THE BREEDING DISTRIBUTION OF NORTH AMERICAN MIGRANT BIRDS: A CRITIQUE OF MacARTHUR (1959)

MARY F. WILLSON

MacArthur (1959) claimed that the eastern deciduous forest has more neotropical migrants than northern coniferous forests or grasslands, and concluded that "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." A reanalysis of data covering part of the area dealt with by MacArthur suggests that the basis for his conclusion deserves reassessment. We certainly expect to find some association of migratoriness with temporal stability of the food supply (Fretwell 1972), but the nature of the "correlation" reported by MacArthur (1959) can be reinterpreted.

For simplicity, the reanalysis deals only with the eastern two-thirds of North America, and only with 3 major habitat types: grassland, northeastern deciduous forest, and northern coniferous forest. Each of these categories clearly encompasses a variety of specific habitats, but in order to compare my results with MacArthur's, and attempt to discern large-scale contrasts, major habitat categories are useful. Summaries of the census data (excluding nocturnal species) are presented in Table 1. The locations of wintering grounds were determined mainly from the Peterson field guides (1947, 1961, 1973), and the range maps of Robbins et al. (1966). Two-tailed Mann-Whitney U tests ($p \leq .05$) were used to test for statistically significant differences between habitat types.

MacArthur (1959) depended greatly on breeding bird censuses found in *Audubon Field Notes (American Birds)*, and I have done the same in order to make possible comparisons with MacArthur's paper. These censuses are notoriously open to criticism, perhaps especially regarding estimates of population sizes, but nevertheless are adequate for criticism of MacArthur's interpretation and statement of a reassessment that suggests alternative hypotheses. All the censuses used by MacArthur (1959) for the 3 habitat categories analyzed here were included in the present study (except those in Audubon Field Notes, Vols. 1 and 2, which were not readily available) and the sample sizes were increased considerably. In choosing censuses to be included, an effort was made to use those from relatively homogeneous study plots.

The discussion is necessarily speculative. The purpose of this note is to *restate* an old hypothesis about seasonal variation of food resources in different habitats; testing of the hypothesis must come later.

TABLE 1

SUMMARY OF PROPORTION OF MIGRANTS IN BREEDING BIRD CENSUSES FOR 3 HABITAT TYPES

Location	Reference	% total migrants		% neotropical migrants	
		Spp.	Individ.	Spp.	Individ.
GRASSLAND					
Manitoba	Jones 1972	100	100	18	33
Minnesota	Hibbard 1972	88	93	38	53
N. Dakota	Johnson 1973	82	99	44	32
N. Dakota	Johnson 1972	100	100	38	31
Wisconsin	Bailey & Ellis 1968	89	90	33	16
S. Dakota	Springer 1965	100	100	56	59
Wyoming	Mickey 1939	67	88	0	0
Iowa	Kendeigh 1941	75	73	25	31
Colorado	Porter 1973	75	43	0	0
Kansas	Zimmerman 1965	55	82	22	41
Kansas	Walker 1965	50	49	0	0
Oklahoma	Howell 1941	60	60	40	50
Texas	Allen & Sime 1939	50	57	0	0
	$\bar{x}$	76	73	24	27
NORTHEASTERN DECIDUOUS FOREST					
New York	Kendeigh 1946	67	91	67	91
Connecticut	Palmer 1973	68	74	57	64
Michigan	Irish et al. 1973	59	61	38	42
Ohio	Williams 1947	59	83	53	81
Indiana	Webster & Adams 1971	47	64	45	62
Indiana	Mannon & Webster 1973	71	68	56	58
Indiana	Adams & Webster 1971a	52	63	46	59
Indiana	Adams & Webster 1971b	59	76	55	72
W. Virginia	Katholi 1973	63	85	56	79
West Virginia	DeGarmo 1948	86	98	71	91
Maryland	Criswell et al. 1973	56	51	47	50
Maryland	Stewart & Robbins 1947	57	80	50	79
	$\bar{x}$	62	75	53	69
NORTHERN CONIFEROUS FOREST					
Northwest Territory	Stewart 1955	53	85	35	58
Northwest Territory	Stewart 1955	63	84	36	44
Saskatchewan	Erskine 1973	79	97	47	76
Manitoba	Erskine 1972a	82	97	44	55
Manitoba	Erskine 1972b	90	99	60	52
New Brunswick	Tull 1973	100	100	76	79

TABLE 1. (*Continued*)

Location	Reference	% total migrants		% neotropical migrants	
		Spp.	Individ.	Spp.	Individ.
Maine	Cadbury & Cruickshank 1941	87	94	63	65
Maine	Stewart & Aldrich 1952	76	93	53	79
Quebec	Erskine 1970	100	100	64	48
Ontario	Kendeigh 1947	68	90	46	81
Ontario	Nakashima 1973	80	90	53	42
West Virginia	Bush et al. 1973	77	94	48	72
	$\bar{x}$	80	94	52	62

Deciduous forests have, on the average, the same percentage (53% of spp., 69% of individuals) of neotropical migrants as coniferous forests (52%, 62% respectively), and the percentage in grassland (24%, 27%) is significantly lower than either of the forests. In contrast, MacArthur stated that the proportion of neotropical migrants was greater in deciduous forest, less in coniferous forest, and least in grassland, but he apparently did no statistical tests on his data. MacArthur called a species a "neotropical migrant" if most of the area of its winter range, as determined from the 1957 A.O.U. checklist, fell within the tropical zone. The major reason for the difference between MacArthur's results and mine is that I included any species that commonly winters in the tropics, whether or not most of its winter range was tropical, for lack of any obvious biological reason to exclude them. Had I used MacArthur's criteria, the results resemble his more closely, but with no difference of statistical significance between forest types. The relative paucity of neotropical migrants from North American grasslands is perhaps not surprising in view of the rather small area occupied by neotropical grasslands. Coniferous forest breeders obviously change vegetation types on the wintering grounds, but this may be a relatively smaller behavioral change than for a grassland breeding bird to shift to a forested winter habitat.

