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# Avian Community Structure along Elevational Gradients in the Northeastern United States

K. P. Able and B. R. Noon

Department of Biological Sciences, State University of New York, Albany, New York 12222, USA

**Summary.** Breeding birds were censused along four elevational gradients in the Adirondack Mountains, New York, and the Green Mountains, Vermont. The bird communities of the four gradients were basically similar in species composition, richness and amplitude patterns. Three measures of species diversity decreased with increasing elevation. Low-elevation communities contained higher proportions of rare species and the relative abundances conformed to the broken-stick distribution. At higher elevations the communities showed greater dominance and the dominance-diversity curves approached geometric series. The species characteristic of high-elevation communities had the broadest altitudinal distributions.

The upper and lower distributional limits of most species were independent of one another except at "ecotones" where marked changes in vegetation structure occurred. On each mountain, slightly more than half of the species' limits coincided with ecotones. This is a significantly greater proportion than has been found in similar studies of tropical forest bird communities. In further contrast to tropical communities, we found no convincing cases of attitudinal competitive exclusion between species. Interspecific competition in the past seems to have been translated primarily into differences in habitat selection by temperate forest birds.

Many of the differences between temperate forest breeding bird communities and tropical ones can be understood in terms of the migratory nature of most of the temperate species and the lower species richness in temperate forests.

## Introduction

Studies of species distribution along environmental gradients have made important contributions to our understanding of natural communities, particularly plant communities (Whittaker, 1967). This approach has recently been applied to birds in the New World tropics (Terborgh, 1971) and New Guinea (Diamond, 1972, 1973). These studies, like most others, have employed gradients of elevation because mountains often encompass a large range of environmental change over a small distance. Regardless of the type of gradient, the distribution of species with respect to each other and in relation to the habitat can be used to evaluate the roles of competition and habitat selection in structuring the communities. Paradoxically, detailed gradient studies of vegetation have been done only in temperate or arid regions, while similar studies of birds have been done primarily in the rivet tropics.

Tropical bird communities differ from temperate ones in a number of important respects. In the highly seasonal environment of the temperate zone, most species are migratory, occupying their breeding ground for only a fraction of the year. An important consequence of this seasonality is that species are subjected to a variety of selection pressures in breeding and wintering areas as well as during the intervening migrations (Fretwell, 1972). Tropical species, by contrast, tend to be highly sedentary and characterized by low dispersal ability. Both alpha and beta diversity (Whittaker, 1960) are considerably greater in tropical forest bird communities and greater species packing is thought to be accompanied by increased interspecific competition. Both environments present formidable barriers to understanding community organization. The migratory nature of temperate birds confounds our attempt to associate selection pressures in one locality with observed species and community characteristics. On the other hand, the overwhelming number of species in tropical areas snakes accurate censuring more difficult and scanty knowledge of species life histories hampers interpretation of data.

With these limitations in mind, we present an analysis of the breeding bird communities on elevational gradients on four mountains in the northeastern United States. This is the first detailed study of bird community structure on temperate elevational gradients. As such, it provides a basis for comparing forest bird communities on similar gradients in temperate and tropical areas. Finally, it permits comparison with gradient analyses of vegetation on some of the mountains.

## Methods

### *The Gradients*

We censured birds on four mountains: Whiteface (1550 m cl) and Nippletop Mountain (1480 m) in the Adirondacks of New York and Mount Mansfield (1300 m) and Camel's Hump Mountain (1300 m) in the Green Mountains of Vermont. These gradients were selected on the basis of several criteria. They were 1) long gradients with 2) gradual, rather uniform slope, 3) vegetation that has not been recently disturbed and 4) ease of access. Siccama (1968) conducted detailed studies of the vegetation of several peaks in the Green Mountains (including Camel's Hump Mountain) and concluded that the forests of those mountains were very similar to the Adirondacks in terms of species composition and zonation. Detailed descriptions of the forests of Whiteface Mountain can be found in Scott and Holway (1967) and Holway and Scott (1969); other studies of Adirondack vegetation are Adams et al. (1920) and Bray (1930).

The vegetation on all of the mountains is basically mature second growth forest, although some areas of virgin spruce-fir remain at high elevations. All where at least partially logged for hardwoods, spruce-fir pulpwood, and yellow birch (*Betula lutea*). Most logging activity occurred during the latter hill of the nineteenth century (Siccama, 1968; Holway et al., 1969). The Adirondacks were protected from tile most destructive logging practices by legislation in 1896. In Vermont, some selective logging persisted into the mid twentieth century, at least on Camel's Hump Mountain (Siccama, 1968). Localized fires have occurred within the past fifty years, and dense stands of paper birch (*B. papyrifera*) occupy burned areas. With the exception of a few areas on Whiteface Mountain, there was little evidence of fire in our sampling areas. Based on his studies of the reproductive status and distribution of the dominant tree species, Siccama (1968) concluded that the present forests are stable in composition and probably constitute the climax vegetation of the region.

The lower elevations of the mountains are covered with mature hardwood forest dominated by sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*) with occasional patches of hemlock (*Tsuga canadensis).* The lower limits of these forests are determined by agricultural disturbance in the valleys. The upper limits of these species occur between 790-920 m; the disappearance of beech may be quite abrupt. Yellow birch occurs from quite low elevations, increasing in abundance with elevation and transcending the zone where sugar maple and beech disappear. It is a dominant tree at the upper reaches of the lowland hardwood forest. Red spruce (*Picea rubens*) occurs as scattered trees in the upper areas of the beech-maple forest. Its abundance increases with elevation as deciduous trees disappear (except for small numbers of white birch, *B. p. cordifolia*). Above about 1060 m it is gradually replaced by balsam fir (*Abies balsami*) which extends upward to timberline (there is no timberline on Nippletop Mountain). Alpine meadows occur above timberline on the other three mountains. They are extensive only on Mount Mansfield (ca. 100 ha; see Vogelmann, 1964, for a description of alpine areas in the Green Mountains).

Although the forests on these mountains seem to the casual observer to consist of at least two discrete types, Siccama (1968) and Scott and Holway (1967, 1969) showed that the vegetation is actually a complex continuum of species populations rather than a mosaic of discontinuous units (see Whittaker, 1967). While species of the lower elevation hardwood forest were entirely absent from the higher elevations, species characteristic of the upper slopes are found in small numbers on the lower slopes. In the so-called transition zone or ecotone between these two forest types species from both areas occur, but no important tree species is limited to mid-slope forests. Despite the essential continuity that characterizes these forest communities, for our purposes three major changes in vegetation physiognomy were distinguished:

1) The area on the gradient in which beech and sugar maple disappeared. Concomitantly, yellow birch and red spruce increased markedly.

2) The virtual disappearance of deciduous trees along with an increase in the proportion of balsam fir.

3) Tree line.

For convenience, we shall refer to these transition zones as ecotones or habitat discontinuities. In practice, Ecotones 1) and 2) could be localized within zones of about 100 m of elevation or less, and tree line was considerably more abrupt.

