# ORNITHOLOGICAL LITERATURE

MEASUREMENT OF BIRD POPULATIONS. By S. Charles Kendeigh. *Ecological Monographs*, 14, January, 1944:67–106.

Using nearly a dozen studies (largely his own) as illustrations, Kendeigh here evaluates a number of techniques in bird-census work and presents a well-organized summary of others that have been developed. Many of the illustrative facts are new, others are brought up to date, still others are analyzed for the first time. They make the paper one that no serious worker in bird ecology will want to miss.

The richness of this report lies in the diversity of the author's experience and the long-term character (measured by present standards) of the census work in which he has participated. Summaries of the University of Illinois censuses of the Trelease Woods involve 11 nesting seasons between 1927 and 1943, and 14 winter seasons between 1924 and 1943; the excellent nest census on the 15-acre Baldwin estate in Ohio spans 15 years (1925 to 1939); the intensive investigation of a House Wren population on the same area covers 24 years (1916 to 1939).

Although Kendeigh feels that work on the House Wren should probably cover a century to furnish sufficient evidence for cyclic trends, his study of this species nevertheless represents one of the most impressive field investigations of birds ever completed in this country. Age, sex, and non-breeding classes are given for 24 years—the longest and most detailed bird census yet to be reported. Part of this material has previously been published (Kendeigh and Baldwin, 1937), but the analysis by age classes is new and of unusual interest. In the House Wren, 70 per cent of the breeding-season population is shown to consist of first-year birds; this class occupies a very important role in the annual fluctuations of the total population. Slightly unbalanced sex ratios (occasionally up to 62:38) do not seem to have affected the population in any consistent manner. An average of 9 per cent of the singing males did not nest in either half of the breeding season. The population curve shows marked low points about 1917, in 1926, and in 1940, with a possible three- to four-year cycle superimposed on these major fluctuations.

The paper contains three especially interesting analyses of bird-census work taken from the literature. In perhaps the most important of these, Kendeigh selects eight examples of breeding-bird communities in "mature relatively undisturbed climax deciduous forest." By eliminating the forest-edge birds (4 to 38 per cent of the populations reported) from these censuses, he obtains an average of about 220 pairs of forest-interior species per 100 acres. This is a new approach that further experience and knowledge may or may not justify. In one atypical example ("No. 3"), Kendeigh subtracts five acres from a 40-acre census tract to correct for edge birds present in the successional vegetation; but the forest birds breeding on these same five acres are averaged in with others breeding on the remaining 35 acres, and a small error in the calculated densities has resulted. Despite this lapse, Kendeigh's method of analysis represents the most practical method so far devised to summarize scattered information on the numerical composition of the bird community in a major biome.

In another analysis, three years of trip records of the Cleveland Bird Club are reviewed at length and evaluated as an index of relative abundance. Indices and numbers observed per hour are found to be more accurate in the winter than in the summer, and to be inconsistent for open-country species. "For ultimate reliable determination of the relative abundance of birds, analysis must be so complete as to put the results on essentially the basis of a true census. For the vast number of trip records compiled by bird students in the past, it is very doubtful if the necessary information is available in sufficient detail to make such analysis possible."

Under "Measurement of Absolute Abundance," Kendeigh includes a third analysis in which he gives additional data on the trend of yearly fluctuations in Bob-white numbers in Ohio from 1908 to 1942. "During these 35 years the total population has varied from less than 1,000,000 to over 4,000,000 birds." As a measure of absolute abundance, the Christmas Bird Counts, on which this statement is based, have most of the inherent weaknesses chargeable to ordinary trip records. Additional imperfections involved in the older lists are obscured by the lack in the present paper of any tabulation of the actual data and by an inadequate table in Kendeigh's earlier account (1933) of the same subject. In 1908, for instance, there were 15 parties reporting. According to *Bird-Lore,* three of these spent only one hour in the field, another only 90 minutes, three others less than three hours each. Only four parties in that year found any Bob-white at all, and the 200 they reported is converted into "a corrected total population" of over 1,000,000 birds. In trying to follow the process of this particular conversion, one further discovers that the distances traveled by 11 of these 15 parties have been estimated in some unstated manner by the analyst. This breakdown of the data is certainly not typical of the more recent Christmas Bird Counts, nor does it invalidate the major trends reported here. The real merit of this part of the study is its value as an index of *relative* abundance. Pronounced lows are indicated for 1915, 1928 or 1929, and 1940, with peaks in 1911 or 1912, 1923 or 1924, and 1935. At least during the period 1908 to 1942, a cycle of about 12 or 13 years is strongly suggested.

