typical *gubernator* mates. Songs of this population were typical of *gubernator.*

We found seven nests, all in the tule substrate rather than in the low sedge community, and noted several instances of flight-singing by males in early morning hours and a near absence of flight-singing at other times. The absence of flight-singing could have been due to the incessant strong winds that blew throughout the day.

Cuernavaca, Morelos

Red-wings inhabit rice fields and are abundant for several miles along both sides of the highway south of Cuernavaca, Morelos. These cultivated fields are interspersed with scrubby hedge growth, and there are scattered tall trees within, and adjacent to, the fields.

The Red-wing population here is pure *grandis* in all characters of plumage and song. The birds place their nests in the rice fields near the ground. Males sing from trees and other prominent song posts near or in their territories. We did not observe flight-singing.

Discussion

In recent years, Orians (1960, 1961a, b) and Collier (Orians and Collier, 1963) have investigated relationships of and between the Red-winged and Tricolored Blackbirds *(Agelaius phoeniceus* and *A. tricolor)* in the Pacific states. The two species are closely related with ranges overlapping in large areas of California and southern Oregon. Tricolor males have white borders to the red epaulets and Red-wing males of most populations have yellow borders. Female Tricolors are more heavily pigmented than most female Red-wings. Tricolors defend only the nest and a small area around it and are highly colonial in their breeding, while Red-wings defend larger territories and are loosely colonial. Vocalizations of the two species are completely different, and there are, in addition, differences in flock movements, foraging, and food habits.

The Great Central Valley of California is the stronghold of the Tricolored Blackbird and probably the place where it has been in contact with the resident population of Red-wings *(A. p. californicus)* the longest. It is also the place where the males of the two species show the greatest difference in plumage. The males of the Red-wings lack almost completely a yellow border to the epaulets and are (as indeed they have been called) "Bicolored" Red-wings. Since the females of both species select their mates, this difference perhaps insures against cross-specific mating and the resulting non-adapted hybrids. Brown and Wilson (1956) have applied the term "character displacement" to this kind of phenomenon. (See also a paper on character displacement by Kenneth C. Parkes in this issue of *The Living Bird.*)

These bicolored Red-wings in California were originally described as one of the two populations of *A. gubernator* and subsequently as a race (*californicus*) of that species (Nelson, 1897:59), the other race being *A. p. gubernator* of the central plateau of Mexico. Although the California bird has long since been known to be conspecific with *A. phoeniceus* because it intergrades with other populations (Mailliard, 1910), the biologically interesting bicolored condition and its implications have continued to intrigue workers. Anyone who is familiar with the competition between Red-wings and Tricolors in California and then confronts Red-wing race *gubernator* of central Mexico, at once wonders what comparable forces have been at work to cause the loss of the yellow margins to the red epaulets, and whether this characteristic might play a role in fitting these birds to co-exist with other blackbirds.

We believe that the known present zones of contact of the forms *A. p. gubernator* and *grandis* are secondary. Movement of one or both populations is probably current or of the recent past. It is nearly certain that *grandis* was not in the Lerma Marshes when Nelson and Goldman collected there in 1892 and 1904 or when W. W. Brown collected there in 1925 while on the Thayer expedition (specimens now at Harvard University). Consultation of a relief map supports the probability that after a period of complete isolation the two forms have been in contact for a comparatively long time in the Tlaxcala-Apizaco area where isolating mechanisms between the two have proved vulnerable. These mechanisms might be intrinsic genetic ones, extrinsic ecological ones (absence of two well-defined habitats suitable for breeding into one of which one form could retreat under competitive and selective forces), or both. The mountain barriers between the exclusive ranges of the two forms in this area are at the low eastern end of the transvolcanic belt, perhaps accounting for the hypothesized early contact of the two here.

The Lerma Marshes, in contrast to the Tlaxcala-Apizaco area, are hemmed in by mountains except in the north. The Rio Lerma flows out of the valley toward the north-northwest, and it was probably along this river that Red-wings (ancestors of the present population of *gubernator*) reached this high mountain marsh. The closest large Red-wing population south of the Lerma Marshes is that of *grandis* near Cuernavaca, Morelos. Although the barrier is steep between Cuernavaca and the Lerma Marshes, it seems probable that the source of the immigrant *grandis* now in the Lerma Marshes, was the Cuernavaca population, because southwest and west of Toluca the country is continuously rugged, lacking broad valleys and appropriate Red-wing habitat almost to the coast, where the resident form is not *grandis*. The Lerma birds are morphologically inseparable from the Morelos populations.

We have discussed previously our beliefs concerning the interrelationship of intrinsic and extrinsic factors in the isolation of these two Red-wings as operative species in the Lerma Marshes and can add only this conclusion: The existence of two well-defined blocs of essentially uniform habitat in this marsh, rather than the existence of only one habitat appropriate for nesting Red-wings, or a more thorough interspersion of the existing habitats, prevents the potential intrinsic isolating factors from being adequately tested. Further support for the suggestion that competitive exclusion accounts for the absence of Red-wings from certain areas of seemingly good nesting habitat must await further investigation.

A line drawn from the Lerma Marshes to Tlaxcala passes through the Valley of Mexico, which, of all three areas, is the most effectively isolated from the south by mountains. Thus far, only *gubernator* is known to breed in the Valley of Mexico, but in the autumn of 1964, Dickerman observed and collected striped female Red-wings there for the first time, indicating that possibly further events await investigation into the relationship between these two blackbird forms.

Summary

The ranges of *Agelaius phoeniceus grandis* and *A. p. gubernator* are in seemingly secondary contact in two areas of central Mexico. The northern race, *gubernator,* has long been known to inhabit the marshes of the headwaters of the Rio Lerma in the Valley of Toluca, state of Mexico. In this race, the males are bicolored (no yellow border to the epaulets) and the females almost solid sooty brown. Recently, the race *grandis* (males with yellow borders to the epaulets, females striped light brown) apparently has invaded the Lerma Marshes.

In the summer of 1964, we studied the two races and found them to be ecologically segregated in these marshes, *gubernator* breeding in low sedge bog and pasture and *grandis* breeding in tule-cattail stands. These habitats occur in two large blocs instead of being interspersed. Between the two large blocs is an area of tule-cattail and *Carex* sedge about 1,000 meters wide and inhabited by no Red-wings. We believe that competitive exclusion operates to produce this hiatus. The two populations were nesting within sight of each other and often flew over, but did not alight in, each other's habitat. Songs of the two forms were perfectly distinguishable from each other. Males of *gubernator* (low sedge and pasture) sang about half their songs in flight, while males of *grandis* sang most often from perches. Breeding of both forms took place from late June to mid-August. Several intermediate-plumaged birds and one "displaced" male *grandis* in *gubernator* habitat provide evidence of current and past genetic introgression. Both forms fed in their breeding habitat and in adjacent cornfields. We saw no evidence of direct competition between members of the two forms. The population of *grandis* was small (less than 20 males counted) while that of *gubernator* was large, although density of the two was similar.

In the general area from Laguna Rosario to the Apizaco-Tlaxcala area, these two Red-wing forms are also in contact. Here they inhabit tule marshes and pastures and produce a "hybrid swarm." All plumage types from "pure" *gubernator* to "pure" *grandis* are represented. Songs of males are intermediate between songs of the two forms where they are allopatric or do not interbreed. We theorized that the source of the *grandis* population in the Lerma Marshes is the area of Cuernavaca, Morelos, over high mountain barriers. The zone of secondary contact in the Lerma Marshes is probably a new one compared to that in the state of Tlaxcala. Barriers between the exclusive ranges of the two forms are lower in Tlaxcala. The Valley of Mexico which is between these two areas of contact is, of the three, the most isolated by mountains from the south. Only *gubernator* is known to breed there, but recently fall specimens of striped female Red-wings were taken there.

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A hard-pencil drawing by Louis Agassiz Fuertes from the author's collection.

TECHNIQUES IN BIRD ILLUSTRATION

DON RICHARD ECKELBERRY

The moment a bird painter depicts a species in accordance with specifications dictated by someone else—when he draws the bird a certain size, shows a particular race or plumage, or demonstrates some action or activity—he is dealing with bird illustration. This differs from bird art which, by its very nature, has to be untrammeled. We can see the difference in the work of John James Audubon by comparing the earlier plates, made when he was painting as he wished and his plans for publication were still a dream, with the later plates when he was his own publisher trying to complete the series. Art, I suspect, is not just a matter of talent but of intent. Illustration, in all but feeling, is usually more demanding.

I had never seen an original painting by a professional bird artist until I was of age and had come to New York, nor had I discussed techniques with others. The purport of this paper is to consider practical methods of procedure in bird illustration in an effort to be helpful, particularly to oncoming practitioners. Having received many inquiries as to the "secrets" of bird painting and letters asking for specific help, I am setting down here my own methods and those methods of my colleagues with which I am familiar, in the hope that they will be of value. Of course, excepting a requisite degree of native talent, the only secret is and always has been *hard work*. In addition, one must keep in mind that there is no "correct" approach to this specialized form of illustration. Each of us ultimately discovers the methods best suited to his own nature and develops his own style.

The greatest difficulty in bird illustration is that its aim is basically in conflict with Nature's attempt, through the devices of counter-shading and disruptive patterning, to destroy the perception of the bird as a form in the first instance and as a unit in the second. Birds are not easy subjects to draw and paint well. They vary greatly in shape, texture, and color. As a rule they will not come near enough, sit still enough, or stay long enough for you to draw, let alone paint them. And since there is no substitute for knowing the bird in life, we must regularly refreshen our impressions in the field. The bird illustrator also has a problem which the ornithological writer does not: what the writer does not know he can simply omit; the illustrator must commit himself.

Field Work

A painting done in the field from observation of the bird in life, or from a fresh specimen in the hand, has a quality that can never quite be duplicated in the studio. Of course, painting in the field has its difficulties. Onlookers

Portrait of a young Osprey

distracting you and blocking your light, insects biting you or crawling across freshly applied paint, perspiration dripping from your brow onto the picture, humidity so high that the pencil engraves the paper and washes simply refuse to dry, and the light waning as you try to finish—such annoyances make one yearn for the comfortable conditions of the studio.

On his Ethiopian expedition, Louis Agassiz Fuertes painted perhaps the finest series of field paintings ever done, the culmination of many years of such work which gave his studio portraits their remarkable authenticity. Since work in the field depends upon circumstance and one paints what comes to hand, the random results of the collection limit their function as finished work. But for Fuertes' untimely death, a selection of his African work might never have been published, and the bulk of them regrettably have not. George Miksch Sutton, who not only followed his mentor in this practice but has gone on to produce many quite finished compositions in the field, has thus far seen very few of his fine Mexican series reproduced. Concerning this he wrote me the following:

"The series of bird paintings which I did in Michoacán (Brown-backed Solitaire, Pygmy Owl, etc.) were all done outdoors. This means, of course, that we had decent weather, and that we were off the beaten track. I had made up a great tablet of Strathmore bond beforehand. I constructed a crude easel wherever I worked. My whole painting outfit I wrapped in a big waterproof *poncho*. I caught birds alive in mist-nets or simply watched them; did all the vegetation, etc., directly from growing plants. I did these pictures sometimes five or six at a time, working for 2-hour stretches at one, then for 2 hours at another, etc., so as to be sure my highlights and shadows made sense. The Pygmy Owl was a morning study, for the bird seemed to enjoy sunning itself each morning in a particular madroño tree near our parked truck. The White-eared Hummingbirds I did at the same time. The luxuriant *Lobelia* plant about which the hummers lived was very close to the truck and the birds fed within inches of my brush, paper, easel, etc. Details of plumage I worked in from specimens that 'stayed put,' but I had living models galore. The orchids in the Brown-backed Solitaire picture grew so high that I climbed after some big bunches of them, pulled loose the bark to which they were attached, and fastened them to a trunk at eye-level, i.e., *my* eye-level. [The paintings to which Sutton here refers are still available in excellent full-size reproductions at the Cornell Laboratory of Ornithology.]

"Throughout the series, I took care to keep the ecology sound. Thus, in my Mexican Trogon study, I waited quite a while to make certain that I was showing in the picture berries that the bird actually ate. Some of my studies are unfinished to this day simply because I did not see what I wanted to see of certain birds or find the right accessory material.

"Every one of those pictures rouses memories. The sprawling cactus in the Ant Tanager study was as much a fight with mosquitoes as it ever was a work of art! And the dog that went along with me could never seem to find a comfortable resting spot that did not include the open paint-box. I had a busy time indeed swatting and scolding and getting up to stretch, etc. That time I sat on the ground, on a hard, hard path where there were (praise be!) no ticks.

"Not all of my Mexican studies are good. I was just plain tired when I did some of them. My hands became stiff or puffy from too much walking. That Black Hawk-Eagle *(Spizaëtus tyrannus)* that I did in San Luis Potosi was a miserable disappointment. I had walked miles. When I started work

Left leg inside

RING-BILLED GULL

Sketched from injured bird, Babylon L.I., N.Y.
Feb. 24/51

Eye: gray-straw
pale

Orbital skin: dark
gray-brown

Subadult character of tail
from above interior
margins more extensively black.

Bill: very gray-green or grayish.
Straw green, yellower
at tip & flesh in gape.

above

Left leg, outside
Legs: greenish-lead

Don R. Eckelberry

it was getting dark. I had other work I felt I should do, etc. When I tried finishing it the following day I felt myself under pressure. In short, one should 'feel right' while working.

"I took care to use sterilized water, since I am a brush-licker. I trained certain brushes to do certain things—but of course every artist does this. My favorite brushes were (always have been) big ones that come to a good point. With a brush of this sort I can start with a fine line and quickly broaden the stroke to match a streak, spot, or bar. My Cooper's Hawk head-sketch [in "The Birds of Arizona," 1964] is a good example of what a painter can do with bars, etc. when he has a good *and big* brush.