Elevation, per se. is not likely to be important in determining the distribution of plants or animals. However, a host of potentially important factors vary with elevation. During the breeding season, air temperature decreases monotonically with increasing elevation (Adams et al., 1920; Siccama, 1968) and precipitation increases up to ca. 1100 m, above which it decreases slightly. Relative humidity increases with elevation in spite of the slightly reduced rainfall at higher elevations. Siccama (1968) noted that the only major climatic variable that changed abruptly with elevation was the length of the growing season (i.e., number of frost-free days), which showed a marked reduction at elevations corresponding with the upper limits of the beech-maple forest.

The gradients we sampled were on the north facing slopes on Nippletop, Whiteface and Camel's Hump Mountains and on the east facing slope on Mount Mansfield. Siccama (1968) and Holway et al. (1969) found that forest composition did not vary significantly with changes in slope direction, although the absolute elevations at which changes in forest type occurred varied somewhat.

### *Sampling Methods*

On each of the mountains except Camel's Hump, sampling stations were established at intervals of about 100 m along the elevational gradient. Stations closer together were sometimes used, especially in the area of ecotones. Because Camel's Hump was accessible only by foot trail, censusing was conducted in a slightly different manner. All sampling was done along the trail, which was divided into a series of segments covering approximately equal changes in elevation. Censuses were conducted on the following dates: Nippletop Mountain, l2 and 13 July, 1973: Mount Mansfield, 7-10 July, 1974; Whiteface Mountain, 11 and 12 July, 1974; and Camel's Flump Mountain, 10 days during June and July, 1974

Birds weir censused during the 3-4 h of peak activity immediately after down. At each station the two observers (K.P.A. and B.R.N.) walked in different directions, counting all birds seen or heard while moving steadily through the two areas for a prescribed length of time (usually 0.5-0.75 h). In general, this gave us 1-1.5 observer-hours per station per day. Efforts were made to avoid duplication between observers in counting individual birds. We consistently employed "squeaking" and "hissing" sounds to attract and excite nearby birds. On successive days, we altered the order in which stations were sampled so as to reduce the bias introduced by time of day. The counts of birds were normalized to numbers of individuals of each species per hour of sampling time at each station. These estimates formed the data base on which the analyses were conducted.

The data are clearly biased in favor of conspicuous, vocal species. However, our methods give reasonable results for territorial species that perform frequent vocalizations. This applies to virtually all of the breeding birds in these forests except raptors and grouse, and these species (perhaps 6-8) were excluded from consideration. We are confident on the following bases that our short-term censuses provided an accurate picture of the bird communities: 1) The great similarity between gradients in species composition, attitudinal distribution, and relative abundance. 2) The first census at each station yielded 77-95% of the total species recorded at that station; no more than two new species were recorded on the last census at a station; in every case this amounted to less than 10% of the species total at the station. 3) Camel's Hump Mountain was censused over a longer period of time (55 observer-hours) than the other gradients, but its patterns were very similar. 4) Noon spent the entire breeding season, 1975, studying thrushes on Mount Mansfield. He recorded only one species not found in 1974, the Olive-sided Flycatcher (*Nutallornis borealis*), a marginal species in mature, undisturbed forest. Patterns of distribution and abundance were essentially the same as in 1974. Because we were primarily interested in making comparisons between stations and mountains, we believe the data are sufficiently accurate and unbiased for our purposes. Certainly, our familiarity with the species likely to be present made it possible for us to obtain far more accurate data than in similar studies in tropical areas (e.g., Terborgh, 1971; Diamond, 1972) where vast numbers of virtually unknown species must be dealt with.

## Results

### Species Composition

The number and kinds of species were very similar on the four mountains censured. The total number of species on each gradient was as follows: Whiteface Mountain, 44; Camel's Hump Mountain, 42; Mount Mansfield, 41; Nippletop Mountain, 38. Differences in the faunas of the four mountains consisted primarily of rare species (e.g., *Picoides tridactylus, Hesperiphona vespertina, Spinus pinus*) or species for which mature forest constitutes a marginal breeding habitat (e.g., *Sayornis phoebe, Oporornis philadelphia, Geothlypis trichas*). However, the Boreal Chickadee (*Parus hudsonicus*) was fairly common at higher elevations on the two Adirondack Mountains, but was absent from the two gradients in the Green Mountains.

We examined the diversity patterns on these gradients using Hill's diversity numbers (Hill, 1973; Peet, 1974):

$$N_0 = \text{number of species;}$$
$$N_1 = \text{Exp}(H');$$
$$N_2 = \frac{1}{\sum p_i^2}\,.$$

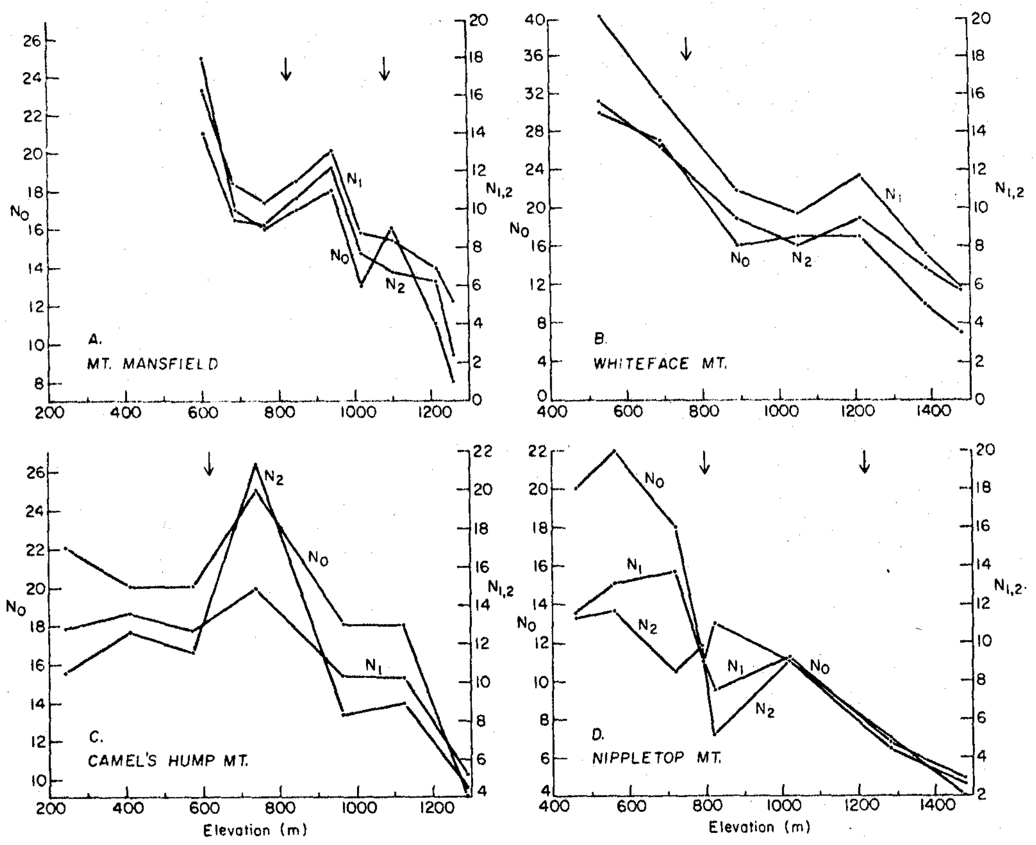

**Fig. 1 A-D.** Plots of species richness and diversity with elevation on the four gradients. $N_0$ = number of species; $N_1$ = Exp ($H'$); $N_2 = 1/\sum p_i^2$