However, there is no apparent reason why seasonal change in food supply should be reflected by the proportion of the avifauna that includes *neotropical* migrants only. *Any* species that commonly leaves its breeding habitat in the non-breeding season probably does so because of seasonal habitat changes, or conversely, seasonality in habitat characteristics is evidenced by any species moving to its breeding grounds, no matter where it comes from. Many North American breeding birds leave their breeding habitat to winter in the southern U.S. or nontropical Mexico. Considering *all* migrants (and some-

time migrants such as the Red-headed Woodpecker, *Melanerpes erythrocephalus*) in the major habitat types, the percent of species in the avifauna that are migrants is rather similar in grasslands (76%) and in coniferous forest (80%), and these percentages are marginally ($.10 > p > .05$) higher than in deciduous forest (62%). The average percent of migrant individuals is about the same in grasslands (73%) and in deciduous forests (75%), and is significantly less in those habitat types than in coniferous forest (94%). Thus, relatively more species in deciduous forest are year-round residents than in the other 2 habitats, and more individuals may be permanent in deciduous forest (and grasslands) than in coniferous forest.

Despite the conspicuous seasonal change in foliage in deciduous forests, any effect on the migratory avifauna is apparently less than in coniferous forests with relatively small seasonal changes in foliage. Seasonal "blooms" of insects in these forests may be more a function of climate (e.g., length of summer) than of foliage type. Very short summers may produce large insect blooms and provide resources for many migrants. Latitudinal differences within a habitat type in the proportion of migrants might be used to test this suggestion. The grassland data presented here suggest such a trend (increasing migratoriness with increasing latitude), but the forest data do not. A larger sample is required to explore this possibility adequately.

Resident populations exploit chiefly bark-dwelling arthropods and fruits or seeds as winter food resources (c.f. Morse 1971). It is possible that the variety of fruits and seeds available in deciduous forest throughout the winter is greater than in coniferous forest. Furthermore, the form of deciduous trees may provide a greater variety of foraging sites than does the form of coniferous trees, even in winter. Woodpeckers partition deciduous tree bark surfaces in part by branch size (Willson 1970 and others). They are relatively rare residents of most kinds of coniferous forest (in the censuses used here, about 1% of the avifauna, compared with almost 10% for deciduous forests), and account for part of the difference between the forest types. Other bark gleaners such as chickadees and nuthatches also contribute to the difference. In sum, the contrast between winter and summer food supply in deciduous forests (total amount and/or accessibility) actually may be *less* than in the other habitats, which is a suggestion directly opposite to MacArthur's. In addition, deciduous forests may provide more roosting holes as shelter from the most severe weather. And winter weather may be slightly milder in the region of deciduous forest: longer times without snowcover on the ground than in coniferous forest and less wind than in grassland, for instance. As a result, demands on the food resources might be reduced.

The situation can also be viewed in terms of just the neotropical migrants to these 3 major habitats. The neotropical migrants in the census data were

categorized as much as possible by their primary nesting habitat (a few species that primarily use open shrubby habitats but occurred in the censuses were not included). Fifty-seven percent (34 spp.) of the neotropical migrants breed primarily in deciduous forest, 37% (22 spp.) nest most frequently in coniferous forest, and the remainder in grassland. More species migrating from the neotropics to the nearctic have exploited the deciduous forest than the coniferous forest or grassland. The advantages of the deciduous forest might include a somewhat shorter distance from the wintering grounds, possibly a greater similarity of leaf shape and spatial distribution to wintering habitat, a greater diversity of nesting sites, and perhaps a wider variety of small, soft fruits as alternate dietary items.

Nevertheless, a significant number of neotropical migrants are adapted to exploit primarily the coniferous forest. Over half of these are warblers (Parulidae, 15 spp.). In comparison, only about ⅓ (11 spp.) of the neotropical migrant, deciduous-forest nesters are parulids. Purely historical explanations for the predominance of parulids as coniferous forest migrants are insufficient; some ecological basis for their prevalence must be involved. Perhaps their small size and slender bills facilitate foraging among the narrow leaves and flexible branch tips of most northern conifers. Some may use deciduous enclaves within the coniferous forest, but more precise census reporting would be needed to ascertain this.

SUMMARY

A partial reanalysis of MacArthur (1959) has shown that (1) North American neotropical migrants are less prevalent in grasslands than in forests (as MacArthur also showed) but that there is no significant difference in the proportion of neotropical migrants in deciduous and coniferous forest (unlike MacArthur's results); (2) coniferous forests have relatively fewer year-round resident individuals than grasslands or deciduous forest, and grasslands and coniferous forests have slightly fewer resident species than deciduous forests; (3) most neotropical migrant birds breed primarily in deciduous forest and most of those that breed in coniferous forest are parulids.

The results suggest that seasonal changes in available food resources may be effectively less in deciduous forest than in coniferous forest (in contrast to MacArthur's conclusion). Possible ecological bases for the habitat differences are suggested, but remain to be demonstrated.

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UNIVERSITY OF ILLINOIS, PROVISIONAL DEPARTMENT OF ECOLOGY, ETHOLOGY AND EVOLUTION, VIVARIUM BUILDING, CHAMPAIGN, ILLINOIS 61820. ACCEPTED 16 SEPT. 1975.