# ON THE BREEDING DISTRIBUTION PATTERN OF NORTH AMERICAN MIGRANT BIRDS

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The first review of the Palearctic migration system as a whole "in its essential aspect as a seasonal ecological adjustment on a gigantic scale" was provided by Moreau (1952). The Nearctic, too, has a migration system and certain aspects of this system can be studied much more thoroughly than is possible at present for the Palearctic, for there is more accurate census data from undisturbed North American areas. It is the purpose of this paper to present information about the pattern of breeding distribution of Nearctic birds which migrate into the Neotropical region.

For present purposes, a Nearctic species will be called a "migrant" if most of the area of its winter range as outlined in the A.O.U. Check-list (1957) lies within the Neotropical Region as outlined by Darlington (1957). (Roughly, as here defined, the Neotropical Region covers all the American continent south of the United States, including the West Indies, but excepting the Mexican highlands; the Nearctic Region is the area north of the Mexican border, plus the Mexican highlands.) The species treated should properly be called "Neotropical migrants," but for brevity the term "migrant" will be used with this meaning throughout this paper.

Although this definition of migrant neglects the many species which move shorter distances within the Nearctic, it is relatively objective, and provides a basis for drawing some general conclusions. Water birds present a rather separate problem from other birds and so are excluded. Game birds and birds of prey constitute such a small proportion of the total number of species or individuals that the question of whether to include them will have little bearing; for consistency they have been included.

It is rewarding to consider an individual about to start its northward migration. Since its destination is presumably a result of natural selection (at least in part), it may be postulated that the individual will tend to breed in the area which permits it the greatest output of reproducing progeny. Figure 1 shows, in black, the proportion of migrant individuals in the breeding populations of various relatively undisturbed vegetation communities in North America. The underlying data are in more detail in Table 1. The extent of the forest biomes (Pitelka, 1941) is shaded in the figure. The proportion of migrant individuals is taken from breeding bird censuses from the areas listed on Table 1. The census species regarded as neotropical migrants are listed in the Appendix. Censuses from obviously

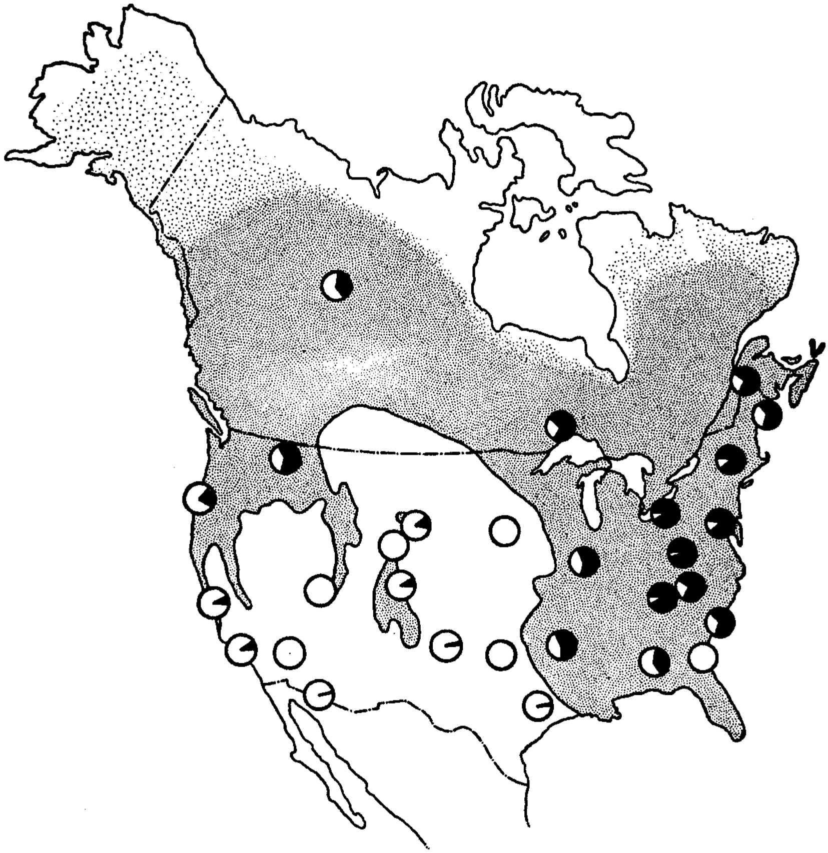

FIGURE 1.—PROPORTION OF NEOTROPICAL MIGRANT INDIVIDUALS. The black sectors of the circles represent the proportion of breeding bird individuals in undisturbed vegetation communities at that locality which will migrate out of the Nearctic region in the winter. The stippled zone is roughly the forested region. The species regarded as neotropical migrants are listed in the Appendix.