We used an unbiased estimate of $H'$ as defined by Hutcheson (1970). $N_1$, like the Shannon-Weaver function from which it is derived, is most sensitive to changes in the importance of rare species, whereas $N_2$, the inverse of Simpson's (1949) diversity measure, is more strongly affected by the commonest species in the sample (Peet, 1974). Plots of diversity along the four elevational gradients, as measured by these three quantities, are presented in Figure l.

In general, the three measures of diversity are highly correlated in these samples. Diversity generally decreased with increasing elevation, almost monotonically on Mount Mansfield and Whiteface Mountain (Fig. 1A and B). Species richness ($N_0$) declines from a maximum of between 22-30 at a single station (usually the lowest station) to 4-9 near the tops of the mountains. The sudden increase in species richness ($N_0$) and heterogeneity ($N_1$) near the middle of the Camel's Hump gradient (Fig. 1C) is due to the existence of small, isolated patches of beech and maple forest in lower pockets or small ravines above the major ecotone between deciduous and coniferous forest (around 620 m). These patches of habitat harbored populations of species characteristic of forests below the

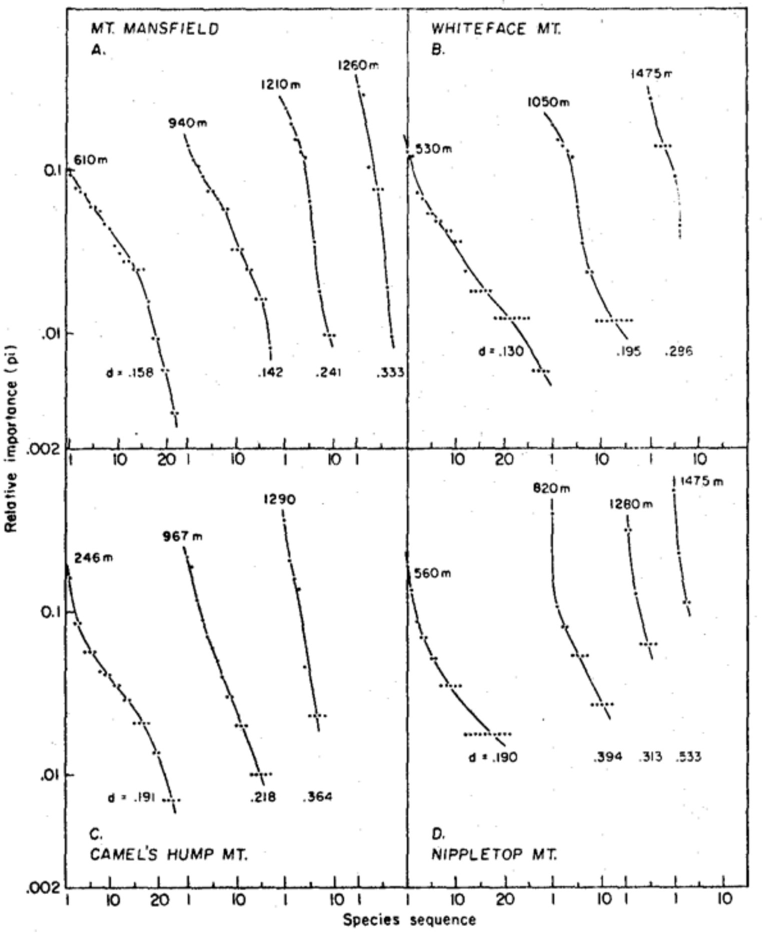

**Fig. 2A-D.** Dominance-diversity curves for selected elevations on the four gradients. Each species is represented by its proportional abundance in the sample ($p_i$) on the ordinate, and its rank in the sequence of species from the most to the least abundant on the abcissa. Indices of dominance, $d = n_{i_{\max}}/N$, are given for each curve

ecotone (e.g., *Vireo olivaceus, Mniotilta varia, Setophaga ruticilla*) that are virtually never found in pure coniferous forest. The confused situation just above 800 m on Nippletop Mountain (Fig. 1D) may be the result of sampling errors. We conclude that species richness and species diversity tend to decrease with elevation along these temperate forest gradients.

Further insight into the make-up of the bird communities can be obtained by examining the dominance-diversity curves shown in Figure 2. The pattern of these curves and their changes with elevation were similar on the four mountains. The curves for lower elevation stations had smaller slopes due to reduced dominance and greater proportions of rare species. The low-elevation curves for the Adirondack Mountains were concave due to the considerable number of species

**Table 1.** Ranking and proportional abundances of the four most abundant species at selected elevations on the four mountains