In a number of lesser studies, Kendeigh brings out many useful facts about bird-census work. Only a few of these can be noticed here. An interesting table summarizes a preliminary measurement of the conspicuousness of birds in the field; another tabulation shows that Palmgren's coefficient of efficiency in the field cannot be arbitrarily used by other investigators. Contrary to Lack, Kendeigh rightly stresses the inadequacy of nest counts as the sole basis of census work, especially in forest communities. In contrast to the 15-acre study plots required in *Audubon Magazine* breeding-bird censuses, he recommends that tracts of 50 acres be used in the study of woodlands and that 75 acres be used in grasslands. My own impression is that greater annual fluctuations in bird populations are being reported from small-sized areas than from tracts of 40 to 65 acres; and I heartily second Kendeigh's recommendation.

In this stimulating summary of the literature, some very remarkable gaps in bird-census work are particularly evident. The scarcity of reliable counts of migrants on a census plot is pointed out, although A. B. Williams' success in this connection seems to have been overlooked. Despite the uneven character of the field work, the University of Illinois winter census stands out as the best such investigation of this kind now in print.—J. J. Hickey.

ECOLOGICAL ASPECTS OF SPECIES-FORMATION IN PASSERINE BIRDS. By David Lack. *Ibis,* 86, July, 1944:260–286.

It has become evident in recent years that new species of birds (and perhaps of most animals) evolve in geographical isolation from the mother species. Most workers have emphasized the point that an overlap of the ranges of two forms originating from the same species can come about only if isolating mechanisms have developed during the period of separation which guarantee reproductive isolation when geographical separation ends. Lack, in the present paper, makes the very important point that reproductive isolation alone is not enough, that at least in most cases the ranges of two closely related species overlap only if the species have developed certain ecological differences—dissimilar habitat or food preferences, for example—that prevent competition with each other.

At first glance many apparent exceptions to this thesis come to one's mind, for example, among eastern North American birds: Downy and Hairy Woodpeckers, Yellow-billed and Black-billed Cuckoos, Gray-cheeked and Olive-backed Thrushes, Prairie and Pine Warblers, Cooper's and Sharp-shinned Hawks, Sharp-tailed and Seaside Sparrows, Red-eyed and Yellow-throated Vireos, Baltimore and Orchard Orioles, and many others, but investigation shows that there are considerable ecological differences between the two members of each of the listed pairs. I do not know of any pairs of closely related eastern North American birds that are even similar in their habitat and food preferences. (The closest competition, in fact, seems to exist often between species which are not at all related, e.g. between Starling and Quail, for food on winter fields, or between Catbird and Robin, for berries.) Lack shows this difference in ecological requirements of closely related species of European and tropical birds. In many cases there is considerable overlap in the requirements, but it is never complete. Cases which I should like to see more closely analyzed are certain species of ducks and herons, hummingbirds and other flower-visiting birds (in particular the New Guinea honey-eaters of the *Meliphaga analoga* group), fruit doves (e.g. the genera *Ptilinopus* and *Ducula*), and white-eyes (e.g. *Zosterops minor* and *novaeguineae*). I should not be surprised if at least in some of these cases the ecological difference were very minute.

As logical as Lack's thesis is, his evidence is of necessity mostly circumstantial. It consists of such facts as different bill sizes, from which feeding differences can be inferred, or the significant observations of Colquhoun that the feeding zones (distance from ground) among closely related species of warblers and titmice are quite different. Equivalent observations in this country are still to be made. It would seem worthwhile to add direct evidence by appropriate analyses of stomach content.

An exception might be taken to some of Lack's illustrations of competition. For example, if the Curlew (*Numenius arquata*) and the more northerly Whimbrel (*N. phaeopus*) replace each other geographically in Great Britain, and if the Whimbrel is contracting its range while the Curlew is expanding northward, this does not necessarily prove that the Whimbrel is succumbing to the competition of the Curlew. Both range changes are perhaps correlated with a third factor, for example, a change in climate, and not directly with each other. It should not be overlooked that the borderline between two neighboring ecological districts is sometimes quite abrupt. I would not attribute it to competition if two closely related species meet along such a line.

The significance of Lack's study lies not only in its contribution to the field of evolution, but also in its bearing on the badly neglected subject of comparative ecology.—ERNST MAYR.

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