man-modified habitats have been omitted, the censuses used being of essentially "virgin" (or at least climax) areas. These undisturbed areas have changed sufficiently slowly and have been present sufficiently long to have their own characteristic bird fauna; this is in contrast to cultivated areas whose fauna has usually come from other habitats such as prairies, shores, and tundra. Thus the censuses from undisturbed areas are more likely to represent the conditions for which the pattern of migration gradually evolved.

## EFFECT OF CLIMATE

The first thing to note is that nearby censuses usually show similar proportions of migrants, except when the habitat changes rapidly; so the distribution is not chaotic. It is also important to notice that there is no simple correlation between climate and the proportion of migrants. Thus, the prairies with severe winters and warm summers have a lower proportion of neotropical migrants than the west coast forests with mild winters and cool summers. The east coast region is intermediate in climate but has a much higher proportion of such migrants than either. Furthermore, at the edge of the prairie the gross aspects of climate such as temperature and rainfall do not show sudden changes, yet the proportion of migrants does. (The proportion of migrants in the avifauna was also compared with the more complicated climate-vegetation classification of Holdridge (1946) with no more success.)

## Correlation with Differences in Vegetation

Roughly speaking, the proportion of neotropical migrants is highest in the deciduous forest of the northeast. At the periphery of this region where the amount of conifers increases, the amount of evergreen oak etc. increases, or the amount of grass and general aridity increases, the proportion of neotropical migrants falls off. In the northern coniferous forests, where most needles are shed when between two and three years old, the proportion of such migrants drops. It is still lower in the west coast coniferous forests which, with their mild wet winter, are much less seasonal in aspect than the boreal coniferous forest. The dry open coniferous forest of the Colorado Rockies and Black Hills has a still lower proportion of migrants, and chaparral, desert, and prairie habitats have virtually none.

On the available evidence, the most reasonable explanation of the pattern shown in Figure 1 is that where change between winter and summer in the supply of food suitable for migrants is greatest, the proportion of migrants is greatest. Since direct measurements of food supply are not available, the following rough indication must suffice. Although some of the suggested explanation seem slightly *ad hoc* or at least tenuous, there is little doubt about their validity for the major effects. There is little doubt that the northeastern forests which are 100% deciduous have great summer outbreaks of defoliating insects, and, on the other hand, that there is much less seasonal change in supply of insects in the western habitats which have virtually no migrants.

A more detailed analysis is as follows. The food increase which governs the proportion of migrants must be moderately predictable. Thus, a summer increase in food depending upon a desert bloom which may take place at various seasons or not at all for several years is of little use to a migratory bird population. The summer food must also last a sufficient length of time to supply the migrant population during its stay in the breeding area. The grasshopper population of the prairies may fail in this respect. Prairie and desert may also provide a large seed crop which the more omnivorous resident species can utilize in the winter. This makes possible a high population of residents, which in turn permits them to use much of what summer insect increase does occur. For these reasons, desert and prairie areas would be expected to provide little summer increase or else little winter decrease in food for migratory bird species. By contrast, the most obvious seasonal change in wooded areas of severe cold or drought is the loss and renewal of leaves. A host of species of defoliating insects and their parasites are an obvious source of food for insectivorous birds, and they do in fact provide the major portion of the food of migrants (Mitchell, 1952; McAtee, 1932). With this in mind it is not difficult to provide tentative explanations of the varying percentages of migrants in the remaining regions of Figure 1. Coniferous trees retain their needles for two or three years and may thus be considered about 40% deciduous, compared with 100% in the angiosperm forests of the northeast. Therefore, the high proportion of migrants in the northeast and the lower proportion in all coniferous forests are to be expected.