"I chose certain paints for certain effects and this is surely important. On one Mexican trip I had yellows not one single one of which was right for certain yellows of bird plumage. This was awful. I tried various combinations of transparent and opaque colors and used anything that seemed to achieve the effect I wanted. Very important is the proper technique in erasing. If I made a bad mistake, I let the paper dry *completely* before touching an eraser to it. For big washes in backgrounds I was obliged to mix really great quantities of paint and some colors behaved far better than others.

"I believe that the design of a picture is a matter of instinct. Something simply told me that a branch of a certain sort would do, that another wouldn't; that a big empty space was just as important as a filled-up space."

Only just recently, in Trinidad, I tried painting from live birds caught in a mist net and placed in a glass-faced wooden box with a screened top. It is not the easiest way to work, because the birds usually jump about a good deal and must be hand-held from time to time to check details and measurements, and because of the pressure of time in insuring their release in good condition. But the compensatory advantages of the live bird, fresh-field impressions, and a wealth of accessory material to select from are considerable. If there is not time to work out an arrangement beforehand or if none comes to mind straight off, it is practicable to spot the bird on the paper and compose the botanical material around it later.

Undertaking in the studio the illustration of any species I have not seen in the field gives me a very uncertain feeling. All of us who are called upon to produce a long series of illustrations must compromise in this matter. Even when I am familiar with the genus involved, experience has taught me to be wary. In Jamaica, for example, there are two species of "robins" common in the Blue Mountains. The White-eyed Thrush *(Turdus jamaicensis)* is a typical *Turdus* in posture; the fact that it sings a strikingly mockingbird-like song does not affect illustration. But its congener, the White-chinned Thrush *(T. aurantius)* looks robin-like only in relaxed perching poses. On the ground, where it spends much time (hence the local name "hopping dick"), it lacks the soldierly robin stance because its tail is usually held up at about a 45-degree angle or even vertically. This essential difference is reflected in my illustration of the species in James Bond's "Birds of the West Indies" (1960). Had I not seen the White-chinned Thrush and drawn the figure on the assumption that intrageneric differences are merely a matter of proportions, size, and color, I should have missed the true species-character.

A more extreme example is that of the large neotropical wood warbler genus, *Basileuterus.* Most of these species— for example, the Rufous-capped Warbler *(B. rufifrons)* in *Mexico*—are birds of scrub or woodland understory and rather resemble our Wilson's Warbler *(Wilsonia pusilla)* in proportions. Both *B. fulvicauda* and *B. rivularis,* which may be conspecific, differ, at least from other members of the genus I have seen, in being ground-loving, streamside species as distinct in life, both in color and habits, as a waterthrush is from a Yellow Warbler. If the illustrator extrapolated on the basis of seeing only the Rufous-capped Warbler, he would err gravely. At the time I did the line drawings for Alexander F. Skutch's "Life Histories of Central American Birds," Volume 1 (1954), I had not seen the Buff-rumped Warbler *(B. fulvicauda)* in life. Later, when I did see it in Costa Rica, I pointed up the risks in my notes: "Redstart-like, especially in a tree. On the ground, head and tail are held rather high, the stance rather like that of the European Bluethroat, i.e., high on straight legs. Pumps tail (which is usually half or three quarters spread) *down* irregularly, in this respect resembling *Euthlypis* of Mexico. Appears shorter and more contrastingly dark and light than my drawing for Skutch."

Illustrating a genus with which one is unfamiliar is even more risky. I could determine from a skin that the Paltry Flycatcher *(Tyranniscus vilissimus)* is a small-headed, long-tailed, and long-legged species, but how could the skin inform me that this bird perches horizontally and cocks its tail like a gnatcatcher? And without field work how would I know that fruiteaters *(Pipreola)* sit rather upright like bluebirds or waxwings and have the same somewhat "angry" expression?

While I have always made sketches from captive birds and fresh specimens, I have given up any consistent attempt to sketch in the field. I find that when memory of the visual experience fades written descriptions are more useful. On looking at a field sketch later, I sometimes wonder just what the point was, but descriptions such as the following from my Argentine notebook serve as permanent impressions:

" 'Araucaria Spinetail' " *(Leptasthenura setaria)*—Found only in the araucaria 'pines,' hence unless seen in young trees it is usually very high up, where located by its high, thin, accelerated trill. It works the 'pines' very much like a titmouse, which it somewhat resembles because of its long, pointed crest. Although the tail is sometimes dragged along a branch, it does not seem to be much employed, and while sometimes cocked a little up or held out straight behind, it is frequently held down at a considerable angle from the body as the bird bends over a branch or hangs upside down. Soft parts: *Iris,* light middle value flesh gray. *Bill,* max. [maxilla] and also tip and terminal portion of cutting edge of mand. [mandible], brown-black; rest of mand. flesh (grayish pink). *Legs,* middle value gray-olive (claws more brownish); heel and hind edge of tarsus slightly lighter, concolor with breast (gray ochre); soles brighter ochre (same value as flanks or under tail coverts). [The vernacular given was my "working" English name on daily lists.]

"Crested Screamer—In flapping take-off, primaries are much recurved. Almost condor-like in flight: deeply slotted fairly long wings held rather flat, broadest in mid-secondaries. Base of primaries (also greater primary coverts?) above and entire under wing coverts, white. Neck short and held straight out (pinched at collar), squarish head, bill often opened wide (loud goose-like double clanging notes, the second higher). Belly rather rounded, legs slightly down, rounded wedge tail. Hundreds seen soaring. Sometimes perch in trees as well as stand in groups, wade or swim. Downy young swim freely.

"Stephanophorus diadematus—Remarkably finch-like for a tanager. Moves sluggishly through trees and low brush. Singing posture and rollicking, rich song, very grosbeak-like. Rather small headed. Sexes alike. Soft

Pionopsitta pileata ♂

Ara maracana ♀

August 31, 1959 near Tobunas,
Misiones, Argentina. DRE

Ramphastos discolorus ♀
Aug. 30, 1959 near Tobunas,
Misiones, Argentina DRE

A preliminary drawing of a Bat Falcon, this is neither a field sketch nor a drawing sufficiently worked out in detail to serve as a working drawing. It is, rather, a studio sketch done from memory which could, with some refinement and definition, be used.

parts: *Iris,* dark brown (appears black). *Bill,* max. and tip (broadly) of mand. lead black, rest of mand. pale plumbeous gray. *Legs,* brownish slate, soles lighter dull ochre yellow."

I often augment such notes with small sketches of postures, flight patterns, details of the way the crest is raised, or other particulars.

I make careful notes and sketches also of the vegetation with which the birds are associated, and in this respect do a good deal of color photography. But no matter how many pictures I take, I find when I get home that I do not have half enough, and regrettably, there is no going outside my studio and plucking exotic flora to work from. Actually, I should photograph a lot more of even the local foliage for reference in winter.

We cannot deny the informational value of bird photography which has influenced all bird painters from Fuertes on. However, I forego the excitement of hunting with a camera and rarely attempt it in the field, largely because it takes too much time. I prefer to discover the "essence" of species-character by general observation rather than by a record of the "instant."

The logic of this view depends entirely upon what one is after. When Arthur Singer and I were working together in Jamaica, he consistently talked about the "gesture" of one or another of the birds we saw and was especially interested in getting pictures of birds in action. While he was photographing, I was just watching, hoping to see a given species often enough to determine the "typical" aspect which is what interests me. It is good that there are such different points of view; Nature is so grand that there is room for endless viewpoints. This variety is just what bird painting needs.

Richard E. Bishop, known for his etchings and oils of waterfowl, uses 16 mm slow-motion pictures to study the action of birds in flight. By splicing a sequence into a loop, he is able to run it continuously through a projector until he has observed it to his satisfaction.

Singer introduced me to the value of zoo photography by means of which, with relative ease and speed, one can collect reference material, especially of less familiar or entirely unfamiliar species. Even here it is necessary to keep in mind that the lens often tends to distort close-ups, that colors, due to diet deficiency, molt, or age, may be far from normal, and that bills and feet are sometimes over-grown. Nevertheless, the camera is a very useful tool and, as the collecting of specimens by museums lessens, illustrators will probably use it more frequently.

My experience with the Rose-breasted Thrush–Tanager *(Rhodinocichla rosea)* points up the limitations of the camera. Paul Schwartz published, in E. Thomas Gilliard's "Living Birds of the World" (1958), two fine photographs of this tanager, a bird of rather ambiguous affinities and one that I was therefore particularly anxious to see. One August afternoon Paul and I went crawling through the thorny scrub near Caracas, Venezuela, where he was able to show me my first *Rhodinocichla.* The bird was indeed mimid-like as Paul's photograph suggested, but, contrary to the impression I had gleaned from the pictures, it was more like a catbird than a thrasher in build. Obviously the birds *did* look as they appeared the moment the shutter of Paul's camera was released, yet somehow I felt that a definitive picture would have shown them otherwise. How many pictures of ourselves and our friends do we see that do not seem to be true likenesses?

Other Working Aids

In studio work a personal collection or access to a good collection of skins is an absolute necessity. Most collections are open to the serious worker. I consider myself fortunate not only in having access to the unexcelled series in the American Museum of Natural History but also in having those persons in charge so unanimously and consistently helpful.

There is nothing deader than a bird skin. On the other hand, with a good skin to provide accurate colors and markings and field work to provide the knowledge of the bird in life, it may be revivified in the painting. In selecting specimens to work from, I avoid those that are under- or over-stuffed, compressed, or stretched, because these deficiencies affect the natural pattern of the feathers and the relation of the wings to the body area. However good the skin, one must not depend on it for form. Only a fresh specimen with its musculature still intact can be relied upon for that, and even then one must take into account the lax plumage of the dead bird.

Over the years I have made a collection of bird wings from dead birds that come to hand. I open the wings and either pin or press them so that when dry they remain spread. These wings have great value for flight pic-

Felt pen drawing reduced.

Horned Owl - captive
Bear Mt Park, N.Y.

Sept. 1949

The above sketch of a male Rose-breasted Grosbeak was done in the field by watching the bird through binoculars and then drawing. It is one of several which did not, probably, take thirty seconds each. Few such sketches work out well, but now and then one, such as this one, sufficiently captures the moment to merit being filed away as a suggested pose for a future picture. A more exact drawing would first have to be made from it.

tures and I wish that museums had similar and more comprehensive collections of this sort. I might add that I avoid making flight pictures of the smaller passerines. Because one's eye does not apprehend their fast, fluttery flight, any stop-action portrayal tends to take on the aspect of high-speed photography.

Walter Ferguson injects dead birds in good condition with formaldehyde and stores them as one does bird skins. While this method causes some shrinkage, it is quick and the birds do retain their shape.

Two other categories of important reference material are a good library—botanical as well as ornithological—and a clipping file. The latter includes pictures of any kind of bird, plant, or habitat from magazines, old books, and other sources. One of the principal values of clippings to a bird painter is to remind him of what has been done and to make him aware of inconsistencies. I have many times avoided mistakes in soft-part renditions—so often inadequately reported, if at all, on skin labels—by checking through color photographs or pictures by other painters. When they do not agree on the proper color, I then go through the literature or check other labels at the museum to determine just what is correct. One can avoid this by painting in the field from the fresh specimen, provided, of course, that the fresh specimen is in typical plumage.

The Drawing Stage

In my own work, the drawing stage is the most important phase, the part on which I usually spend the most time. To some extent this is because I do not paint in a very detailed manner, preferring to suggest feathers rather than to delineate them all; but it is also due in part to the importance which I ascribe to the drawing and composing stage where the picture-to-be is formed and fixed. It is not unusual for me to do six or ten drawings, some simply variations of a single theme, before getting one that satisfies me. I file the others away for possible future use.

I begin very roughly with a soft pencil (e.g., an F to 2B lead or Wolff Charcoal) on tracing paper (available in pads of various sizes) and work until I get something promising. Then I put another sheet of tracing paper over this "rough" and trace off and add to the best features of the sketch. Successive layers follow until I achieve a final working drawing. The earlier sheets are discarded. As I said above, I am then very likely to start off again on another tack. I put the finished drawing on the studio wall in the hope that I can see some further way to improve it while moving on to another subject.

The point of working on paper other than the painting surface is to keep that surface clean. This is especially important in preparing illustrations for bird guides where many figures must go on one plate with a white ground. For such a plate I cut a sheet of tracing paper to working size and juggle the individual drawings about until I get the best possible arrangement. The outlines of the drawings are traced onto the sheet as a guide. Sometimes this means redrawing one or two figures for better composition. That is about the extent of aesthetics on such a job. I draw all birds reversed to the way they are to appear finally. The transparent tissues are then flopped and traced onto the painting surface, following the guide sheet of outlines for exact placement. It is thus impossible to lose the quality of the drawing or the compositional balance of the plate.

When I have to do one or two figures in a natural setting, I work out the composition in thumbnail sketches, then draw the birds on separate sheets of tracing paper, the foreground accessories on still another, and the whole is finally combined on the working surface. The background, unless unusually complicated, I sketch in lightly, leaving it to be worked out directly in paint.

When working in oil the approach is quite different. I commonly make a series of small sketches of the picture composition until I am satisfied with the design. I then draw the birds directly onto the canvas, or other support, in charcoal or Wolff pencil. Where a group of birds such as shorebirds or ducks must appear—particularly where the paint is to be handled thinly—I may transfer the drawings on in a fairly rough stage. This allows me to play with the arrangement and perhaps improve upon the compositional sketch without too much wear and tear on the painting ground. When I am free to paint for fun, I sometimes start directly on canvas with only the small sketch as a guide, drawing with a brush dipped in pigment much thinned with turpentine.