| Species | $p_i$ | Species | $p_i$ | Species | $p_i$ | Species | $p_i$ |
|---|---|---|---|---|---|---|---|
| Mount Mansfield | | | | | | | |
| El. (m) 610 | | 770 | | 1020 | | 1260 | |
| Red-eyed Vireo | 0.1573 | Red-eyed Vireo | 0.1770 | Blackpoll Warbler | 0.2353 | Wh.-thr. Sparrow | 0.3333 |
| Amer. Redstart | 0.0941 | Dark-eyed Junco | 0.1416 | Wh.-thr. Sparrow | 0.1765 | Blackpoll Warbler | 0.2941 |
| Ovenbird | 0.0787 | Amer. Robin | 0.1416 | Winter Wren | 0.1029 | Nashville Warbler | 0.1078 |
| Wood Thrush | 0.0754 | Hermit Thrush | 0.1327 | Swainson's Thrush | 0.1029 | Yel.-rump. Warbler | 0.0784 |
| Camel's Hump Mountain | | | | | | | |
| El. (m) 245 | | 575 | | 965 | | 1290 | |
| Amer. Redstart | 0.1904 | Wh.-thr. Sparrow | 0.1579 | Blackpoll Warbler | 0.2178 | Dark-eyed Junco | 0.3636 |
| Red-eyed Vireo | 0.1628 | Blackburnian War. | 0.1316 | Wh.-thr. Sparrow | 0.1881 | Gray-ch. Thrush | 0.2045 |
| Veery | 0.0849 | Yel.-rump. War. | 0.1053 | Yel.-rump. War. | 0.1188 | Wh.-thr. Sparrow | 0.1590 |
| Bl.-cap. Chick. | 0.0849 | Gold.-cr. Kinglet | 0.1053 | Winter Wren | 0.1010 | Blackpoll Warbler | 0.1364 |
| Whiteface Mountain | | | | | | | |
| El. (m) 530 | | 890 | | 1210 | | 1475 | |
| Amer. Redstart | 0.1302 | Dark-eyed Junco | 0.1930 | Wh.-thr. Sparrow | 0.2111 | Dark-eyed Junco | 0.2857 |
| Red-eyed Vireo | 0.1255 | Blackpoll War. | 0.1404 | Blackpoll Warbler | 0.1555 | Wh.-thr. Sparrow | 0.1429 |
| Veery | 0.0744 | Gold.-cr. Kinglet | 0.1228 | Swainson's Thrush | 0.1111 | Blackpoll War. | 0.1429 |
| Chest.-sid. War. | 0.0683 | Canada War. | 0.1228 | Gray-ch. Thrush | 0.0666 | Gray-ch. Thrush | 0.1429 |
| Nippletop Mountain | | | | | | | |
| El. (m) 460 | | 720 | | 1020 | | 1475 | |
| Red-eyed Vireo | 0.1764 | Red-eyed Vireo | 0.2068 | Wh.-thr. Sparrow | 0.1515 | Wh.-thr. Sparrow | 0.5555 |
| Wood Thrush | 0.1568 | Bl.-thr. Blue War. | 0.2068 | Blackpoll Warbler | 0.1515 | Blackpoll War. | 0.2222 |
| Bl.-cap. Chick. | 0.0784 | Swainson's Thrush | 0.1034 | Swainson's Thrush | 0.1515 | Dark-eyed Junco | 0.1111 |
| Wh.-br. Nuthatch | 0.0784 | Gold.-cr. Kinglet | 0.0862 | Red-br. Nuthatch | 0.1212 | Gray-ch. Thrush | 0.1111 |

**Table 2.** Elevational amplitude rankings of the five species on each mountain with the broadest distributions on the gradient

| Amplitude Rank | Mount Mansfield | | Camel's Hump | |
|---|---|---|---|---|
| | Species | Amplitude | Species | Amplitude |
| 1 | Dark-eyed Junco | 660 m | Winter Wren | 1045 m |
| 2 | Winter Wren | 660 m | Yel.-bel. Sapsucker | 1045 m |
| 3 | Bl.-cap. Chickadee | 610 m | Dark-eyed Junco | 885 m |
| 4 | Wh.-thr. Sparrow | 495 m | Wh.-thr. Sparrow | 885 m |
| 5 | Hairy Woodpeckers | 495 m | Hairy Woodpecker | 885 m |
| 6 | Robin | 495 m | | |

| Amplitude Rank | Nippletop Mountain | | Whiteface Mountain | |
|---|---|---|---|---|
| | Species | Amplitude | Species | Amplitude |
| 1 | Dark-eyed Junco | 960 in | Dark-eyed Junco | 925 m |
| 2 | Winter Wren | 960 m | Wh.-thr. Sparrow | 660 m |
| 3 | Wh.-thr. Sparrow | 960 m | Swainson's Thrush | 560 m |
| 4 | Swainson's Thrush | 850 m | Red-br. Nuthatch | 560 m |
| 5 | Purple Finch | 850 m | BL-thr. Gr. Warbler | 560 m |

with low importance values. Several of the low elevation samples conformed to MacArthur's (1960) broken-stick distribution. With increasing elevation the slopes of the curves increased and tended to become linear, approaching geometric series. Accordingly, the communities were characterized by greater dominance of the most abundant species. Values of a simple index of dominance in a community (May, 1975),

$$d = n_{i_{\max}}/N$$

are shown in Figure 2. The values of $d$ for the lower elevation samples are also characteristic of the broken-stick model for communities of these sizes (see May, 1975).

The ranking of species abundances showed considerable similarity from gradient to gradient. Table 1 shows the proportional abundances of the four commonest species at selected stations on the mountains. At the lowest stations, the Red-eyed Vireo (*V. olivaceus*) and American Redstart (*S. ruticilla*) were usually the two most abundant species, and on each mountain a thrush (either *Hylocichla mustelina* or *Catharus fuscescens,* but not both) ranked among the four most numerous species. At higher elevations the Blackpoll Warbler (*Dendroica striata*) and White-throated Sparrow (*Zonotrichia albicollis*) were the two dominant species. Again, a thrush (*C. ustulatus*) was among the four most numerous species on three of the four mountains. The faunas at the tops of these peaks were depauperate and dominated by White-throated Sparrows, Dark-eyed Juncos (*Junco hyernalis*), Blackpoll Warblers and Gray-cheeked Thrushes (*C. minimus*).

### *Species Amplitudes*

Several species were very generalized in their habitat preferences and were found over nearly the entire gradient. The species showing greatest amplitude tended to be similar on each of the mountains (Table 2). The Dark-eyed Junco and White-throated Sparrow appeared on all the lists and the junco had the greatest elevational range on three of the four mountains. On Whiteface Mountain and Mount Mansfield it was found at all sampling stations. The Winter Wren (*Troglodytes troglodytes*) ranked high in amplitude on three of the mountains and had the largest amplitude on Camel's Slump Mountain.

A number of species were found over very narrow elevational ranges. Some of these were rare species and their amplitudes were probably broader than our census data indicated. Most were concentrated at the lower end of the gradients. Some species were quite abundant even though they occurred only at the lowest elevations: the American Redstart, Wood Thrush and Veery occurred only at the lowest one or rarely two stations, but were among the most numerous species in those areas (Table 1). Thus species may have high importance values near their distributional limits.

Some conspicuous species seemed to be characterized by narrow ranges. The Golden-crowned Kinglet (*Regulus satrapa*) on Mount Mansfield and the Canada Warbler (*Wilsonia canadensis*) on Nippletop Mountain were both found near the middle of the gradients, but nevertheless had narrow amplitudes of between 100-150 m. These are both conspicuous species for which our census data should be accurate.

The mean amplitude of the species at each sampling station increased with elevation and decreased with species richness on all the mountains. The regressions of amplitude on elevation and species richness are shown in Figure 3. The data from Mount Mansfield are poorly fitted by the regression, but more than 80 percent of the variance in the three other data sets is explained. The slopes of the regressions of the two Adirondack mountains are significantly ($P$ <0.01) greater than those of the two gradients in the Green Mountains; mean amplitude increased more rapidly with elevation on Nippletop and Whiteface Mountains.

