

# SEASONAL CHANGES IN THE HABITAT DISTRIBUTION OF TRANSIENT INSECTIVOROUS BIRDS IN SOUTHEASTERN ARIZONA: COMPETITION MEDIATED?

RICHARD L. HUTTO

*Department of Zoology, University of Montana, Missoula, Montana 49812 USA*

**ABSTRACT.**—The distribution and abundance of 26 migratory insectivorous bird species were recorded over an elevational habitat gradient in the Chiricahua Mountains, Arizona for the spring and fall migratory seasons. Most of the species used this area only during migratory passage, and 54% exhibited significant shifts in the habitats occupied from spring to fall. The majority (69%) of species also exhibited significant changes in density within habitats between seasons. Using pairwise correlations of bird densities from 7 habitat types and 2 seasons, I identified 5 groups that contained species whose seasonal distributional patterns were similar to one another but independent and distinct from members of the other 4 groups. Despite independence among groups in the seasonal patterns of habitat distribution, the combined density of all species was significantly positively correlated with a measure of food availability taken from each of the habitat types in each migratory season. Consequently, the spring-to-fall change in insect density within each habitat also was significantly correlated with the seasonal change in bird density over each of the habitat types. The hypotheses that best explain these correlations include that in which competitive adjustments among the migratory birds enable a close match to food resource availability and that whereby noncompetitive adjustments occur in response to the diversity (itself correlated with food abundance) of food types available. *Received 7 May 1984, accepted 18 August 1984.*

EXPLANATIONS for patterns in bird community structure routinely have been sought from knowledge of food resource distributions and abundances (MacArthur 1969, 1970, 1972; Cody 1974). This stems logically from the idea that natural selection should lead toward the utilization of currently underutilized resources, and competition among species should determine both the number and relative abundance of species that use those food resources. More recently, however, Wiens (1977, 1983) suggested that the match between resource levels and species utilization patterns will be less than perfect because unpredictability or instability in resource levels cannot be tracked rapidly enough by bird populations (but see Cody 1981). In fact, recent experimental evidence (Emlen 1978, 1979, 1981; Emlen and DeJong 1981) suggests that birds are rather fixed in their foraging behaviors and that a close tracking of resource levels is impossible. This means that, except for the occasional year of an ecological crunch when resources are scarce, many aspects of community structure would result as much from stochastic processes as from deter-

ministic ones (Wiens 1977, 1981; Rotenberry and Wiens 1980a, b).

Although most of the discussion and uncertainty about the role of food resource levels in controlling bird community composition revolves around breeding populations, a unique situation for testing whether birds respond, in an ultimate sense, to seasonal changes in food levels exists with migratory birds. Changes in vegetation structure and food resource levels from spring to fall are not of equal magnitude among habitat types. This provides the opportunity to ask whether bird community structure changes in response to changes in the distribution of food resources.

In this paper I outline the patterns of habitat use by small, insectivorous bird species of southeastern Arizona during both migratory seasons and test whether the habitat distribution of these birds is independent of migratory season. This is followed by an analysis of the relationships between bird densities and various habitat parameters, including food availability. If interspecific and intraspecific competition for food are important during the

migratory seasons, then the combined density of similar-sized, insectivorous birds would be expected to match the relative food resource levels among habitats within a season and, therefore, to match any seasonal changes in relative food levels among habitats. If food is of little ultimate importance in determining bird community composition, or if food levels are important but changes in food levels are impossible to track closely, then independence between bird densities and food densities would be expected.