Francis Lee Jaques tells me that when working in oil he makes his drawing on paper and transfers only the outline onto the painting surface, since "the detail is lost once you start to paint." He goes on to say, "In doing my museum backgrounds I found it advisable to pin up cutouts of birds for size and position, and this proves to be useful for *any* painting It is easier to draw on paper than on canvas, corrections can be made, and when cut out with the scissors they can be adjusted for composition and in relation to proper perspective." I know that Perry Wilson, in working on habitat groups, often spots his birds on the finished oil background and then cuts the bird *out* of the sheet of paper, stippling the flat silhouette on from this stencil; then he works out the form and detail by brush.

Fuertes did many fine sketches such as the one in hard pencil of the meadowlark shown at the beginning of this article. These sketches appear to be studies rather than working drawings. In any case, many of the working drawings in his later opaque work were of birds hardly more than outlined on rough paper and transferred to the watercolor surface by smudging the drawing's reverse side with a soft pencil and tracing it on. George Sutton follows the same method.

Arthur Singer works out a rough, comprehensive sketch the size of the final work and usually in color (pastels). Since his work is almost entirely in tempera, he does not work out a detailed drawing because here again such detail would be painted out in laying in the flat color areas upon which value transitions, texture, and detail are added. Singer thus spends much more time in painting and much less in drawing than I.

A few general comments are in order here about drawing birds. The most common weakness, I observe, is in the placement of the eye in relation to the bill and gape. Walter Ferguson points out quite correctly that this error occurs frequently where the bird is in three-quarter view facing out or into the picture. In the first case, the distance from the eye to the bill is increased (not foreshortened in perspective) because the eyes and bill are on different planes. The width of the skull sets the eyes out beyond the center skull line. In the second instance, the foreshortening is correspondingly exaggerated for the same reason. Equally important is the way the eye is set into the head—not just flat, in all circumstances, against the plane of the head (see my study of the Ring-billed Gull illustrated in this article).

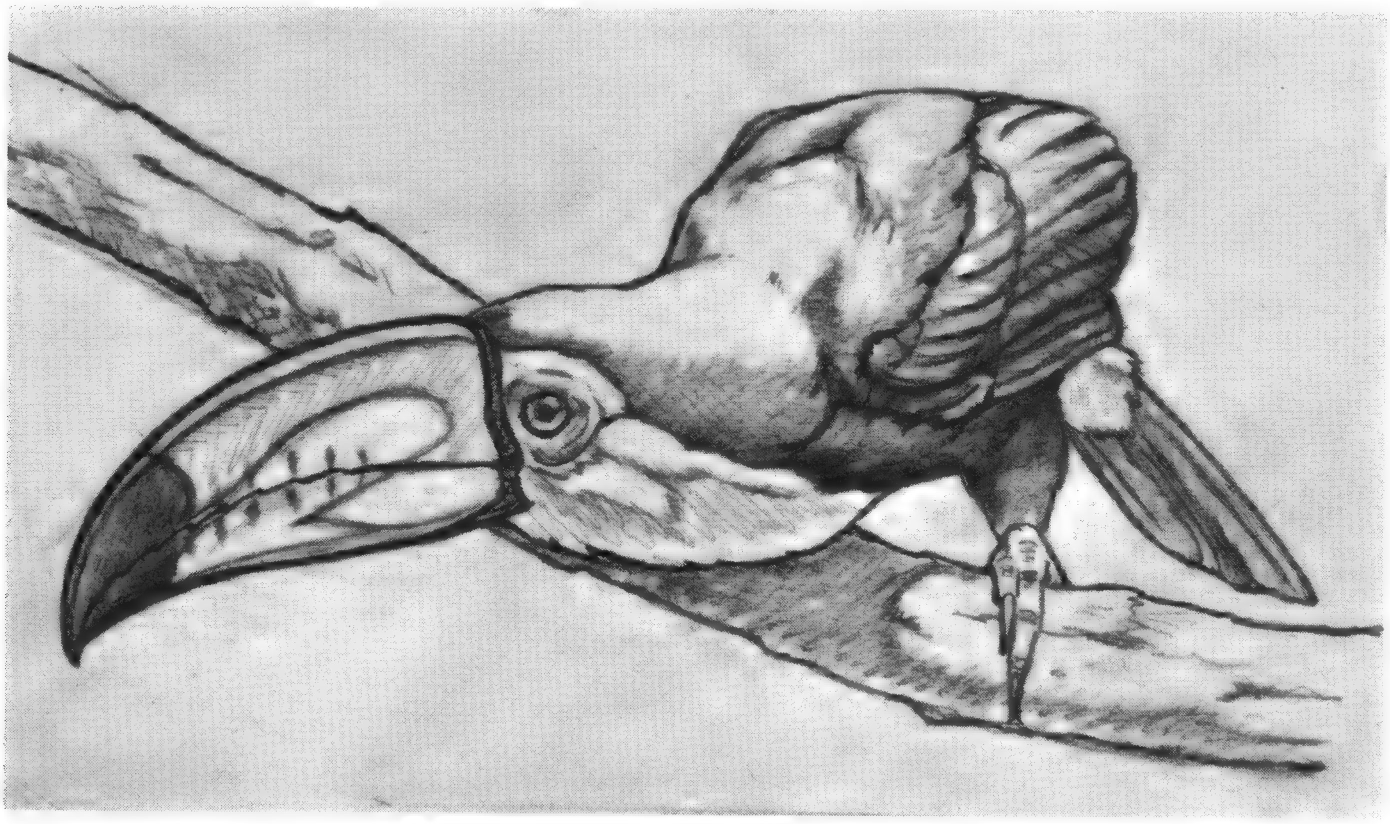
Boat-billed Herons (tempera on Whatman Board, 8½ x 11 inches). The basic requirement here was simply to illustrate the adult and immature plumages of the species, *Cochlearius cochlearius*. (Reproduced by courtesy of Western Printing and Lithographing Company.)

Next to neglecting avian expression, bird artists too frequently draw legs and toes poorly. Legs (tarsi) are not properly described by two parallel lines; their thickness varies from heel to toes. And many a bird has been illustrated with an extra joint midway along the hind toe, even in the most recently published books. Birds do not, as a rule, clutch a perch in the "death grip" so often depicted.

One would think that however inexperienced the ornithological illustrator, whether working from the live bird, the skin, photographs, or the work of his predecessors, he would at least use his own eyes enough to see the way feathers overlap. Yet we regularly find feathers misrepresented. The most obvious error is the incorrect arrangement of the upper-wing coverts in relation to the flight feathers. The greater coverts overlap, as do the primaries, secondaries, and tertials, in one direction while the middle and lesser coverts overlap in the reverse direction.

Such determinable variations as the number of toes and their positions in front of a branch or behind, the number of primaries or tail feathers—these and other details may not be noticed by the general viewer, but let any serious ornithological illustrator slip (and sometimes we do!) and he will shortly be called to account. It is perfectly all right to paint in a way that does not define the number of feathers involved in a particular area because these distinctions are not always visible, but if one does, he must show the right number.

There is also a tendency we must all watch out for—that of averaging out proportions. A kingfisher is more likely to be drawn with a head too small rather than too large, a Louisiana Heron with a neck too thick rather than too thin, a turnstone with legs too long rather than too short.



The working drawing of a Keel-billed Toucan for the fifty-cent full-color stamp in a twelve stamp series commissioned by the government of British Honduras.

Finally, the draftsman should take care in the matter of visual logic in combining background with foreground. His tendency often is to go to extremes, to include a great range of mountains behind a tiny sparrow.

Painting Media

Watercolor is both the fastest and most difficult medium. The larger the painting, the more difficult it is to use and, where backgrounds are involved, the more loosely it should be handled. Since all the sparkle comes from the paper's surface, one cannot mess about with it or it will go dead. It is necessary to think out, to know, what you want to do and how you are going to do it *before* touching brush to paper; and once having painted, to realize that you must leave it alone. Watercolor is essentially a value rather than a color medium. Fuertes, Sutton, and John Henry Dick have used it for the bulk of their work. So have I.

Gouache, the addition of white opaque pigment to transparent colors, is less brilliant, and any over-use of white tends to produce chalky effects. Robert Verity Clem and J. Fenwick Lansdowne work in this medium with entirely different but excellent results. Gouache is half way between pure watercolor and tempera and is particularly suited for toned grounds. I have not been able to examine the original work of the great English illustrator, Archibald Thorburn, but his technique, from reproductions, looks to be in this method rather than the next. It also appears that Fuertes' illustrations for "Birds of Massachusetts and Other New England States" (1925-27) border between this medium and the next.

Tempera, the medium most commonly employed for bird painting, is essentially a color rather than a value medium. Using it, you discover all sorts of hues you are scarcely aware of when working transparently. Tempera can be handled semi-transparently as well as fully opaque. Any large areas require much more time to cover, particularly where color or tonal transitions are involved. Tempera provides colors which transparencies cannot, but it inclines to flatness and decorative effects. Allan Brooks adopted tempera for use on toned grounds early in his career. Roger Tory Peterson and Singer use it almost exclusively, but mostly on white grounds. Both Sutton and I sometimes combine an opaque background with a transparent foreground or with only the bird in pure watercolor. However, Sutton informs me that he always paints the bird and any other transparent passages first and the background later, while I always do it the other way round.

Oil is the slowest and most anti-linear, but at the same time the most plastic and symphonic medium. The larger the painting, the easier oil is to execute. Thus it is best adapted to broad effects and large birds. Athos Menaboni contradicts all this by his use of oil glazes on paper. Bruno Liljefors, Jaques, and Peter Scott—all artists interested in large, powerful effects— have done most of their painting in the more typical opaque method.

These color media pretty well cover the field. Of course there are others such as pastels, colored inks, casein, and the new acrylic-vinyl pigments.

Painting Equipment

I cannot stress too strongly the importance of using good materials. This is obvious to the professional, but I mention it because *so* much work, brought to me for criticism, is done with and on materials so wretched that no one could have done anything with them. Painting in itself is difficult enough without unnecessary handicaps.

Reduced from the life-size original, this is a "working drawing" of an immature male Aplomado Falcon for a color illustration to be published in Dean Amadon and Leslie H. Brown's "Hawks of the World."

Working drawings, from which final illustrations are made, need not show three-dimensional form, but provide the contour and action, and indicate color- and feather-area definitions which are to be brought out by the paint. Comparison of this original size (smaller than life) motmot drawing with the National Wildlife Federation stamp (to be published) will indicate how it relates to the final color treatment.

Painting surfaces, even of the best quality, will be acceptable to one artist and not to another, depending upon their preferred medium, their way of handling it, the amount of "tooth" they find sympathetic, and so on. Each painter must experiment to find compatible surfaces. George Sutton, for example, achieves his fresh results for the most part on 3-ply Strathmore Bond, a surface much too smooth and non-absorbent to suit me. The only general statement that I can make is that the smoother (less "toothy") surfaces are better for tempera and the rougher textures better for watercolor, especially when the picture is large or where not quite so much sharp delineation is required.

Most of *my* work is done on Whatman Board—No. 1 Surface (light tooth), Cold Pressed (medium tooth, most used), and Rough (coarse tooth for large, loosely handled pictures). When the papers are mounted thus, they have added absorbency and resiliency and are better protected for handling and shipping. The same papers may be obtained unmounted or in blocks, the latter being simply a number of sheets glue-bound all around. Blocks tend to buckle somewhat when subjected to many washes but are practical for field work where weight is a consideration. When using loose sheets, I invariably stretch them. This is done by thoroughly soaking the paper in water, holding or hanging it up to allow the excess water to drip off, and then spreading the sheet onto a drawing board. With a clean sponge one can more or less flatten the now limp paper and then seal it onto the board all around with wide, gummed-paper tape. It will dry taut by the following day.

I know of no toned ground available in a good, textured stock, but a watercolor tone can be laid heavily onto Whatman with a very large brush and sponged off after it has dried. The pits of the paper retain some color and the tonality can be controlled both by the value of the wash and by the degree of sponging. Illustration boards are available in gray tones. They are too smooth and water resistant to be quite satisfactory for my way of working, even for opaque or semi-opaque handling. Charcoal papers in various colors may be used for gouache and tempera and, if mounted on cardboard with photo-mounting film (such as Kodak's Thermount Tissue), will take more punishment. Lansdowne uses charcoal paper with success as his direct and economical work does not involve saturating the paper.

Years ago at Audubon House I examined a number of fine hummingbird plates that Fuertes did to illustrate Frank M. Chapman's extensive series of papers on North American birds in *Bird-Lore.* They were done on a gray paper unfortunately no longer available, but the remarkable thing was that the gorgets (at least on *some* of the males) were painted on a smoother (white?) stock and pasted on! Whether this was planned or resulted from his dissatisfaction with earlier attempts beneath, I cannot say. But it worked!

The selection of oil surfaces is also personal. A wide range of canvases, both linen and cotton, are available in tones of gray or tan as well as white. And a white canvas can be toned down before painting begins by scrubbing a turpentine-thinned color over the surface. Gesso panels are very good for detail as are the various canvas boards which I have tried, but nothing is quite as satisfying to me as the spring of the brush on taut canvas. I sometimes paint in oil on Whatman Board (Rough) by first isolating the paper, and the drawing on it, with a synthetic resin varnish—now marketed in a spray can (such as Weber's Univar Varnish)—which prevents the oil from sinking in. I did the egret, tern, spoonbill, and some other illustrations for "Our Amazing Birds" (1952) in this manner as well as the Double-crested Cormorant painting shown in this article.