Within the coniferous forest, there is a variation in the proportion of migrant individuals, northern spruce-fir forest having more migrants than the pine and redwood forests farther south. A tentative explanation is as follows. Spruce and pine have about equal densities of insects per unit volume of compressed foliage (Kuusisto, 1941), but the ratio of foliage to wood in spruce is 1.5-2 times that for pine (Baker, 1950, page 284). Thus the insect-eating bird might be expected to comprise only half to two-thirds as large a percentage in pine as in spruce. (This explanation is only partly correct; the relative importance of spruce and pine cones and of the under story surely complicate the exact answer.) A difference in shade tolerance is the most likely explanation of the greater foliage/wood ratio in spruce than in pine. Trees, such as various spruce species, that are quite shade tolerant can maintain a thicker layer of foliage before the inside leaves suffer from the lack of light. If this is correct, it may, along with simple food preferences, explain the low numbers of migrants in oak-gum communities of the south and oak forests of the midwest. Oaks are quite intolerant of shade (Baker, 1950) and probably have a small foliage/wood ratio. It is also true that the season when the

TABLE 1

BREEDING BIRD CENSUS DATA OF HABITATS REPRESENTING UNDISTURBED CONDITIONS

| *Habitat* | *Location* | *Reference* | *% migrant† individuals* | *% migrant† species* | *Ratio migr. ind. to migr. sp.* |
|---|---|---|---|---|---|
| Desert | | | | | |
| | California | Hutchinson, 1942 | 0 | 0 | |
| | Utah | Fautin, 1946 | 0 | 0 | |
| | Arizona | Hensley, 1954 | 3 (–14)* | 7 (–13) | .43 |
| Prairie | | | | | |
| | Oklahoma | Howell, 1941 | 0 | 0 | |
| | Wyoming | Mickey, 1939 | 0 | 0 | |
| | Iowa | Kendeigh, 1941 | 0 | 0 | |
| | Texas | Allan & Sime, 1939 | 8 | 12.5 | .67 |
| Chaparral | | | | | |
| | California | Cogswell, 1948 | 0.5 | 6 | .083 |
| Oak Savanna | | | | | |
| | Texas | Dixon, 1957 | 5 | 10 | .5 |
| Dry Pine | | | | | |
| | Colorado | Thatcher, 1956<br>Hering, 1956<br>Snyder, 1950 | 5,10,19,20 | 20.5,20,7,30 | (.7)** |
| | S. Dakota | Whitney, 1956 | 13 | 30 | .43 |
| | Georgia | Fleetwood, 1948 | 0 | 0 | |
| Redwood | | | | | |
| | California | Pugh & Pugh, 1957 | 16 | 11 | 1.43 |
| Sitka Spruce | | | | | |
| | Oregon | Fables & Fables, 1957 | 27.5 | 17 | 1.62 |
| Northern Coniferous | | | | | |
| | N.W.T. | Stewart, 1955 | 37 | 25 | 1.48 |
| | Ontario | Kendeigh, 1947 | 74 | 40 | 1.85 |
| | Idaho | Longley, 1944 | 63 | 50 | 1.26 |
| | Maine | Stewart & Aldrich, 1952 | 72 | 48 | 1.50 |
| | Maine | Cadbury & Cruickshank, 1941 | 62 | 33 | 1.88 |
| Oak-Gum | | | | | |
| | Alabama | Imhof, 1948 | 43 | 53 | .81 |
| | Illinois | Snyder et al, 1948 | 62 | 59 | 1.05 |
| Hammock | | | | | |
| | S. Carolina | Mellinger, 1948 | 63 | 65 | .97 |
| Oak-Pine | | | | | |
| | Arkansas | Hoiberg, 1957 | 59 | 47 | 1.23 |
| Hemlock | | | | | |
| | N. Carolina | Odum, 1947 | 75 | 59 | 1.27 |
| Northeastern Deciduous | | | | | |
| | New York | Kendeigh, 1946 | 82 | 61 | 1.34 |
| | Ohio | Williams, 1947 | 87 | 50 | 1.74 |
| | Maryland | Stewart & Robbins, 1947 | 82 | 60 | 1.37 |
| | Tennessee | Aldrich & Goodrum, 1946 | 84 | 67 | 1.25 |
| | W. Virginia | DeGarmo, 1948 | 89 | 71 | 1.25 |

† See Appendix for species regarded as "migrants," i.e., neotropical migrants.