Mean amplitude at a sampling station was inversely correlated with the number of species occurring at that station. Interpretation of this relationship is confounded by the fact that species richness is also inversely correlated with elevation. Thus the depauperate faunas at the tops of the mountains were characterized by species with much larger than average amplitudes on the gradient. Several other observations are pertinent to an understanding of these patterns: 1) No species reached maximum abundance at the upper end of these gradients, suggesting that none was optimally adapted to this zone. 2) The most abundant species of the high elevation communities had both greater dominance and absolute abundances than the dominant species of loaner elevations. 3) In general, those species that had high abundances also had large amplitudes, giving rise to the positive correlation between mean amplitude at a station and elevation. 4) Species diversity was lowest at high elevations. This was correlated with reduced foliage height diversity and relatively small areal extent of the habitat.

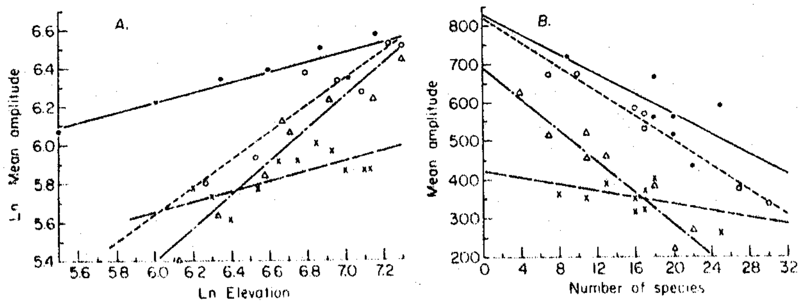

**Fig. 3A and B.** Regressions of mean species amplitude at given sampling stations on elevation and the species richness at the station. x Mount Mansfield; ● Camel's Flump Mountain; ○ Whiteface Mountain; Δ Nippletop Mountain

## *Community Structure*

To determine the similarity in species composition of the sample stations along the gradient we have used the coefficient of similarity, $S=2w/(a+b)$, where $w$ is the number of species shared by two samples and $a$ and $b$ are the total numbers of species in each of the respective samples. The coefficients were converted to percent similarity (100 $S$). Similarities between adjacent stations and between the lowest station and each succeeding higher one are shown in Figure 4. The ecotones are indicated by arrows. If the limits of species distributions occur independently of one another the points showing species similarity between the lowest station and each progressively higher one should describe a descending line of constant slope. An increase in slope indicates a more rapid turnover of species in that area of the gradient.

On each of the mountains the slopes of the curves increased near ecotones. This was particularly true at the lower ecotone on those mountains where two noticeable habitat discontinuities occurred. On Mount Mansfield increases in slope were associated with the higher ecotone as well. Both types of plots indicated increased species turnover at similar positions on the gradients. Because the data from all four mountains showed definite increases in turnover at ecotones, we conclude that these habitat discontinuities had a significant influence in determining the limits of species on the gradient.

The species similarity coefficients used above ignore the relative abundances of the species. Therefore, we also employed a dissimilarity index described by MacArthur (1972, p. 189):

$$M=\frac{2}{1+\dfrac{2\sum p_i q_i}{\sum p_i^2+\sum q_i^2}},$$

where $p_i$ and $q_i$ are the proportions of species $i$ in samples $p$ and $q$, and $1 \leqq M \leqq 2$. We have computed the similarity between the lowest elevation station and each successively higher station (Fig. 5). The functions should increase as the distance

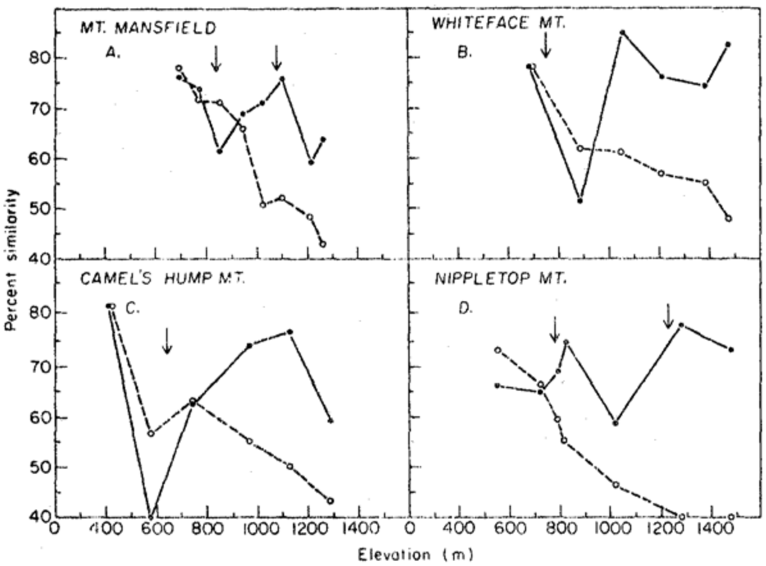

**Fig. 4A-D.** Plots of the coefficient of species similarity, $S = 2w/(a + b)$, The solid line connects points denoting the similarity between each sampling station and the next higher station. The dashed line connects similarity coefficients between the lowest elevation station and each succeeding higher station. Arrows denote the approximate elevations of ecotones

between the stations being compared increases. An increase in the slope of the line indicates a greater change in community composition between two stations.

The addition of information on relative abundance considerably clarified the patterns revealed by the plots of species similarity. Large increases in dissimilarity (i.e., increases in *M*) were associated with ecotones on all of the mountains, whereas the slopes of most of the curves tended to be much smaller or approach zero across stations remote from habitat discontinuities. It is interesting that on Mount Mansfield, the steepest of the four mountains, the two ecotones appear to have been treated as a single discontinuity by the birds. The same changes in vegetation on the other mountains were associated with two distinct changes in faunal composition. The proximity of the two ecotones on Mount Mansfield is probably responsible for this difference. The greater similarity between stations 1 and 4 than between 1 and 3 on Camel's hump was due to the isolated patches of beech-maple forest in the vicinity of station 4 discussed earlier.

Both types of similarity measures suggest a major influence of ecotones in setting the distributional limits of species on this gradient. The magnitude of this effect is revealed in Table 3. On each mountain slightly more than half of the species' distributional limits occurred at stations associated with an ecotone. These figures exclude distributional limits dictated by the upper and lower termini of the gradient. For purposes of comparison with other studies, we have converted these data into the proportion of species limits per ecotone sampling station.