The range of colors in one's palette is less important than color quality. Regardless of medium I consistently use the finest grade of Winsor & Newton, Grumbacher, or other fine colors. Of course it is necessary to have a good range of the primary colors: red (rose carthame, scarlet lake, alizarin crimson, etc.), yellow (lemon, spectrum yellow, cadmium yellow), and blue (cerulean, cobalt, ultramarine), plus a range of earth colors (yellow ochre, burnt sienna, burnt umber). For reproduction from aqueous media, I find ivory or lamp black better for deep darks than mixing deep reds and blues as one would in oils. For certain effects in watercolor, such as the intense gorgets of hummingbirds, I use Grumbacher-Schmincke Brilliants which come in caps or button-pans and which are highly transparent, almost inklike. All other colors I buy in tubes. The transparent colors are squeezed as needed to keep them full, into pans in a regular painting box. In starting to paint it is a good idea to flood the box at the sink in order to wash off mixed pigments and to soften the colors for better handling. The tubes of designers' gouache (tempera colors) are only squeezed out as needed into ceramic trays, because they harden rather quickly and larger quantities of pigment are required than for the same area in transparents. I like a very large water container or even two, one for rinsing out brushes.

As for brushes, it is better to use larger ones (red sables) which will come to a fine point and carry more color than smaller ones which require frequent reloading. I rarely use a watercolor brush smaller than Number 4. Perhaps Number 6 is the size most constantly employed. The very largest sizes available are used for carrying washes over large areas and flooding on water preparatory to painting wet on wet. Old brushes which have lost their points are often still useful for washes and for softening edges of applied paint. For oils, I supplement flat-tipped sable and bristle brushes in many sizes with the smaller, pointed sables for detail. Filberts (rounded but not pointed brushes) are fine for drawing in paint and I find a blender (fanned brush) helpful in softening transitions or reducing definition.

Methods in Painting

Watercolor, being transparent, allows for underpainting. By the time I had read Sutton's account of Fuertes' method *(Audubon Magazine,* 1941), I had arrived at much the same approach—that of painting in the form and defining the feather tracts (auriculars, lores, malar region, throat, scapulars, etc.), wing, tail feathers, and the like in rather neutral tones. This included some dry-brush texturing, the pigmented brush being applied with the tip more or less fanned (by wiping or "heeling" it first on another surface or by splaying it by pressing the base of the hairs between one's fingers), laying down feather texture (often by cross-hatching) as a base for the final, exact color wash. A clean, damp brush will then pick up the highlights where they have not been gone around as in, say, the white bars formed by the tips of the wing coverts. A dampened, blunt, old brush can then be used to soften the edge of the bird against its background. When I am illustrating a yellow-breasted bird, for example, I first lay on either a neutral or a darker yellow tone representing the shadow (contour) of the underparts, then I soften the slightly darker inner edge, and apply a flat yellow mixed to exact color over the whole area. The underpainting provides the form. Where deep darks are overpainted with a wash, a certain amount of final accenting is necessary.

I now tend to paint more directly with final color, or to apply washes of deepening values of the same color—that is to say, building to value with

Pulsatrix melanota Koeniswaldiana

Tobunas, Misiones, Argentina
Sept. 8, 1959

exact hue. And I am less of a purist than I once was. Where an opaque color will give a closer effect in a generally transparent illustration, I do not hesitate to use it. But when it is used to salvage a passage gone wrong, it becomes a crutch. My honeycreeper-tody plate for Bond's "Birds of the West Indies" was executed in this mixed treatment. I painted the very different blues of the male Red-legged Honeycreeper and Orangequit and the green upperparts of the todies in tempera and the rest of the plate in transparent watercolor.

The wet-on-wet technique requires considerable control. In pure watercolor I might use it both for certain areas on certain birds—for example, the blurry, soft markings on the chest of a Great Horned Owl—and, more frequently, for backgrounds where I want to set that plane away by playing softness against crisp, foreground delineation. In any case, one has to learn how much lighter the color will dry when pigment is applied to a damp surface. For backgrounds, water is flooded onto the paper around the bird and the foreground accessories. Where the background is broken up into isolated sections—a condition to be planned for in composition—such sections can be handled one at a time, thus simplifying the problem. Once the edges of the foreground material have been carefully "painted" with water, more brush-loads are applied until the given area is quite saturated. This should be done with the working surface flat. The color that is to go on must be mixed with a minimum of water and be darker than the result intended, as the wet surface will not only soften but lighten the hue. Paint freely and quickly at the moment when the paper no longer shows surface water but is still moist. If any dryish spots show before starting, a little water may be added and will spread, but do not add water once the painting is begun. When quite dry you may darken the tone by covering the whole area with one or more washes, or you may lighten it slightly with a kneaded eraser. India ink and tempera may be used in the same manner, though in the latter medium transparent passages are rather risky.

Dry-brush technique goes to the other extreme. After the brush is dipped in paint, it is wiped off on a piece of paper before application. Where I want a very fine texture and especially for higher keyed, less "dry" effects, a moderately loaded brush may be splayed out (fanned) either by "heeling" it onto the scrap paper or by squeezing the base of the brush. Under humid field conditions, washes often refuse to dry, and here a more extensive use of the dry-brush technique can be especially helpful. As a rule it is used for transparent underpainting or for heavy or opaque overpainting.

Where I apply broken areas of color in the ordinary course of painting as, say, on the striped back of a sparrow, I usually first put down the blackish median portions of the feathers. Then, after softening the edges with a clean, damp brush, the intermediate brownish color (bordering the black) is put down, defining also the overlap of feathers and again softening the outer edge. The pale buffy edges may then be tinted in. All this usually takes less time to do than to describe. I do not suggest that this is *the* way to proceed, but that it is one way to try.

Gouache and tempera, where used on toned grounds, give you the advantage of being able to work toward both light and dark value extremes from an established middle value. This helps in holding the picture together tonally. On *white* paper it is practical to begin with a thin, flat application of the local colors and work up and down in value on this pre-established tone. In gouache it is effective to work transparently for values darker than the ground color and opaquely for those lighter.

Oil is so little used for book illustration that the work of Jaques stands almost alone in the field in this country. His paintings for the original "Florida Bird Life" (1932), many of which were done in this medium, are a landmark in the presentation of a logical association of birds dominated by their background, thus conveying the habitat-group effect (for which he is also well known) in small compass. Jaques writes me that he paints "birds, or any object in oils on canvas *first,* because it is much easier, and somehow they come forward better and the outline can be cleaner, which in specific birds is, to me, desirable. I paint trees first. Sky showing through trees looks better and has a better shape when painted last or over the trees. Otherwise the tree branches, etc., look obviously painted last and the sky areas have little sharp corners which should then be laboriously filled up. But there is a limit beyond which the detail would be too great, and painting over the background or sky works too. If . . . some parts of the bird are lost against the background, they can easily be altered later. I do the painting as far as I can go, first—study it a few days or preferably longer, then after the painting is dry, make corrections by dragging stiff color or values, not completely covering the underlying color. Highlights can be brightened and clear color can be used with a clean brush where desired."

Where the background is an important element of the picture, *I* have usually worked the other way round, just as I would in watercolor, and perhaps out of that habit, as I like to get the whole sweep of the background in and establish the values of the landscape before moving up to the birds and extreme foreground detail. In doing this I, admittedly, run the risk of executing the background so strongly that there is no "power" left for the foreground elements, so it is necessary to keep this always in mind. Wherever possible I paint around the birds drawn on the surface, but without much care. This can be tidied up when the birds are painted in. The difficulty of drawing or tracing birds onto a finished background is that the birds are apt to look just that way—superimposed—because of the reduced surface texture resulting from the additional application of pigment. Where I am painting from the aesthetic rather than the scientific viewpoint, I usually work all over the picture, building it up rather evenly, until *it tells me* I am finished, which is often sooner than I had planned and sometimes later.

Methods in Line

Ordinary pen-and-ink techniques are so well known and so generally applicable that I need say little here. In their relation to bird illustration, I would only point out that the work of Earl L. Poole and George Sutton,

An example of wet-on-wet background technique. The Yellow-billed Cuckoo, the tent caterpillar nest, and the rest of the foreground were painted last.

Oldsquaws from a color original, 6 x 22 inches — an example of mixed media. The entire background is transparent and was allowed, in the process of painting, to invade the birds drawn in, so that the free handling of the near-shore waves was not inhibited. The heavier washes overlapping the figures were then minimized by picking up most of the color with a clean, damp brush, and the birds painted in, largely with tempera handled opaquely. (Reproduced by courtesy of Western Printing and Lithographing Company.)

This Snowy Owl, painted in tempera, is reproduced original size but somewhat trimmed. Done as a large stamp for the National Wildlife Federation, and reproduced by their permission, it illustrates both the freedom and limitation of painting for a particular purpose. As the stamps are quite small, the bird figure must be large but may be painted rather loosely. Not intended to be an identification picture, though it must be identifiable, it was possible here to use backlighting and a contrast of warm (background) and cold (owl) colors to create form and space. It is not usual to paint a white bird dark, but it is perfectly realistic to do so, so long as it still *appears* to be white.

and the two English illustrators, D. M. Reid-Henry and R. A. Richardson, is particularly worthy of study.

Scratchboard is, I think, more generally used today because of its greater plasticity than straight pen work. It allows not only for black on white but also for white on black by virtue of surfacing cardboard with plaster which will accept a coating of black pigment to be scratched into. Scratchboard is available in both smooth and textured surfaces, the latter for halftone effects. C. F. Tunnicliffe in England and Jaques in this country are the leading exponents of the medium. Tunnicliffe is much more texturally oriented and works well within the extremes of value range. Jaques pushes values to black and white extremes with a minimum of intermediate tones. His illustrations in the attractive books written by his wife, Florence Page Jaques, demonstrate the point, as will "Shorelands Summer Diary" (1952) and other books by Tunnicliffe. Roger Peterson's work and T. M. Shortt's illustrations for "Arctic Birds of Canada" (1957) are also worthy of study.

Jaques, who uses black opaque watercolor applied with a brush, writes: "When dry, cut the lines with, say, a knife blade point. Lines which, when a brush is used, are thick and lumpy, just scrape the edges until they are thin." I personally have always used India ink and employ scratch knives (both pointed and rounded types), inserted like the pens they resemble into the ends of a double-headed pen holder.

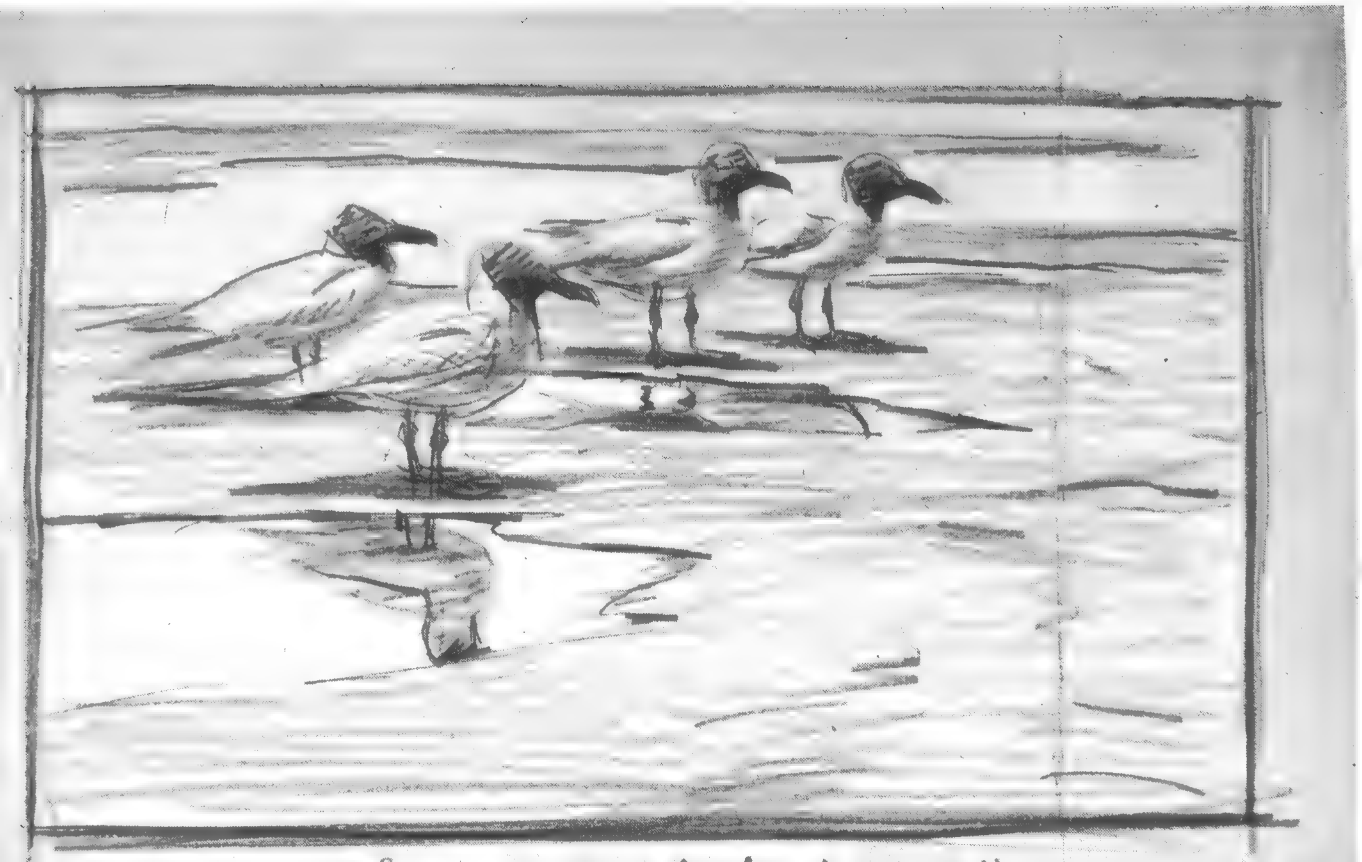
My experience has led me to a few cautions with regard to line work in general. Do not try to duplicate a full range of values. Aside from pure black and white, select only two or three or, at the most, four values of gray for translation. In short, it is best not to try to convert line into a full halftone effect. With much labor it can be done, but rarely without the loss of those crisp and strong qualities which are the advantages of the medium. Whether the line is black on white or the reverse, the strokes should be applied in conformity with the shape of the object in order to enhance the illusion of form where form is desired.