* The figures in parentheses hold if Wied's (Arizona) Crested Flycatcher (*Myiarchus tyrannulus*) is considered a migrant.

** Refers to a mean of the ratios of the four habitats.

leaves are on the trees is much longer in the south, at least, which may make less probable a seasonal insect bloom of the type utilized by migrants. Thus, the information supports the suggestion that migrating birds tend to breed in the areas with the greatest available food supply during the nesting season.

## Correlation with Latitude

There is another interesting feature summarized in the table of censuses. For the more northern undisturbed vegetation types censused, the proportion of individuals which migrate to the neotropics is greater than the proportion of species which do not so migrate, as evidenced by ratios greater than one of migrant individuals to migrant species (see Table 1). That is, migrants constitute a greater proportion of the total individuals than of the total species. This means that, in the northern areas censused, the average abundance of the neotropical migrant species is greater than that of the residents and species which move short distances, which are in the table called "non-migrant." (This is not to say that no migrant is rare or no non-migrant abundant; it refers only to averages.) In southern areas, on the other hand, the tendency is reversed, as evidenced by ratios less than one, meaning that, on the average, "non-migrant" species are commoner. The trend with latitude seems quite consistent and appears to be nearly independent of the nature of the particular undisturbed habitats censused. No one explanation of this pattern is obviously correct; a proper weighing of the possibilities will probably have to wait until a better understanding has been achieved of the factors controlling relative abundance of species.

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## Summary

1. Over a variety of undisturbed habitats throughout the continent, the density of breeding individuals of species migrating to the Neotropics seems to correlate with the contrast between winter and summer food supply in the given habitat.

2. In the undisturbed northern habitats considered, the average migrant to the Neotropics is commoner than the average species which fails to make this journey. The reverse is true in the southern habitats.

## APPENDIX

### Nearctic Land Birds, Occurring in the Censuses, Here Considered Neotropical Migrants

Accipitridae: *Buteo platypterus.* Pandionidae: *Pandion haliaetus.* Cuculidae: *Coccyzus americanus, C. erythropthalmus.* Caprimulgidae: *Caprimulgus carolinensis, Chordeiles minor.* Apodidae: *Chaetura pelagica.* Trochilidae: *Archilochus colubris, Selasphorus platycercus.* Tyrannidae: *Tyrannus tyrannus, Myiarchus crinitus, M. tyrannulus, M. cinerascens, Empidonax flaviventris, E. virescens, E. traillii, E. minimus, E. difficilis, Contopus virens, C. sordidulus, Nuttalornis borealis.* Turdidae: *Hylocichla mustelina, H. ustulata, H. fuscescens.* Vireonidae: *Vireo griseus noveboracensis, V. flavifrons, V. s. solitarius, V. olivaceus, V. philadelphicus, V. gilvus.* Parulidae: *Mniotilta varia, Protonotaria citrea, Helmitheros vermivorus, Vermivora peregrina, V. r. ruficapilla, Parula americana, Dendroica petechia, D. magnolia, D. tigrina, D. caerulescens, D. coronata, D. virens, D. occidentalis, D. cerulea, D. fusca, D. dominica, D. pensylvanica, D. castanea, D. striata, D. discolor, Seiurus aurocapillus, S. noveboracensis, S. motacilla, Oporornis formosus, O. philadelphia, O. tolmiei, Geothlypis trichas brachydactylus, Wilsonia citrina, W. p. pusilla, W. canadensis, Setophaga ruticilla.* Thraupidae: *Piranga ludoviciana, P. olivacea.* Fringillidae: *Pheucticus ludovicianus, Passerina cyanea, P. ciris.*

When not all North American subspecies of a listed species are neotropical migrants, the particular subspecies considered a migrant is listed; otherwise, only the species name is given. Some species included *(e.g., Dendroica coronata)* are possibly doubtful; however, their numerical abundance is sufficiently small that their inclusion makes little difference to the data. Many highly migratory species (*e.g.,* most orioles and swallows) are not included, because they did not occur in any of the censuses considered.

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