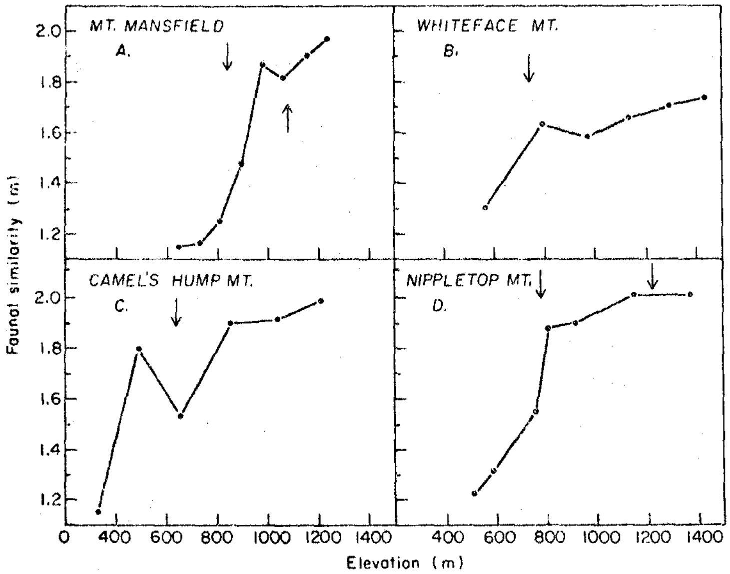

**Fig. 5A-D.** Plots of the index of faunal dissimilarity between the lowest elevation station and each succeeding higher station for the four mountains. Arrows denote the approximate elevations of ecotones

**Table 3.** Elevation limits of species distributions in relation to ecotones on the four mountains

| Mountain | No. of limits excluding termini | No. at ecotones | Proportion at ecotones | Proportion of limits/ ecotone station |
|---|---|---|---|---|
| Whiteface | 35 | 20 | 0.570 | 0.285 |
| Nippletop | 34 | 18 | 0.530 | 0.177 |
| Mansfield | 39 | 20 | 0.510 | 0.170 |
| Camel's Hump | 39 | 20 | 0.510 | 0.255 |

Another factor that seems to be important in limiting the altitudinal distribution of many species is interspecific competition. It is reasonable to expect competition among closely related species. Warblers and thrushes had the largest numbers of species on our gradients. Representative species abundance curves for these groups are shown in Figure 6. To provide convincing evidence that distributions are influenced by interspecific competition, species abundance curves should drop precipitously at the point of contact between two species. Furthermore, the species should reach maximal or near-maximal abundance adjacent to the zone of contact and this zone must not coincide with an ecotone.

The Wood Thrush and Veery were common at low elevations and tended to reach their upper limit on the gradient together, at the lower ecotone. The Hermit Thrush (*C. guttatus*) also occurred at low elevation and was sometimes abundant there, but its numbers were variable and it extended above the lower ecotone

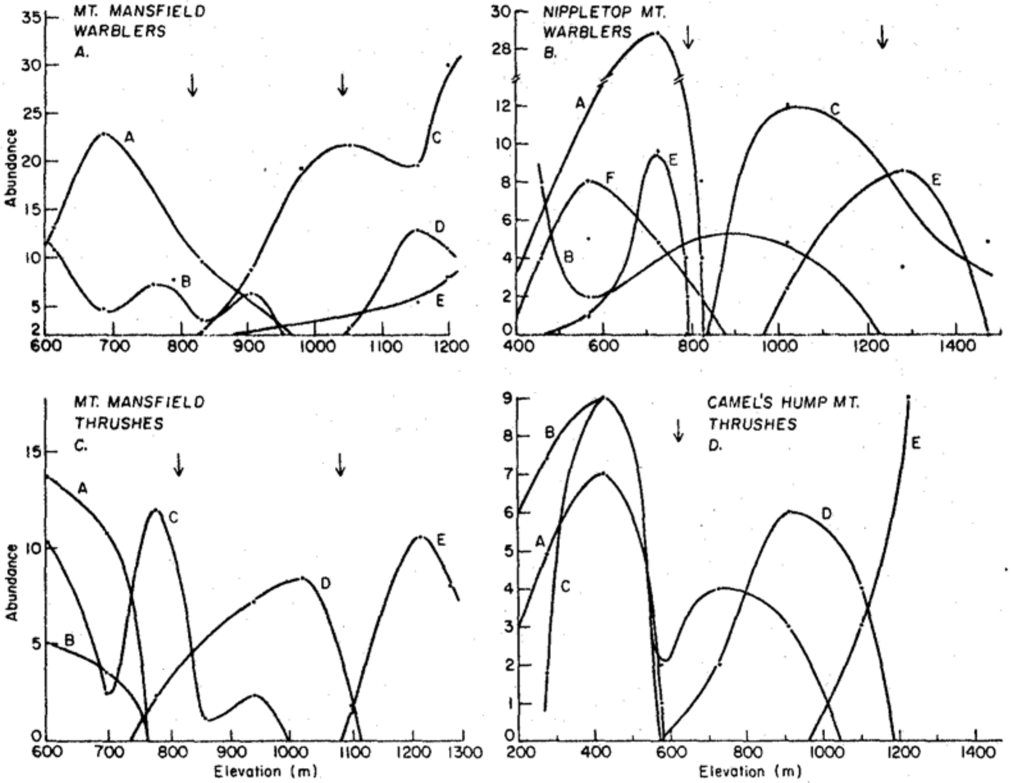

**Fig. 6A-D.** The abundances of warbler and thrush species on the elevational gradients. **A** Warblers on Mount Mansfield. **B** Warblers on Nippletop Mountain. **C** Thrushes on Mount Mansfield. **D** Thrushes on Camel's Hump Mountain. Species of warblers are denoted as follows: *A* Black-throated Blue Warbler; *B* Black-throated Green Warbler; *C* Blackpoll Warbler; *D* Nashville Warbler; *E* Yellow-rumped Warbler: *F* Blackburnian Warbler. Species of thrushes are denoted as follows: *A* Wood Thrush; *B* Veery; *C* Hermit Thrush; *D* Swainson's Thrush; *E* Gray-cheeked Thrush

into the middle elevations of the gradients in reduced abundance. At higher elevation, the Swainson's and Gray-cheeked Thrushes tended to inhabit mutually exclusive ranges. Overlap between them was confined to a single sampling station on each mountain, except Whiteface where they co-occurred at two stations. Unfortunately, the importance of competition is unclear in this case because the point of contact between these species sometimes coincided with the upper ecotone as on Mount Mansfield (see Fig. 6 C). However, this was not always the case, and on Nippletop Mountain intense interspecific aggression was observed on one occasion. This species pair may provide an example of spatial competitive exclusion reinforced by interspecific territoriality and we are examining the relationship between these and the other thrush species in greater detail.

The foliage-gleaning warblers can be divided into two groups: Black-throated Blue (*D. caerulea*), Black-throated Green (*D. vireos*), and Blackburnian Warblers

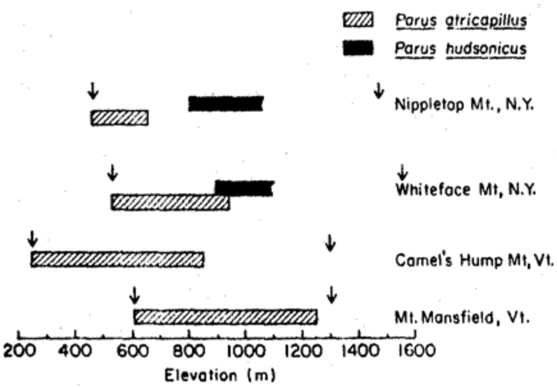

**Fig. 7.** The distribution of the Black-capped and Boreal Chickadees on the four mountains. The species are sympatric on Nippletop and Whiteface Mountains; only the Black-capped Chickadee was found on Camel's Hump Mountain and Mount Mansfield. Arrows indicate the upper and lower termini of the gradients

(*D. fusca*) and Americal Redstarts occurred primarily below the first ecotone; Yellow-rumped (*D. coronata*), Blackpoll and Nashville Warblers (*Vermivora ruficapilla*) occurred from the first ecotone to the limits of trees on the tops of the mountains. Repulsion interactions (Diamond, 1973) were not apparent among these species. The upper limit of the low elevation species group tended to coincide with the first ecotone.