With scratchboard it is important that the board be quite dry following the application of pigment. If it is not, the scratched lines will dig in raggedly and too deeply. On damp days, hold the board over a burner or put it in the oven for a few minutes. Use a brush wherever possible in preference to a pen as, with a brush, there is less building up of pigment. Be direct and avoid reworking.

While not precisely a "line" technique, dry-brush ink drawing *is* a black and white method reproduced as line and so may be mentioned here. The handling is much the same as for dry-brush color work except that the pointed brush is employed more frequently. To retain a point, when draining the brush of excess ink, roll the tip of it on scrap paper. The texture can be controlled by the tooth of the paper. My Ferruginous Pygmy Owl drawing on page 194 of *The Living Bird* (1964) was done on white charcoal paper and reproduced original size. Such fine texturing would not stand much reduction.

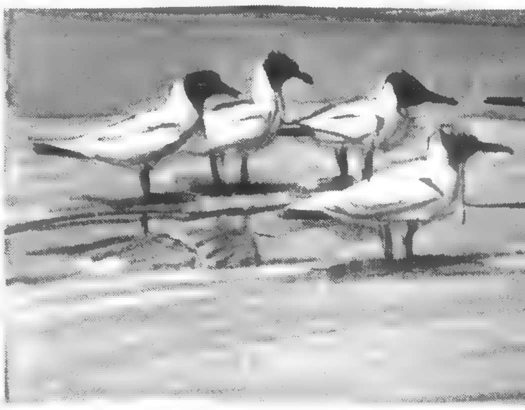
Reproduction

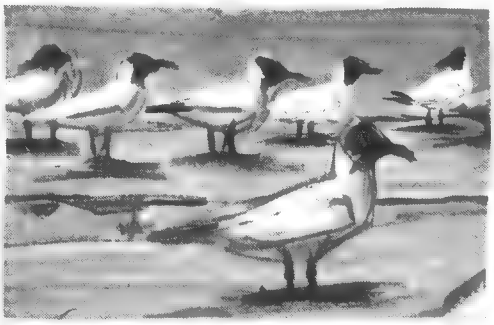
One learns early that some degree of quality is almost invariably lost in reproduction—all too often a depressing degree. This is particularly true of serial work for book illustration where, for cost reasons, whole groups of plates, almost sure to have a range of colors beyond the scope of the usual



high keyed: darkest darks not black (bellies picking up warm reflections from mud)

very textured – lush color





These small compositional sketches are ty
of those I make in working out the design
picture before going on to finished draw
for illustrations or, for more creative w
freer drawing and painting on the final
face. The gull sketches are concerned
pattern, while that of the Barred Owl is
turally oriented.

four-color process, are photographed as one. The reproduction of individual plates stands a much better chance. Even when the proofs are quite good, one must expect a substantial loss in the press run.

To compensate for this, it is important to make illustrations as strong as possible. This may require some exaggeration—for example, I paint the irises black in species where they are really dark brown. Not only does this give a bird a more "alive" effect but, as one of the field notes quoted earlier indicates, this "distortion" is closer to the life aspect.

In both color and halftone work I sometimes instruct the engraver, by an outline of such areas on a tissue overlay, that pure whites should be etched out. This is important for white plumage areas where one or more screens remain over the "white" background which, because of the screens, will appear slightly toned. At times, when I use a rough paper and am not sure that white plumage areas can be etched out, I paint these untouched paper areas with opaque white so that the pits in the surface texture, by virtue of having been filled in, will photograph whiter.

Wherever possible it is best to work natural size in the original. This makes it easier to hold to true proportions and, where a number of species are shown together, to maintain their relative size. In a series it is often necessary to hold to one or a few sizes in the originals so that a group of plates may be "shot" at one time, or because it is impractical to do the larger birds life size.

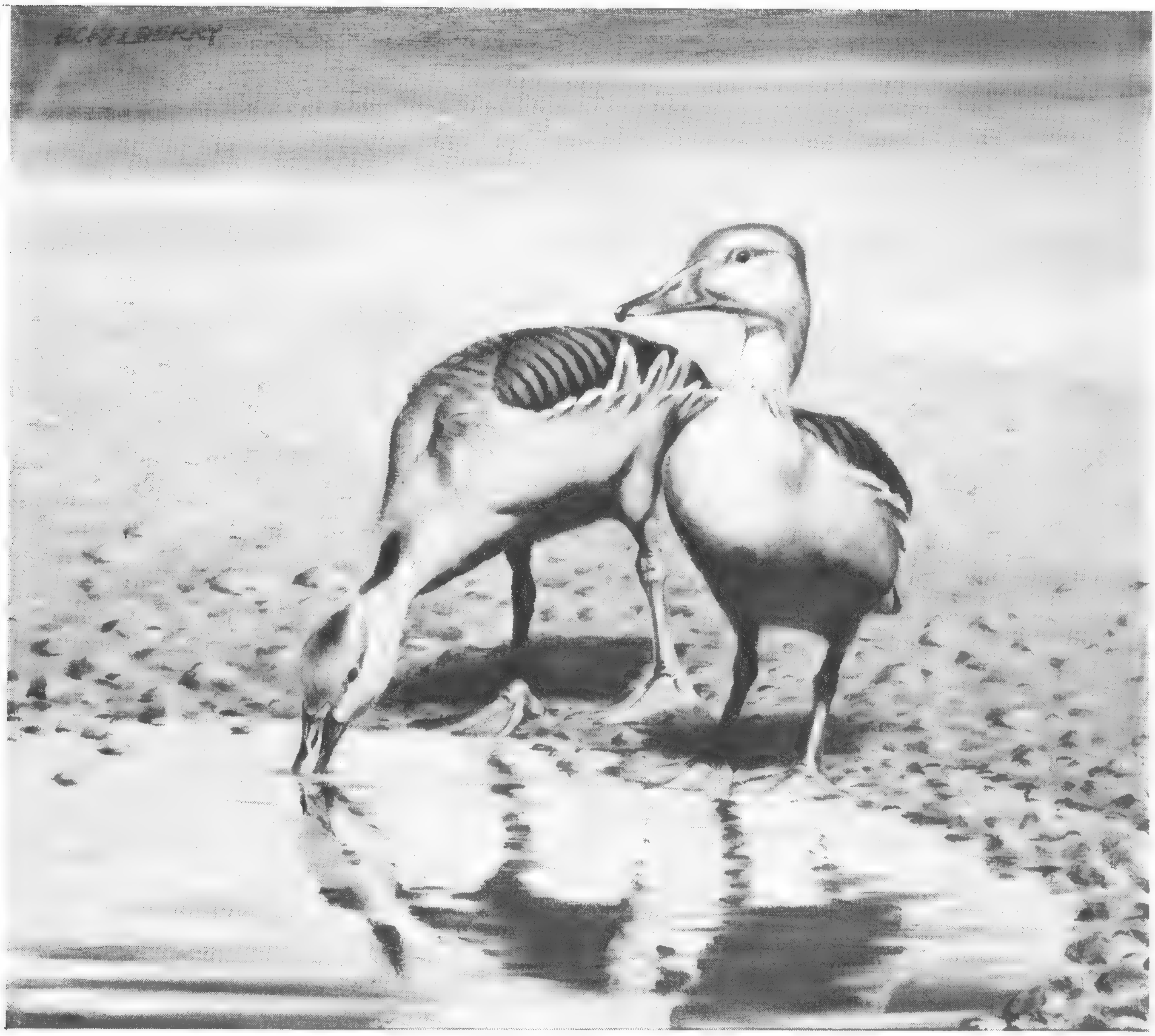
It is perfectly satisfactory to work at reproduction size where you are not reduced to miniature painting, but the usual course is to work somewhat larger, even up to double size. Extreme differences between working and plating sizes risk much loss in texture and detail. It is never a good idea, for illustration purposes, to work larger than life size.

I think it may be fairly said that in this country not more than two dozen bird books have been produced with a substantial number of color plates which really present the artists' works with fidelity. Three of these would certainly include Fuertes' illustrations for "Birds of New York" (1910), "Birds of Massachusetts and Other New England States" (1925-27) completed by Allan Brooks, and "Artist and Naturalist in Ethiopia" (1936). I would also include Fuertes' and Brooks' work for The National Geographic Society's "The Book of Birds" (1932), Sutton's paintings for "Birds of Western Pennsylvania" (1940) which might be considered the finest reproduction of all, and Singer's illustrations for "Birds of the World" (1961). Of the books I have listed, only the plates for the last named were originally produced by a regular commercial publisher and to them I make a profound bow.

Style

Bird illustrators are all "realists." Yet the work of each is as identifiable to even a slightly practiced eye as is their subject matter. The total effect of the painter's preferred surfaces, his color palette, his drawing, his manner of handling paint—all these combine into a kind of handwriting or, to be more exact, handpainting which makes it unnecessary to look at the signature. This is a part of personal style. Beyond this there are some elements in a wholly different category which we should look into for instructive purposes. The terms here are rather arbitrarily employed:

Stylization is a mannered way of painting and therefore is, I suspect, at least partly conscious. Audubon's histrionics, which we may ascribe to the Romantic tradition, and his rhythmic devices, together with the enrichment



Fulvous Tree-Ducks (oil on canvas, 19½ x 21½ inches). Drawn directly on canvas, the exact size detail at right indicates how rough the finished work may be when the painting is not approached from an illustrational viewpoint.

Double-crested Cormorants on their nests (oil on Whatman Board, 14 x 18½ inches). Crests are not shown simply because I have not seen them elevated, even on breeding adults. The painting is an attempt to get away from conventional illustration both in lighting and in composition. Rather atypically, the sky was painted *first* because a very evenly graduated background was important in achieving a misty effect. The entire drawing was then transferred on and painted. (Reproduced by courtesy of Western Printing and Lithographing Company.

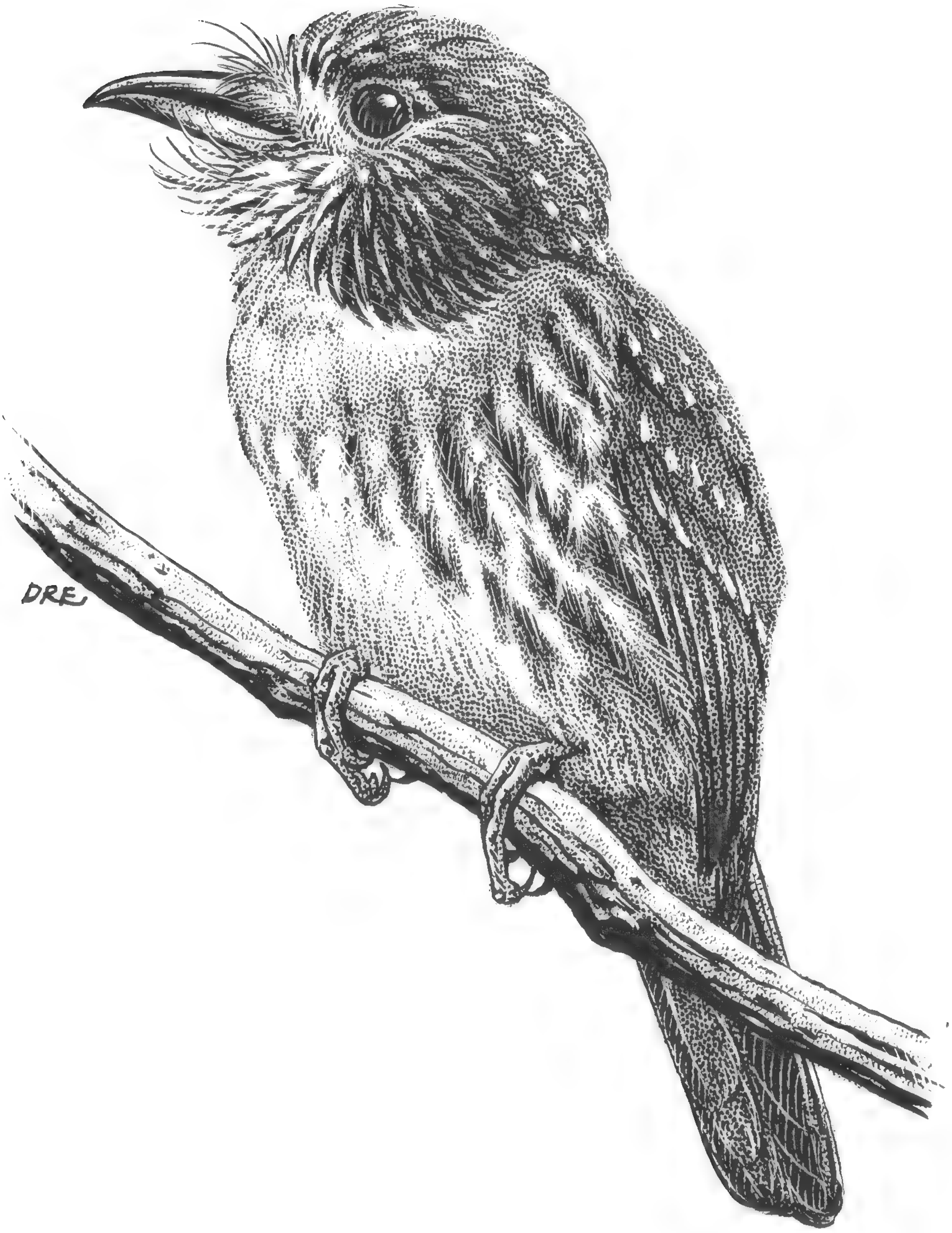
of surface textures and a certain amount of distortion, typify the approach. As I have discussed Audubon's work at some length in *The Living Bird* (1963), there is no point in going into it here.