#### STUDY AREA AND METHODS

I conducted bird censuses and recorded vegetation parameters and insect densities in each of 7 homogeneous habitat types in the Chiricahua Mountains, Arizona (Fig. 1). The 7 sites occurred along an elevational gradient and ranged from low and simple to tall and complex in vegetation structure. The first site (desert flat) was located 2 km northeast of Portal (31°55'N, 109°07'W) at an elevation of 1,402 m and was dominated by desert scrub vegetation, including *Acacia constricta*, *Larrea tridentata*, *Chilopsis linearis*, and *Prosopis juliflora*. The second site (desert wash) was located along lower Cave Creek 2 km northeast of Portal (31°55'N, 109°07'W) at an elevation of 1,433 m and contained many of the vegetation elements that characterized the desert flats plus scattered *Platanus wrightii* and dense sections of *Fallugia paradoxa* and *Chrysothamnus nauseosus*. The third site (creek bottom) was located along the south fork of Cave Creek 7 km southwest of Portal (31°52'N, 109°11'W) at an elevation of 1,631 m; this site was dominated by *Pinus ponderosa*, *Quercus arizonica*, *Q. hypoleucoides*, and *Picea engelmanni*. The fourth site (pine-oak woodland) was located behind the American Museum's Southwestern Research Station 7 km southwest of Portal (31°53'N, 109°12'W) at an elevation of 1,676 m and was dominated by *Pinus leucophylla*, *Quercus emoryi*, *Q. arizonica*, and *Juniperus deppeana*. The fifth site (pine-oak-juniper woodland) was located 12 km west of Portal (31°57'N, 109°16'W) at an elevation of 2,286 m and was dominated by the same vegetation elements as the pine-oak woodland, plus *Pinus cembroides*, *P. ponderosa*, and *Quercus gambelii*. The sixth site (pine forest) was located at the turnoff to Barfoot Park 12 km west of Portal (31°55'N, 109°16'W) at an elevation of 2,512 m and was dominated by *Pinus ponderosa*. The last site (pine-fir forest) was located at Rustler Park 13 km west of Portal (31°54'N, 109°17'W) at an elevation of 2,682 m and was dominated by *Abies concolor*, *Picea engelmanni*, *Pseudotsuga menziesii*, *Pinus ponderosa*, and *P. strobiformis*.

*Bird censuses.*—I censused birds in each site by walking a 1-km line transect beginning at daybreak and recording birds detected by sight or sound within a fixed width that varied from 25 to 30 m, depending upon the habitat involved. The fixed-width transect method provides bird density estimates that are thought to be quite reliable relative to other commonly employed transect census techniques (Amman and Baldwin 1960, Robinette et al. 1974, Franzreb 1981, Tilghman and Rusch 1981). At least 4 censuses were conducted in each site during each season (a number deemed adequate for comparative work; Anderson and Ohmart 1977). For each site the 1975 censuses were combined with 1978 censuses for the fall sample. In all but 2 cases, a single 1975 census was combined with 3 or more 1978 censuses. In the 2 exceptions (desert flats and pine-oak woodlands), 2 censuses were conducted in 1975 and the rest in 1978. Because the distribution of bird densities among species did not differ between years (ANOVAs,  $P > 0.05$ ), I feel that combining fall census data from the two years is justified.

Although the same census route within a site was used each time, for statistical purposes I treated each census as an independent estimate of the bird density in a given habitat because (1) stopover periods for transients (the large majority of birds in this study; see Results) rarely exceeded 4–6 days (unpubl. banding records) and (2) successive censuses in a given habitat were spaced at least one week apart due to the rotation of censuses among sites.

For the purposes of this report I have restricted my analyses and discussion to the small, insectivorous, foliage-gleaning bird species that belong to the families Remizidae, Aegithalidae, Muscicapidae (Sylviinae only), Vireonidae, and Emberizidae (Parulinae only; A.O.U. 1983).

*Bird residence status.*—A bird species was classified as transient in a given study site if it could be found there only during one or both migratory seasons. The breeding status of each species in each site was determined from breeding census data provided by Balda (1967), M. Cody (pers. comm.), and K. Garrett (pers. comm.), each of whom conducted censuses close to, if not precisely within, my study sites.

*Vegetation measurements.*—I measured some vegetation parameters that have been shown through previous work (James 1971, Whitmore 1975) to be important in distinguishing bird species that co-occur within a restricted geographic location. On a single occasion in each site during the fall of 1975 and the spring of 1976, I counted the number of times foliage hit an extendable pole that was raised through the vegetation at 100 points (1 every 10 m) 5 m to one side of the census route, alternating left and right from one point to the next. An imaginary extension for taller habitats was provided by a camera and telephoto lens. I used the total number of hits as an es-

timate of vegetation density (VEGTOT), the total number of hits from ground level to 1 m as an estimate of understory density (VEGONE), the proportion of points that contained at least 1 hit at >5 m as an estimate of canopy cover (CANCOV), the number of perennial plant species hit as an estimate of plant species richness (PSRICH), and the maximum vegetation height at each point averaged over all points as an estimate of mean vegetation height (HEIGHT).