We have also failed to find any clear-cut examples of competitive exclusion among several species pairs. The two vireos, *V. olivaceus* and *V. solitarius,* and the Dark-eyed Junco and White-throated Sparrow (considered congeneric by some workers) overlap broadly in distribution. The flycatchers *Empidonax minimus* and *E. flaviventris,* the chickadees *Parus atricapillus* and *P. hudsorticus,* and the nuthatches *Sitta carolinensis* and *S. canadensis* usually showed no spatial overlap, the pairs being confined to broad-leafed deciduous forest and coinferous forest, respectively.

A less direct way of searching for evidence of competitive interactions in the community is to compare the amplitudes of species having likely competitors on the gradient with the amplitudes of species lacking obvious competitors. We compared the mean amplitude of all species lacking congeners with the mean amplitude of all species with congeners on each gradient. No significant differences were found. We also arranged species into guilds following Willson (1974) and asked if the species comprising large guilds had smaller amplitudes. Again, no differences were found.

The faunal similarity of these mountains precluded most comparisons of species' distributions in the presence and absence of competitors. However, the chickadees *P. atricapillus* and *P. hudsonicus* were sympatric and reasonably common on the two Adirondack Mountains, but the Boreal Chickadee was absent from Mount Mansfield and Camel's Hump Mountain. In fact, the species is apparently absent from the entire southern part of the Green Mountains of Vermont, which has similar elevation and habitats and is at the same latitude as the nearby Adirondacks. On the Adirondack Mountains, the two species showed little or no overlap in distribution (Fig. 7). On the Vermont mountains, the Black-capped Chickadee had larger absolute and proportional amplitudes; on Mount Mansfield a Black-capped Chickadee was seen near treeline at 1250 m. On both of these mountains Black-capped Chickadees extended upward across the lower ecotone into coinferous forest; on the Adirondack gradients the species stopped below the top of the lower ecotone. The evidence is largely qualitative, but we suggest that the Black-capped Chickadee showed ecological release in the form of habitat expansion in the absence of its congener.

## Discussion

Habitat selection in passerine birds appears to be influenced by the physical structure of the vegetation without particular regard to the plant species present (MacArthur and MacArthur, 1961; MacArthur et al., 1966; Cody, 1968; Wiens, 1969; James, 1971; Shugart and fatten, 1972; Anderson and Shugart, 1974; etc.). It is reasonable, therefore, that the distributions of birds on these elevational gradients were influenced by noticeable changes in the physiognomy of the forests (e.g., from mixed to pure coniferous). Although these vegetation transitions are undoubtedly illusory (Whittaker, 1956, 1967), changes in only a small proportion of the tree species can effect a large change in the structure and appearance of the forest if those changes involve the dominant tree species in the community. If avian habitat selection is based primarily on responses to structural features of the habitat, bird communities along an elevational gradient could show discontinuities even though the underlying forest obeyed the continuum hypothesis. This explanation appears to account for the distributions we have found among the bird species.

In general, species diversity measured in several ways decreased with increasing elevation. Most of this decrease can be accounted for by the decrease in species richness. In this sense, our results parallel those of Tramer (1969). However, there was also a systematic change in the equitability of the bird communities along the gradient, with communities at higher elevations exhibiting a higher degree of dominance. Correlated with the reduced species richness and evenness of the high elevation communities was an increase in the average amplitude of the species comprising the samples. Decreasing species richness with elevation seems to be a general rule on mountains in forested regions (Terborgh, 1971; Diamond, 1973), although its causes remain unclear.

The broken stick model of MacArthur (1960) has recently been reviewed by May (1975). The pattern of relative abundance predicted by this model has been found in a number of bird communities (MacArthur, 1960; King, 1964) as well as in other taxonomic groups. In general, the distribution characterizes groups of taxonomically similar species in competition that more or less evenly divide some major resource axis. It is not surprising that the lower elevation communities on our mountains fit this model. At high elevations the bird communities showed high dominance and a geometric series or logseries species abundance distribution. This pattern is very similar to montane plant communities (Whittaker, 1965) which, like the bird communities in question, consisted of a few species in a harsh environment. In general, this distribution should describe a community governed by some dominant factor in which niche preemption by the dominant species occurs. These two extremes, one implying even division of some resource among species and the other a strongly hierarchical resource partitioning, appear to grade into one another with elevation. This pattern suggests fundamental differences in the evolution of niche relations within the communities at the extremes of our gradients.

It is of interest that no species was confined to or most numerous in the floristically distinctive alpine tundra. This is true of the entire Appalachian range. The total area of such habitat is small and the patches of it are relatively isolated in contrast to alpine tundra in the mountains of the western United States where a distinctive high elevation bird fauna exists. The lack of such a fauna atop the eastern North American mountains can be adequately explained by the insular nature of the habitat and the accompanying high extinction rates predicted by MacArthur and Wilson (1967).

The bird fauna of the highest elevations of the mountains was primarily a subset of that characterizing lower elevations. Some of the commonest high elevation species (e.g., White-throated Sparrow and Dark-eyed Junco) extended down to the first ecotone or below. Many species from lower elevations failed to reach the tops of the mountains, however, and the reduced species richness at high elevations can probably be accounted for by the decreased structural complexity and productivity of the habitats.

In addition, the tops of these mountains are frequently shrouded in clouds and subjected to high winds and cold rain even in mid-summer. That the species inhabiting these rigorous habitats have larger than average amplitudes on the gradient is possibly in part a reflection of broader tolerance limits in terms of gradient variables. If this was the complete explanation, however, we might predict that overall bird density would be markedly reduced in high elevation areas as Terborgh (1971) found in Peru. However, this was not the case. Total density of individuals showed some decline with elevation, but the most rapid decrease occurred between the lower stations. The most abundant species of the high elevation communities had both greater dominance and absolute abundances than the dominant species of lower elevations. Species adapted to a wide range of conditions on the gradient have been better able to exploit the rigorous high elevation habitats and showed some density compensation under reduced competition.

Many of our results are similar to Terborgh's in the Peruvian Andes and Diamond's in eastern New Guinea. However, there are some important and interesting differences. Most noticeable among these was the virtual absence on our mountains of distinctive spatial competitive exclusion patterns between congeneric pairs or series. In Peru these interactions accounted for approximately two-thirds of the distributional limits of the species (Terborgh and Weske, 1975); many groups of congeners showed no spatial overlap and gaps occupied by neither species were not infrequent.