Conventionalization appears to be less a deliberately mannered style than a matter of construction showing through painting. It contrasts with stylization in the stripping away of textural interest and in the standardization of form, though both tend toward decorative effects. The illustrations of Allan Brooks demonstrate this point of view. Almost from the start, Brooks developed a basic approach reminiscent of what one sees in books on "How to Draw Birds" in art supply stores. The body is egg-shaped, the head a ball stuck on the body, the tail a pliant stick attached to the pointed end of the egg. While this works well enough for chickadees, kinglets, and the like, it does not work so well for hawks and many other groups. Take any collection of illustrations by Brooks and regardless of the order, the family, or the species you will almost invariably find that the line from the bird's shoulder to the tip of its usually flared tail describes a shallow S-curve, a "sliding-board" back. Foliage and branches also tend to fall into rhythmic arcs. He was nearly as conventional with light, for his birds show pretty much the same clarity against sunsets, stormy skies, or other conditions of light. Since Brooks was very much a field man and collected specimens, one is rather at a loss to explain this monotonous and stereotyped style other than on grounds of deliberate intent or a lack of feeling for the nuances of drawing and light. At the same time, it is only fair to say that his atmospheric backgrounds are often very evocative.

Within the limits of our discussion, to what extent is the painter conscious of his style? And is this to be sought or avoided? I recognize that some would equate style with art. I do not. I think the reason Brooks' work looks "dated" while Fuertes' does not, revolves around this point. Audubon, while mannered, was so aesthetically oriented that he is still in style, a style now classical.

I think it is best for the bird illustrator and vital for the bird artist to be aware of these distinctions but, in his own work, to paint the way he sees and feels, allowing his own style to take shape naturally. We all develop clichés and habits. It is good to become aware of these too, to put them aside after a time, and to strike out in some new direction. Dissatisfaction with one's work is surely the necessary goad to growth; without improvement any effort becomes a bore.

Jaques once remarked to me that the trouble with bird painting is that all the good positions have been taken. He was speaking of doing *illustrations* of North American material, much of which has, indeed, been done to death. From an identification standpoint a profile of a bird is the perfect position. It is also perfectly dull. But the moment one departs from the profile, he is showing some aspects of the bird twice and others not at all. Thus the latitude in functional positioning is always limited and sometimes exhausted, as Jaques said. This is particularly true of those groups of birds of rather indifferent "personality" such as vireos, warblers, and thrushes. Finches, wrens, and the like also may not show much more individual anatomy than a wad of cotton, but they do have a wider range of postures and do more with a tail than just let it stick out behind! Certainly the "dickey birds" have less character than the lower families and for that reason are perhaps more difficult to paint well. Any strongly stylistic treatment will surely overpower them, as Audubon's plates clearly demonstrate.



A life-size drawing of a female White-whiskered Puffbird on textured scratchboard, reproduced actual size. Aside from illustrating the effect of lithographic crayon and ink on this surface, it illustrates also some of the complicated situations in which the bird painter can find himself. Alexander Skutch had asked me if I would provide the illustration for his paper which had been accepted for publication by *The Ibis*. I agreed and sent this drawing to the editor, only to receive word from him that it agreed neither with skins nor with anything mentioned by Skutch in his life history account and that, since he must go to press on schedule, he would not use the illustration. Since I had based my drawing upon observations made at Skutch's farm, I reported the matter to him and enclosed the proof. He shortly replied, "Just this morning I saw a male *Malacoptila* whose whiskers were very much as in your drawing—loosely formed rather than forming 'walrus tusk' moustaches."

Acknowledgments

For their information and suggestions I want to thank Francis Lee Jaques and George Miksch Sutton who have, as always, extended their help. My thanks go also to J. Fenwick Lansdowne, with whom I corresponded on this subject, and to Guy Coheleach, Walter Ferguson, and Arthur Singer, with whom I discussed it personally. Unless I have quoted directly or indirectly, the statements represent my views and do not necessarily agree with the views of my colleagues. Also, I should add that I selected examples of the work of my fellows in the profession merely to prove particular points. The inclusion or the exclusion of names means that and nothing more.

180 WOODSOME ROAD, BABYLON, NEW YORK

Loon, textured scratchboard.

DISPLAYS AND SONGS OF A HAND-RAISED EASTERN MEADOWLARK

MARGARET MORSE NICE

On 20 August 1948, in Jackson Park, Chicago, I came upon Mr. and Mrs. Theodore Brauer releasing a young meadowlark that refused to be deserted. In mid-June their son had rescued the bird from a dog on the golf course; the meadowlark might have been ten days old at that time. During the bird's stay of approximately nine weeks at the Brauers they had made a great pet of him. He followed the family all over the house. And, when the Brauers were out, he seemed content to stay with their dog.

I brought the bird home and installed him on our sun porch in a cage four feet long, three wide, and two high from which I frequently let him out on the porch. We called him "Little Lark" and I referred to him as LL in my notes.

The meadowlark was fully imprinted on human beings. Whenever anyone appeared on the porch he came running, waving a wing, and peeping. This location call he uttered until at least the age of 13 or 14 weeks. In the wild, Lanyon (1957:48) last heard the juvenile location note from a 33-day-old meadowlark.

On 1 September, we first heard the alarm chatter, *dzert-tet-tet-tet-tet* (G. B. Saunders, 1932), that identified our bird as the eastern species, *Sturnella magna.* He gave the chatter in response to alarming or startling events, including coughs or sneezes by one of our family.

LL roosted on the floor of his cage. He was a very light sleeper, like two other ground-living species I have raised—a Bobwhite *(Colinus virginianus)* (Nice, 1939) and a Killdeer *(Charadrius vociferus)* (Nice, 1962)—and in marked contrast to the shrub- and tree-living species I have kept. For example, our adult female Black-and-white Warbler *(Mniotilta varia)* (1950b) slept so soundly that she did not awaken when we turned on the lights, talked, or even touched her gently. Both the meadowlark and the Killdeer were greatly disturbed by movement *above* them outside the windows, such as men climbing ladders or trucks standing in the back yard.

Play Activities

Three activities of this meadowlark might be designated as play: Play-hunting, Play-fleeing, and Play-fighting.

Play-hunting.—LL constantly probed in all sorts of situations where no food was found. On 14 November 1948, I noted: "LL found a small hole in my sweater and immediately enlarged it. Pounds on newspaper; then enlarges holes." He liked to make holes in the couch cover.

Play-fleeing.—I first noted this activity on 29 August 1948: "LL gave big jumps with sudden turns." By 1950, Play-fleeing usually started with crouching, after which the bird dashed wildly about, always on foot. My last record for this activity was on 3 October 1952, nine days before we gave him to the Brookfield Zoo. Konrad Lorenz considers this "play-fleeing" or "frolicking" to be "emotion-dissociated fleeing movements" (Nice, 1943:67; 1962:168). Eibl-Eibesfeldt (1950:315) writes in regard to his hand-raised badger *(Meles meles)* that "Each sudden change of direction is in my opinion an inborn movement element of escape."

Play-fleeing has been recorded in three other passerines: the Song Sparrow *(Melospiza melodia)*; Red-winged Blackbird *(Agelaius phoeniceus)* (Nice, 1950a); and our hand-raised Blue Jay *(Cyanocitta cristata)*, and also in a number of species of eight families in six other orders: Struthionidae, Ardeidae, Anatidae, Megapodidae, Phasianidae, Rallidae, Charadriidae and Scolopacidae. In mammals various investigators have observed Play-fleeing in seven species of five families in five orders: Mustelidae, Muridae, Leporidae, Cervidae, and Equidae (Nice, 1962:168).

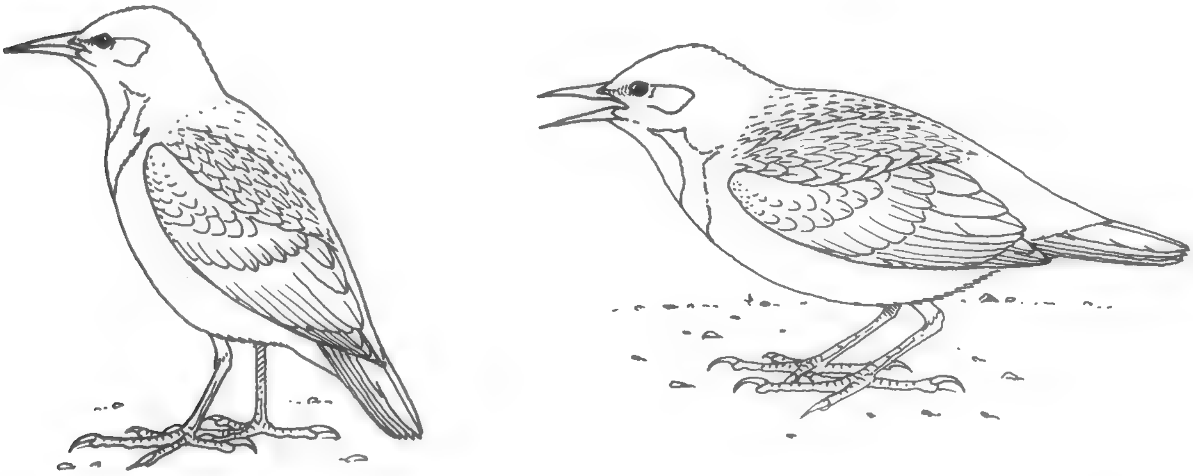


Figure 1. Left, Eastern Meadowlark in normal, "at ease" stance. Right, ready to fight.

Play-fighting.—I saw this in the meadowlark's first fall. According to my notes for 6 September 1948: "LL fought with a piece of potato skin, falling on his side and lying there for perhaps 20 seconds. Did much the same thing with my hand, putting one claw on it and pecking." 8 September 1948: "Gave him a big withered sunflower leaf. He attacks it, *lying on his back,* holding it with both feet." 20 October 1948: "He fights with our fingers thus: When a finger is raised and lowered, he crouches, opens his bill [see Figure 1], rises, strikes with one foot, often over-balancing himself and falling on one side. May grasp the finger with both feet, falling on his side." And 9 May 1949: "Suddenly attacking and fighting the southwest corner of his gravel box, falling over on his side outside. Renews attacks, falling on his back inside, feet in the air! Then fights different corners of the box."

Concerning real fighting in meadowlarks, Dr. George B. Saunders wrote me: "The use of their strong feet in fighting is typical. They can be vicious fighters. The males, battling over territorial rights, will at times lock their sharp claws in each other's plumage or pectoral muscles as they lie side by side on the ground."

Displays

Five displays of this meadowlark will be described: territorial threat; courtship; nest-invitation; nest-molding; and food-carrying.

Territorial threat.—In the spring of 1950 the customary response of LL to the appearance of most human beings was a "bill-raising" display. Andrew (1961) recorded the same display in reproductive fighting for some 34 passerine species. "Most, perhaps all, of the Icteridae give a sleeked bill-raised display in reproductive fighting" (page 327). Lanyon (1957:31) tells of "bill-tilting" in meadowlarks; Nero discusses it in his papers on the Red-winged Blackbird (1956:12-13) and Yellow-headed Blackbird *(Xanthocephalus xanthocephalus)* (1963:382-386). Vogt (1937) vividly describes this display between two male Eastern Meadowlarks in a territorial border dispute.

The characteristics of this display are: *body elongated vertically; head and neck feathers sleeked; bill pointed up* (Figure 2A). Occasionally, when highly motivated, LL turned his back towards the intruder and spread and closed his rectrices.

Our meadowlark indulged in bill-tilting when he was in his cage or on the sun porch, not on the rare occasions when he was in the front of the house. He customarily "bill-tilted" to my husband, my daughters, and all strangers, but seldom to me, the exceptions being when I did something out of character, such as tapping on the sun-porch window. Only twice did we see him displaying in this manner to other birds; in each of these instances there was an element of surprise or of a specially strong stimulus. On 20 March 1951, he postured thus momentarily at our nine-month-old Blue Jay that had suddenly flown into his cage. On 7 November 1951, a Robin *(Turdus migratorius)* was brought onto the porch; she escaped, then screamed as I caught her. LL went to the farthest corner of his cage and lifted his bill to the zenith.

Courtship display.—This behavior was far more pronounced in LL's third, fourth, and fifth summers than in his second. It was largely directed towards me and only once to any other member of the family. Copulatory behavior was first noted 30 October 1948. It was characterized by wing fluttering and warbling (Lanyon's "rehearsed song" (1957:22)) and was fairly frequent in the following spring and summer. It usually took place upon my hand.