Three vegetation variables were statistically significantly ( $P < 0.05$ ) intercorrelated: VEGTOT with CANCOV ( $r = 0.78$ ), VEGTOT with HEIGHT ( $r = 0.74$ ), and CANCOV with HEIGHT ( $r = 0.96$ ). I retained all variables in my analyses, however, because they were different enough to reveal differences in the significance of their correlations with bird density. None of the vegetation variables was significantly correlated with the index of insect abundance (defined below).

**Food availability.**—I did not attempt to sample the same prey species that foliage-gleaning insectivores capture. Even samples that include only prey species captured by the birds would not be immune from criticism that the prey cannot be captured in the same manner that birds capture them and, therefore, that such samples still might fail to provide an accurate measure of food availability. Instead, I used a more general sampling scheme (below) and made the assumption that the calculated values were correlated with actual prey availability.

Prey availability was estimated from counts of flying insects caught on  $10 \times 10$ -cm plastic squares coated with Tanglefoot® that were hung in vegetation at 0.5-m height intervals to 2.0 m [see Hutto (1980) for discussion of the efficacy of this method]. At each site and in each season (1975 and 1976), 20 boards (5 stations with 4 boards each, every 200 m along the transect route) were left hanging for 24 h before I counted the insects. The boards were hung in precisely the same spots in both seasons. The number of insects captured per board is in itself an insufficient estimate of prey availability to foliage-gleaners in different habitats, unless differences in vegetation density (foraging-substrate availability) are taken into consideration. Assuming independence of insects captured and vegetation density between habitats, I calculated a relative index of the number of available insects/unit volume of vegetation (ADJINS) by multiplying the number of insects captured/site times a measure of vegetation density (VEGTOT/100) within the site. The assumption that insect abundance is independent of vegetation density is reasonable if different habitats are involved. For example, a juniper woodland of the same vegetation density as an oak woodland would have many fewer insects available to birds (Balda 1967). This assumption also is directly supported by a lack of correlation between the unadjusted index of insect abundance (as determined from sticky board samples) and either VEGONE ( $r = 0.23$ , NS) or VEGTOT ( $r = -0.35$ , NS).

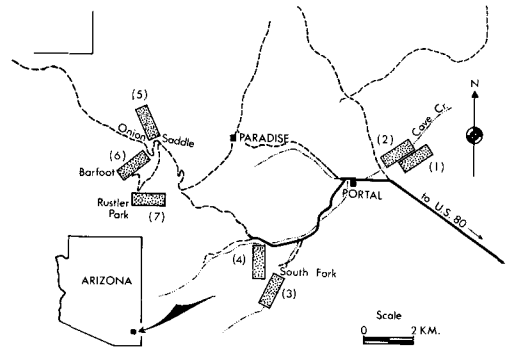


Fig. 1. Locations of the 7 study sites in the Chiricahua Mountains, southeastern Arizona. (1) Desert flat, (2) desert wash, (3) creek bottom, (4) pine-oak woodland, (5) pine-oak-juniper woodland, (6) pine forest, (7) pine-fir forest.

## RESULTS

A total of 26 small, insectivorous, foliage-gleaning bird species was recorded from the spring and fall migration-period censuses (Table 1). With the exception of the creek-bottom habitat, the number of bird species in each of the habitat types was greater in the fall than in the spring. The greatest number of species (16) was recorded during both spring and fall in the creek-bottom habitat and during the fall in the pine-fir forest.

Within a given site in either season, an average of 55% of all bird species of concern was wholly transient; that is, these species were found in these sites only during spring or fall migration. This average is conservative because an unknown proportion of individuals of some species were considered summer residents when, in fact, they were transient individuals that bred farther north than the Chiricahua Mountains. For example, one can be confident that some (or most) of the Black-throated Gray Warblers (*Dendroica nigrescens*) sighted in the creek bottom during spring were transients, but because the species is known to breed in that site, I (conservatively) called them all residents. It probably is reasonable to assume that 70–80% of the species or individuals in a given site during either spring or fall were transient, but the only certainty is that the proportion exceeded 55%. The bulk of individuals that contributed to the patterns described in this