Particularly in light of our greater ability to identify likely competitors among the well-known species inhabiting our mountains, this difference between the studies is so great that we are confident it is real. Both Diamond (1972) and Terborgh (1971) studied the avifauna of virgin forests and Diamond stressed that strict altitudinal segregation in New Guinea breaks down in disturbed areas. The forests we have studied are not virgin for the most part, but are not recently disturbed. However, there are some possible sources of bias that should be mentioned. Terborgh's sampling of birds was done entirely with mist nets and was, therefore, limited to within 2 m of the ground. If species whose activities are confined to the stratum very near the ground are more likely to partition the habitat horizontally than those utilizing higher strata in the forest (Cody, 1974), Terborgh's results will be biased. It is interesting that the most suggestive case of horizontal separation we found was between two species of thrushes that forage on or near the ground.

In further contrast to the tropical forest bird communities described by Terborgh and Diamond, we found a much greater change in species distributions associated with changes in forest vegetation. On Terborgh's gradient, less than twenty percent of the species' limits coincided with ecotones compared with slightly over half the limits on each of our four mountains. However, the data must be normalized for comparison because a higher proportion of our sampling stations were associated with ecotones. When we compared the percentages of distributional limits per ecotone station in the two studies we found that each of our mountains differed significantly from Terborgh's 6.2 percent of the total limits per ecotone station (*t*-test; $0.05 > P > 0.01$). There is no reason to believe that the ecotones on the Peruvian gradient were more gradual than ours. In fact, Terborgh's descriptions and discussions with J. P. O'Neill, who has traversed the gradient, suggest that the vegetation discontinuities were quite abrupt, especially the ecotone between montane rain forest and cloud forest.

On the basis of these differences between avian communities on temperate and tropical mountains we hypothesize that the temperate species respond more strongly to habitat. Based on the noticeable absence of spatial competitive exclusion among our birds, we infer that competition is either less severe in temperate forests or that it is translated into a different result in temperate areas (habitat selection) than in tropical ones (intra-habitat spatial exclusion). We will explore these possibilities further.

On their face, many of our observations are consistent with Fretwell's (1972) general model of avian breeding distributions. The general absence of obvious competition effects on the distribution of the species on our gradients, as compared to similar situations in the tropics, is predicted by Fretwell. Most other students of bird communities have regarded interspecific competition as an important shaping force in both temperate and tropical regions (this view most recently expounded by Cody, 1974). On small islands off the coast of Maine, Morse (1971) studied several of the same warblers (*Dendroica* spp.) examined by MacArthur (1958) on the nearby mainland. In the absence of some of the species, the others showed significant expansion in their foraging niches. These data clearly support the importance of competition in temperate forest breeding bird communities ,and cannot be explained by Fretwell's model. In this study the amplitude expansion of Black-capped Chickadees in the absence of Boreal Chickadees and the relationship between amplitude and species richness implicates the role of competition. The weight of current evidence indicates that the action of competition, at least in the past, is responsible for much of the pattern we see even in temperate bird communities.

if we grant that interspecific competition hits been an important force on our gradients, we are left with the task of accounting for the differences between our results and those obtained in the tropics. It appears that at least one of the outcomes of competition in the tropics, intra-habitat spatial exclusion, is quite rare in temperate forests. This is also confirmed by Cody's (1970, 1974) data from temperate Chile and California mountains. One possibility is that this difference is a function of the much greater species richness and consequent niche packing in much of the tropics. In this regard, it is of interest that Diamond (1973) found altitudinal segregation on tropical Pacific Islands with more than 66 species, but no segregation on islands with fewer species. The faunas of these small islands are, of course, not a random subset of the New Guinea source fauna (Diamond, 1974), and are not fully representative of a tropical mainland or large island. Therefore they do not provide a completely satisfactory test of this hypothesis. We hope to test this idea further along a gradient of diversity on a mainland.

In New Guinea, Diamond (1972) found a positive correlation between morphological similarity and the strictness of altitudinal segregation and suggested that it is a first sorting mechanism among congeners experiencing secondary contact. With time, altitudinal overlap becomes possible as morphological divergence proceeds and other mechanisms such as vertical stratification and microhabitat segregation evolve. There is, however, no reason to believe that our temperate forest bird communities contain proportionately fewer species of recent derivation than tropical forests.

In addition to the difference in diversity, the fauna we have studied differs most noticeably from tropical ones in that it is nearly entirely migratory. Somewhat less than ten percent of the species on our mountains are resident and several of these were rare. The fact that most of the species are only seasonal occupants of these montane forests has no doubt influenced the patterns of community structure and the mechanisms responsible for them. For example, the very sharp boundaries between putative competitors in the tropics (the so-called repulsion interactions) seem unlikely to be the result of exploitation competition (Miller, 1967). Diamond (1973) pointed out that the line separating two species may consist of the territorial boundary between two interspecifically territorial individuals, and it is likely that some kind of behavioral interaction (interference competition) is required to produce the sharp boundaries that have been observed. If we assume that interspecific territoriality necessitates a significant expenditure of time and energy above that required for intraspecific defense (Orians, 1971), we may see why it would be a less viable mechanism for resolving competition in a community made up largely of migratory species. Spatial relations would have to be established anew each year, just at the time when the other demands of breeding in a seasonal environment are impinging upon the individuals. In the tropics where most species are resident, interspecific territorial boundaries could be stable for long periods of time, enhanced by the sedentary nature of the individuals and the consequent opportunity to become familiar with local terrain and landmarks. In addition, the sparse distribution of many tropical forest passerines reduces the burden of intraspecific territorial defense.

In further contrast to birds on tropical elevational gradients, the birds we studied showed noticeable responses to habitat discontinuities. We interpret these data as indicating that habitat selection based on vegetation structure is more prevalent in temperate forest birds than in their tropical counterparts. It has been well demonstrated that the presence or absence of temperate species can be predicted on the basis of measures of habitat structure (Shugart and Patten, 1972; James, 1971; MacArthur et al., 1963). Distributional data (Terborgh, 1971; Diamond, 1973; Cody, 1974) indicate that these techniques would be much less successful in the tropics. Most tropical species show small proportional amplitudes compared to their temperate counterparts. This fact, coupled with the greater niche packing and within and between-habitat diversity in the tropics has given rise to the idea that tropical species show finer horizontal habitat selection (Klopfer, 1967; Karr and Roth, 1971). When analyzed in terms of habitat distributions rather than simple amplitudes the data from elevational gradient studies do not support this notion. Diamond (1973) has pointed out that because of the patchiness of species distributions, tropical forest birds may select habitat not on the basis of structural features of the vegetation, but the presence of conspecific individuals and the absence of competitors. If the common tropical mechanism of horizontal separation is not a viable solution in temperate forest areas, we might expect competition to have more frequently translated into separation based on structural habitat features. Our data indicate that this is the case.

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