The full courtship display was seen only twice in 1949, but occurred frequently in the three following years. The bird *stood erect, raised his crest, puffed out his left breast, held his wings out from his body,* and at times *spread and flipped his tail* (Figure 2B). Lanyon calls this "strutting" (1957: 39). LL took *short, quick steps* and occasionally made *little flights upwards*—"jump-flights" (Lanyon, 1957:38). He *warbled* loudly and then attempted to copulate. Afterwards he usually gave a series of single, high whistles. Such whistles are uttered by wild meadowlarks during periods of "intense excitement . . . the presence of a hawk over the territory . . . [and] immediately following copulation" (Lanyon, 1957:11-12, 40). Our bird also uttered them when held in the hand for close examination.

LL's courtship display differs in one respect from the typical behavior described by Lanyon (1957:39) where the male holds "the bill pointed downward toward the expanded chest." I never saw this with LL but noted it in May 1953 with the Lanyons' first hand-raised male Western Meadowlark, *S. neglecta*—"Reds"—when he was trying to copulate with a fledgling meadowlark in the Lanyons' trailer.

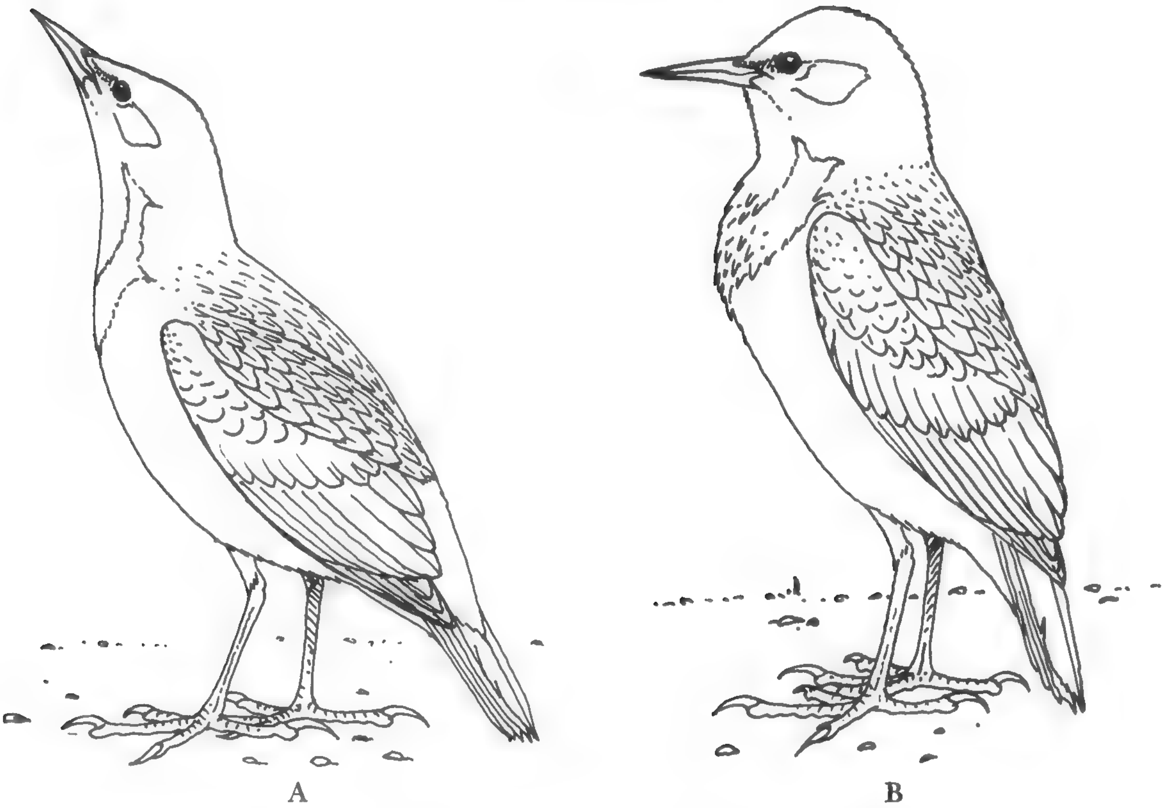


Figure 2. A, male Eastern Meadowlark in bill-tilting display—a threat to territorial rivals. B, male in full courtship display.

Andrew (1961:576), on Lanyon's (1957) authority, shows neither species of meadowlark as singing during courtship, contrary to the behavior of the 11 other icterids in his table. He seems to base this conclusion on Lanyon's description (page 40) of copulation between a *neglecta* pair where the male mounted and the birds "remained in this position for seven seconds, during which time both birds were silent." Nevertheless, Lanyon writes (page 22): "The circumstances under which rehearsed song [warbling] was delivered were similar in the two species: [for instance] . . . during courtship activities." In answer to my query, Dr. Lanyon wrote me that rehearsed song "was often given by males during the activities preceding copulation, i.e., jump-flights and 'strutting'."

On 20 June 1949, I saw courtship behavior when a box of mealworms was introduced into his cage and on 21 September when I brought a female Black-and-white Warbler near his cage. In 1950, he showed courtship behavior to me nearly every day from 21 May to 14 July; four days later he started to molt. When a young Robin recently out of the nest was exhibited to LL on 29 May, he went into an extravagant display on my hand and a little later displayed to the Robin. On 6 July, he displayed when a young Blue Jay was brought next to his cage; and again, on 14 July, he was stimulated by the sight of a large leaf.

Eight times in his third to fifth summer sperm was emitted during displays, the earliest occasion being 13 May, the latest 21 July. The special stimuli setting off such extreme behavior were as follows: a fledgling Robin; a fledgling Blue Jay; a mounted Song Sparow (three times); a handful of crumbs; a rolled up silk stocking; and nothing extraneous. I showed him these objects. After each of these experiences, as well as after many of his copulatory attempts, LL gave a series of the clear, high whistles, from 24 to 121 at a time, the last series lasting for ten minutes.

In late July 1951, we performed three experiments on the courtship behavior with other individuals besides myself offering LL a stimulating object.

17 July: "Constance [my daughter] shows him the mounted Song Sparrow. Wild warbling; copulatory attempts on her wrist. 92 whistles afterwards, lasting 8 minutes."

24 July: "Dr. L. E. Richdale presents a red sock. LL warbles; assumes copulatory attitude. Then stops. Seems confused. Hops down. Then bill-tilts a little. No whistles."

26 July: "Dr. Richdale offers the Song Sparrow mount. LL flies on his hand, steps on mount, fluttering and warbling; tries to copulate 3 or 4 times. 63 whistles in 4 minutes."

LL typically indulged in courtship when I returned to the house after an absence of several hours. In 1952, I was away at Delta, Manitoba, for three and a half weeks, and, in 1951, for six weeks; yet both times he remembered me perfectly. That he recognized us by our voices as well as by sight was shown on two occasions.

19 May 1951: "Constance and I had returned from a two-hour absence; she went out on the porch and I called to her from the front of the house; at once LL jumped down from his perch and started to rush up and down along the north side of the cage. I came on to the porch and he immediately put on an extreme courtship display."

18 April 1952: "LL hears Constance speak in the front of the house. Gives loud chatter, then bill-tilts. Hears my husband's voice. The same response."

Mingled with courtship was a great deal of aggression directed toward me. LL pounded my hands, my arms, my ankles, and my shoes with great vigor during all four springs and summers. Lanyon (1957:40) states that males of both Eastern and Western Meadowlarks "sometimes exhibited considerable aggression prior to, and during, copulation." He told me that his hand-raised *neglecta* male—Reds—used to peck his and Mrs. Lanyon's hands when they reached into his cage; he would court, pound, court, and try to copulate. Dr. Lanyon added that in nature males may be very rough when copulating; they may seize their mates by the back feathers and shake them! Dr. George B. Saunders, on the contrary, writes me that he had observed "no very rough treatment" of females by their mates.

Other people were also treated to LL's attacks including at times my husband and occasionally Constance. However, such attacks were not motivated by courtship. The absences of Constance and myself at Delta (from 21 May to 1 July in 1951, from 10 June to 6 July in 1952) were hard on our bird. Both times, despite the efforts of my husband in caring for him, he went into a kind of depression. He stopped singing, bill-tilting, attacking; instead he hid in corners of his cage, head down, and tail up. Upon our return he became once again his spirited, vocal, out-going self.

Nest-invitation.—Nest-invitation was one of two distinct "symbolic nesting" displays shown by our meadowlark, the other being "Nest-molding." Bill-tilting and courtship display became prominent in LL's third summer and, closely connected with the courtship display, "Nest-invitation" also appeared. I saw it, in 1950, from 21 May to 6 July; in 1951, from 24 April to 19 May, again from 2 to 31 July; and in 1952, from 15 April to 9 June and again from 7 to 9 July.

Very often, right after the courtship display, LL went into this entirely different display: With *body horizontal, tail stiffly erect, wings held out*

Figure 3. Nest-invitation display of male Eastern Meadowlark. With body horizontal, tail stiffly erect, and wings held out (top), he settles on the nest (center), and sometimes bills a piece of grass (bottom).

and *flipped,* he walked slowly to his "nest corner" where he settled down (Figure 3) and gave soft *purring* notes never heard on other occasions. He pushed his head under the surrounding grass and lifted blades; sometimes he billed pieces of grass and tucked them under him (Figure 3).

My desk was next to LL's cage with a window between us. While I was working at my desk, he often gave this nest-invitation display, looking up at me and flipping a wing. When I left my chair and went out of his sight, he flew to a perch and gave a brief song, over and over. As soon as I returned to my desk, back he went into his nest corner and resumed the display with the characteristic notes.

Nest-molding.—This display was first seen on 9 June 1949, and was often repeated from then on till 29 July. In 1950, it occurred from 14 June till 29 July; in 1951, from 6 July to 8 August (I was absent from 21 May to 1 July); and in 1952, from 10 June to 21 July.

With *head up, tail down,* and *wings outspread,* he lay in his nest corner and *kicked vigorously backwards* (Figure 4). No vocalization accompanied this display. Sometimes he lifted blades of grass. On 8 July 1950, I noted: "He seems to be a little shy about 'molding' when I'm looking." In 1952, I wrote on 1 June: "Hear him 'scrabble'; first time this year. Hear him scrabble twice again, but won't continue when I look out the window."

This display started a year earlier than Nest-invitation; in three years it was first seen in June in contrast to April and May for Nest-invitation, but each year it lasted later in the season than the other. Nest-molding (with the omission of 1951 when I was absent in June) covered an average span of 50 days per season; Nest-invitation a span of 78 days.

This "molding," "scraping," "kicking," "scratching," "trampling," "scrabbling," or "stamping" is well known among Charadriidae and various other ground nesters. It also occurs in passerines and other families that build nests above ground, such as the American Robin (Herrick, 1911), European Sparrow Hawk *(Accipiter nisus)* (Bal, 1950), and even among builders of pensile nests, such as the Red-eyed Vireo *(Vireo olivaceus)* (Herrick, 1911) and Long-tailed Tit *(Aegithalos caudatus)* (Maxse, 1951). In a very incomplete list I have noted the occurrence of Nest-molding in 26 species (17 of them passerine), in which the male is involved in 12 cases, the female in 20.

Neither of these symbolic nesting displays appears to have been reported for wild meadowlarks. Nero has described two symbolic nesting displays for the male Red-winged Blackbird and one for the Yellow-headed Blackbird.

In the first of these displays of the Red-wing, which Nero (1956:21-22) calls "nest-site selection," while the female watches, "the male *crawls,* still holding his wings partly upright," breaks off bits of nearby cattail blades and manipulates them like a female building a nest. He gives a "low, harsh, buzzing 'hahh' during the display." Our meadowlark's Nest-invitation corresponds to this display in the slow, horizontal gait to the nest-site, in wing action, in manipulation of nesting material, and in vocalization, as well as in the orientation of the display to the mate.

The "symbolic nest-building" of the Red-wing is described thus: "While the new female watched, he went inside the [old] nest and then went through the motion of building, forming it with his chest, lowering his head into it, and picking here and there, meanwhile holding his wings erect." This would seem to correspond fairly well with the meadowlark's Nest-molding, except for the position of the wings and the apparent absence of "trampling."

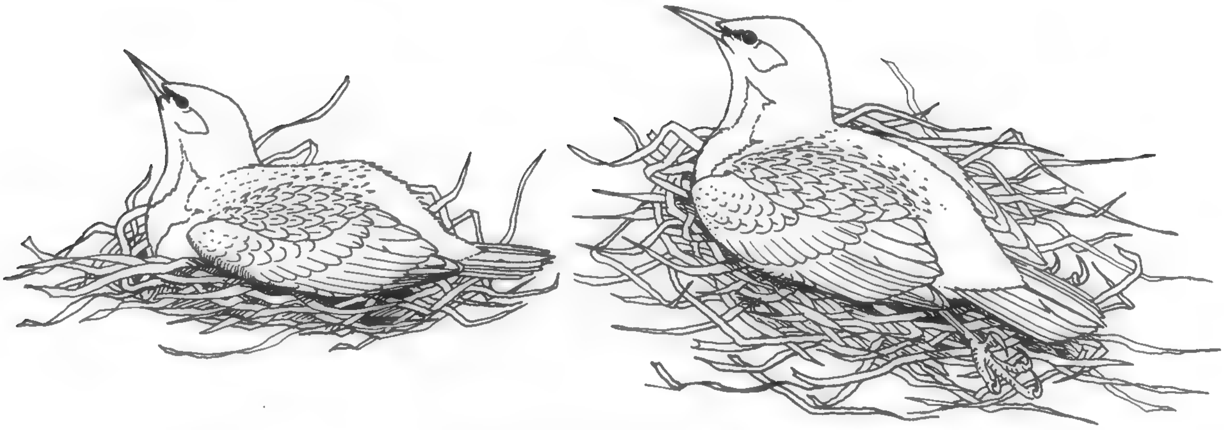


Figure 4. Nest-molding display of male Eastern Meadowlark. With head up, tail down, and wings outspread, he sits on the nest (left) and kicks vigorously backwards (right).