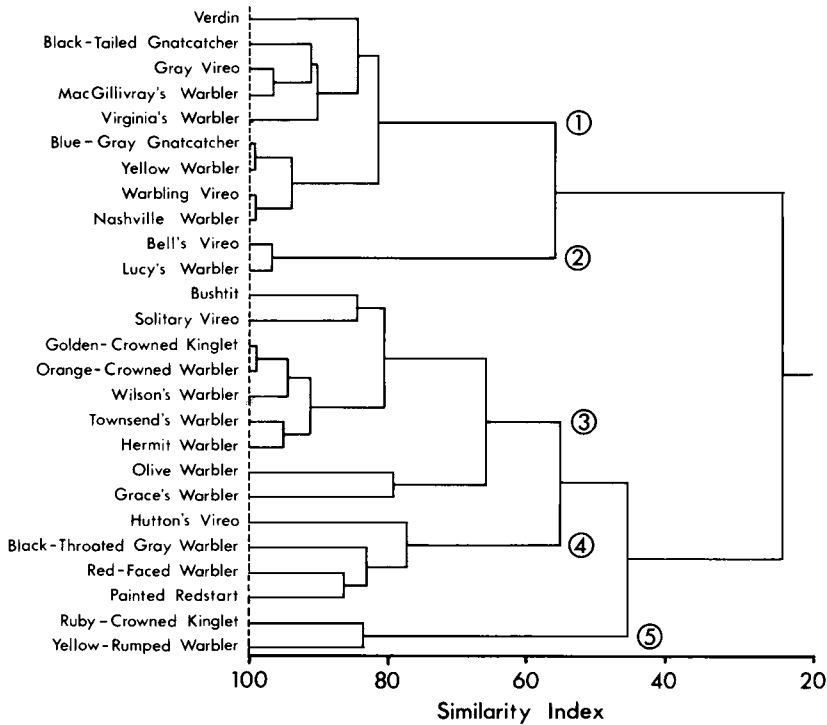


Fig. 2. Cluster dendrogram based on similarities in the seasonal distributions of 26 bird species. The 5 groups of species referred to in the text are indicated numerically.

paper are, therefore, transient species, although the analyses include resident species as well.

There was a significant (ANOVA, season  $\times$  habitat;  $F = 2.7, P < 0.05$ ) shift in the occupancy of the various habitat types from spring to fall, as evidenced by the combined bird densities; birds were relatively more abundant in desert flats and, especially, pine-fir forest in the fall relative to the spring (Table 1). Moreover, these changes in density were the result not only of significant changes in the densities of bird species that were present at a given habitat during both seasons (69% of the bird species exhibited significant changes in density between seasons), but also of some pronounced seasonal shifts in the kinds of species that used each habitat type. On average, there was over 30% turnover (defined in Table 1) in species from spring to fall in a given habitat. Considering each species separately, 14 of 26 species (54%) exhibited significant seasonal shifts in habitats occupied (ANOVAs, season  $\times$  habitat;  $P < 0.05$ ).

Rather than consider each of the 26 species

separately to analyze their seasonal patterns of habitat use, I identified fewer ecological groups that contained species with similar habitat distributions in both seasons. This was done, first, by looking for correlations between the densities of all pairwise combinations of species using all habitats in both seasons. Sixty-four (20%) of the possible 325 pairwise correlations were significant ( $r > 0.53, P < 0.05$ ), and only 2 of those were negative.

I next identified groups of species with similar patterns of habitat use by transforming the correlation coefficients into similarity indices (arccosine transformation) and then subjecting the similarity indices to a cluster analysis (average linkage; Hartigan 1981). At the 60% level of similarity, 5 distinct species groups emerged (Fig. 2). These appear to be biologically meaningful groups rather than groups that were merely forced into existence through the clustering procedure. The distribution and abundance patterns that characterize each group are outlined below.

**Group 1.**—There are 3 characteristics shared by the 9 species belonging to this group (Fig.

TABLE 1. Mean bird densities ( $n/10$  ha) during spring (S) and fall (F) migratory periods for each of the 7 habitat types.