In answer to my inquiry, Dr. Nero informs me that he has never seen trampling in either of the blackbirds he has studied.

Only one "symbolic nest-building" display is mentioned by Nero for the male Yellow-headed Blackbird (1963:395-401). We read of his "Elevating, Flapping, Dropping, Bowing, Crawling, and Pecking or Building" as being "remarkably similar to that of the Redwing." In both his studies Nero discusses the occurrence of symbolic nest-building displays by male icterids (including meadowlarks) and other species where the males take no part in building the nest nor incubating the eggs. He found, in the two species that he studied, that the males used symbolic nesting displays both in courtship and in "reassuring" mates frightened from their eggs.

Food-carrying.—Although our meadowlark never tried to feed any of the young birds that at times shared the sun porch, in two seasons he responded to their presence by carrying food about in his bill.

On 9 July 1949, on the arrival of the 10-day-old Red-winged Blackbird, LL carried mealworms about in his bill for some 10 minutes.

In 1950 he treated a young Robin just out of the nest as a sexual object and did the same when I brought the young Blue Jay near him. After this he treated the Blue Jay with hostility, pecking it when opportunity occurred.

In 1951, strangely enough, his parental instincts were activated by the arrival of two Coots *(Fulica americana)* and two Franklin's Gulls *(Larus pipixcan)* from six to eight days old. At the beginning the gulls weighed about as much as LL but they grew to be twice as heavy. The Coots, originally less than half his weight, increased to two to three times his weight during their stay. Yet as long as these four birds were present—from 1 to 23 July—LL regularly carried three or four mealworms about for 10 to 30 minutes each day, although otherwise he seemed to pay no attention to these young birds.

In 1939, my year old Song Sparrow—Y—carried mealworms around from five to 18 minutes for three days after the arrival in the study of three fledgling Song Sparrows and a 17-day-old Brown-headed Cowbird *(Molothrus ater)*. Several times he approached one of the Song Sparrows; the little birds did not beg and Y failed to deliver the food.

Songs

Meadowlarks do not inherit their songs; they learn them. Scott (1904) reported that the song of his Eastern Meadowlark, a bird that had been raised with a variety of other species, "was quite dissimilar to that of a wild meadowlark"; its most striking feature was an imitation of the European Blackbird *(Turdus merula)*. George B. Saunders wrote me: "None of my meadowlarks [Eastern or Western], raised in Oklahoma City, knew the songs of their species." One of them, raised beyond hearing of meadowlarks but near a Cardinal *(Richmondena cardinalis)* adopted the latter's song. This was over 30 years ago—before Starlings *(Sturnus vulgaris)* had reached Oklahoma City.

On 8 March 1949, while at the Trailside Museum, Riverside, Illinois, I was surprised to hear a young Eastern Meadowlark singing much like his ancestors. He had been brought to the Museum the preceding summer as a "featherless" chick; he had been kept with a group of Robins, Blue Jays, Mourning Doves *(Zenaidura macroura)*, and Starlings in quarters that were heated all winter. There were also plenty of wild Starlings just outside the Museum. One of the most common songs of the local Starlings appears to be an imitation of what A. A. Saunders (1929:152) calls "one of the commonest songs" of the Eastern Meadowlark. This is illustrated in Figure 50 (1929), as well as in Figure 130, Number 1, in his later book (1951). On 1 May 1950, I again heard the Trailside Museum bird singing. I noted: "Whistles very loudly, but with almost no variety to his song." He had adopted two notes from his Robin companions: a *peep* which appeared to express displeasure at my interest in him and also a version of the characteristic scold.

To return to LL. He had been warbling the "sub-song" and "rehearsed song," described by Lanyon (1957:21), from late August 1948 through the fall and winter in his unheated quarters on our porch.

26 February 1949: "Warbling sweetly, more loudly than before. More single notes. One morning thrillingly lovely—like a Wood Pewee! Possibly gets some stimulus from Starlings."

5 March: *"Opens his bill a little when singing!* Single, high sweet notes."

15 March: *"Sings like a meadowlark* occasionally. *Sings with bill wide open.* Also warbles with bill closed."

10 April: *"Sings like a meadowlark at times.* Many other songs, not assignable."

He sang much in May and June, was rather silent during the molt, and sang much again in late September and into October. He was silent from November through January.

In 1950, he began to warble softly in February, singing aloud on the 23rd in response to very mild weather. There was much singing from late March to early July; little in the fall. In 1951, he first sang aloud on 6 March, in 1952, on 3 March; his pattern of singing followed that of the previous years.

Our meadowlark had the advantage of being able to hear a linguistically gifted Starling with a notable repertoire that roosted for two years—1949 and 1950—just across the street from us. During the next two years LL adopted several new songs from other Starlings and at times used phrases from the song of a Cardinal.

Although I was watching for the rendition of alternate songs as mentioned by A. A. Saunders (1951:224), it was not until 2 October 1952 that I heard an example from LL. "Sings alternately, i.e., one song once or twice, then back to the first and so on. A lovely, thrush-like effect."

LL customarily sang when any of us—either friend or foe—left the sun porch; upon our return he fell silent. He also used to sing after the Blue Jay flew into the house from the porch. Apparently both birds and people on the sun porch served in some measure as social companions, though LL appeared to pay no attention to them.

I recorded his songs during three separate hours in 1951 and one hour in 1952. The total number of songs for each hour were 83, 152, 197, and 281. The highest count came on 9 May 1951, when LL sang for 54 minutes during the hour. As to rate per minute, 63 counts ranged from 5 to 8, with a median of 6. Series of songs lasted from 3 to 10 minutes. In 52 counts the number of songs in a series ranged from 8 to 68 songs, the median being 19.

Unfortunately, I have few comparable data on Eastern Meadowlarks singing in the wild. On 29 March 1952, a bird in the McGinness Slough Forest Preserve of Cook County, Illinois, sang 7, 18, 8, and 10 songs per series. On 3 May 1964, a bird near Kalamazoo, Michigan, sang the same very short song 26 times, uttering 11 songs in one minute. Reynard (1963:142) timed 40 *Sturnella magna* while in "relatively continuous song"; the average speed of delivery was 8 songs per minute.

A. A. Saunders (1951:224) writes in regard to the Eastern Meadowlark: "In the height of the singing season, in the latter part of April, I have recorded fifty-three different songs from a bird in less than an hour, and I believe every normal male bird is capable of singing at least one hundred different songs." Mr. Saunders is a specialist in the study of bird song; gifted with "absolute pitch," he can record accurately time, pitch, intensity, quality, and phonetics—all feats that are beyond me. With his superior abilities of discrimination he apparently classifies as different songs utterances that I would call variants of one song.

In the four hours that I recorded, LL gave 5, 8, 8, and 10 clearly different songs. Five of these were very distinctive. Half a dozen were good Eastern Meadowlark songs. Of one my husband remarked: "That takes me back to my boyhood in Ohio when I used to harness up the horse to go plowing." Several songs appeared to be exact imitations of our nearby Starlings. Unlike Lanyon's hand-raised meadowlarks that learned their songs only late in their first summers and in early fall, our bird remained in a somewhat plastic stage and we believe he added new songs to his repertoire as late as 1951 and even 1952. On 18 May 1951, I noted: "It is impossible for me to distinguish many of his songs. Perhaps he has 40 or more, depending on how one classifies them."

LL was a distinguished songster with a wide and varied repertoire. Lanyon (1957:19) writes: "Extreme variation of primary song [i.e., "the loud, specific song," page 15] within the individual, as well as extreme variation within a given population, is characteristic of *magna*. . . . There is no evidence to suggest such extreme variability in the primary song of an individual *neglecta*." He found that nine individual males of *neglecta* averaged seven songs in their repertoires; one had eight and another nine during two years. He gives sonagrams of the complete song quota of one male as heard during two years.

Dr. Lanyon hand-raised at least four *neglecta* males that adopted songs of the Red-winged Blackbirds living next to the Lanyons' trailer. "The critical period of song learning appeared to fall between the start of sub-song, at about four weeks of age, and the first winter" (1957:50). He wrote me on 21 January 1953 that his first hand-raised Western Meadowlark, Reds (not mentioned in his book), was singing regularly by the fifth month of age perfect imitations of the Red-wing, Wood Pewee *(Contopus virens)*, Baltimore Oriole *(Icterus galbula)*, Yellowthroat *(Geothlypis trichas)*, and Catbird

(Dumetella carolinensis), all common species nesting near their trailer. No meadowlarks or Starlings were heard in the vicinity, although Yellow-throated and Warbling Vireos *(Vireo flavifrons, V. gilva)* were "obvious and loud singers but he didn't appear to have been impressed with them." All of Reds' songs *appeared several months after he had heard them during the summer.*

On 16 May 1953, my husband and I visited the Lanyons. During our mid-day dinner Reds continually sang the Red-wing's *conqueree* and nothing else! Later he was used in the field as decoy in the capture of both species of meadowlarks but, like the others with similar experience, he never developed the songs of either madowlark species (1957:51). Dr. Lanyon wrote me that Reds "continued to sing primarily Red-wing songs with lesser emphasis upon the songs of the Wood Pewee, Yellowthroat and Baltimore Oriole."

Summary

A male Eastern Meadowlark, hand-raised from the age of about 10 days, became completely imprinted on human beings.

He exhibited Play-hunting (probing), Play-fleeing, and Play-fighting.

In spring and summer he treated most people with bill-tilting, the threat to territorial rivals.

His courtship behavior was directed primarily towards me. This was accompanied by marked aggression, partly due, we suggest, to frustration from the absence of the correct response from his chosen mate. He remembered me after absences as long as six weeks.

He exhibited two symbolic nesting displays: "Nest-invitation," directed to me; and "Nest-molding." These do not appear to have been reported for male meadowlarks in the wild. The occurrence of Nest-molding in other species is discussed.

In two seasons he responded to the presence of young birds of other species by carrying mealworms in his bill, but never attempted to deliver them.

Meadowlarks do not inherit their songs. They learn them between the age of about four weeks and their first winter, according to experiments by Dr. Wesley E. Lanyon.

Our meadowlark was a talented and diversified songster, his songs largely learned from Starlings but many of them changed and amplified. He continued to add new songs to his repertoire, even in his fifth summer.

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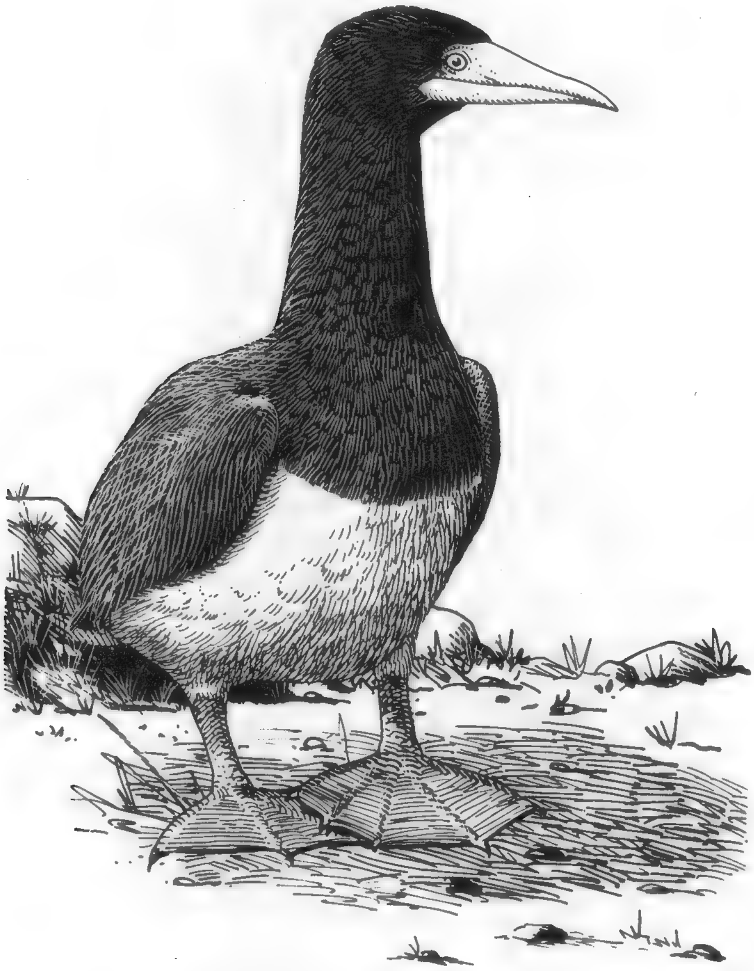

Brown Booby

THE LIVING BIRD

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A separate department within the administrative complex of Cornell University, the Laboratory is primarily concerned with scientific and educational activities. For several years its research was conducted mainly in the fields of bird behavior and biological acoustics. Recently the Laboratory has broadened its research to include: (1) The acquisition, through field and laboratory observations and experiments, of any new information on life histories of bird species. (2) The acquisition, through the cooperation of many hundreds of observers in the United States and Canada, of statistical data on the nesting of all North American species, and the analysis of such data to determine population trends, rates of survival, and other phenomena. (3) Research on the ecology and distribution of birds with emphasis on the controlling factors of the physical and biotic environment. (4) The study of local and worldwide migratory movements of birds at all seasons of the year.

An important part of the Laboratory's educational work is the production of motion-picture films and phonograph records of birds with matching color slides for use in schools and adult organizations.

The Laboratory is essentially self-supporting, obtaining part of its funds for research and educational activities through the sale of phonograph records and record-albums, matching color slides to accompany the records, and books and other printed materials.

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