Species	Desert flats		Desert wash		Creek bottom		Pine-oak		Pine-oak-juniper		Pine		Pine-fir	
	S	F	S	F	S	F	S	F	S	F	S	F	S	F
	Verdin ( <i>Auriparus flaviceps</i> )	15.0	14.3	10.1	7.7	—	—	—	—	—	—	—	—	—
Bush-tit ( <i>Psaltriparus minimus</i> )	—	—	—	1.2	4.8	11.3	2.4	22.9	—	—	—	2.4	—	17.6
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	—	—	—	—	—	—	—	—	—	—	—	—	1.2	11.6
Ruby-crowned Kinglet	0.3 <sup>a</sup>	—	3.6 <sup>a</sup>	—	16.0 <sup>a</sup>	0.3 <sup>a</sup>	5.2 <sup>a</sup>	1.9 <sup>a</sup>	3.0 <sup>a</sup>	17.5 <sup>a</sup>	1.8 <sup>a</sup>	—	19.1	3.7
Blue-gray Gnatcatcher ( <i>Poliopitila caerulea</i> )	0.3 <sup>a</sup>	3.2 <sup>a</sup>	—	8.3 <sup>a</sup>	0.4	—	—	—	—	—	—	—	—	—
Black-tailed Gnatcatcher ( <i>P. melanura</i> )	1.0	2.4	—	1.2	1.2	—	—	—	—	—	—	—	—	—
Bell's Vireo ( <i>Vireo bellii</i> )	—	0.4 <sup>a</sup>	5.4	0.6	—	—	—	—	—	—	—	—	—	—
Gray Vireo ( <i>V. vicinior</i> )	—	—	2.4 <sup>a</sup>	1.2 <sup>a</sup>	2.1	2.7	5.2	1.8	—	—	—	1.2	—	5.6
Solitary Vireo ( <i>V. solitarius</i> )	—	—	—	—	3.5	5.3	4.8	2.4	—	—	—	1.2	—	—
Hutton's Vireo ( <i>V. huttoni</i> )	—	—	—	3.0 <sup>a</sup>	—	1.7 <sup>a</sup>	—	—	—	—	—	—	—	—
Warbling Vireo ( <i>V. gilvus</i> )	—	2.8 <sup>a</sup>	—	—	—	—	—	—	—	—	—	—	—	—
Orange-crowned Warbler ( <i>Vermivora celata</i> )	—	0.4 <sup>a</sup>	4.8 <sup>a</sup>	—	0.6 <sup>a</sup>	0.3 <sup>a</sup>	—	—	—	—	—	2.4 <sup>a</sup>	—	32.9 <sup>a</sup>
Nashville Warbler ( <i>V. ruficapilla</i> )	—	1.2 <sup>a</sup>	—	1.2 <sup>a</sup>	—	0.3 <sup>a</sup>	—	—	—	—	—	—	—	—
Virginia's Warbler ( <i>V. virginiae</i> )	—	6.0 <sup>a</sup>	1.8 <sup>a</sup>	3.0 <sup>a</sup>	3.1	0.7	—	—	—	—	—	—	—	0.5
Lucy's Warbler ( <i>V. luciae</i> )	4.4	—	13.7	5.4	—	—	—	—	—	—	—	—	—	—
Yellow Warbler ( <i>Dendroica petechia</i> )	—	1.2 <sup>a</sup>	—	3.6 <sup>a</sup>	—	0.7 <sup>a</sup>	—	0.5 <sup>a</sup>	—	—	—	—	—	—
Yellow-rumped Warbler ( <i>D. coronata</i> )	1.0 <sup>a</sup>	—	2.4 <sup>a</sup>	—	0.6 <sup>a</sup>	—	10.3 <sup>a</sup>	1.0 <sup>a</sup>	29.8 <sup>a</sup>	3.6 <sup>a</sup>	7.1 <sup>a</sup>	9.5 <sup>a</sup>	2.5	10.6
Black-throated Gray Warbler ( <i>D. nigrescens</i> )	—	0.8 <sup>a</sup>	—	1.8 <sup>a</sup>	14.8	4.0	11.5	4.3	—	2.4	—	0.6 <sup>a</sup>	—	0.9 <sup>a</sup>
Townsend's Warbler ( <i>D. townsendi</i> )	—	—	—	—	0.4 <sup>a</sup>	1.3 <sup>a</sup>	—	2.4 <sup>a</sup>	0.6 <sup>a</sup>	4.2 <sup>a</sup>	1.6 <sup>a</sup>	7.7 <sup>a</sup>	3.7 <sup>a</sup>	11.6 <sup>a</sup>
Hermit Warbler ( <i>D. occidentalis</i> )	—	—	—	—	0.6 <sup>a</sup>	0.7 <sup>a</sup>	0.4 <sup>a</sup>	4.8 <sup>a</sup>	—	2.4 <sup>a</sup>	2.4 <sup>a</sup>	3.6 <sup>a</sup>	1.9 <sup>a</sup>	12.5 <sup>a</sup>
Grace's Warbler ( <i>D. graciae</i> )	—	—	—	—	2.7	1.3	4.4	4.3	—	3.0	7.9	3.6	0.6	2.8
MacGillivray's Warbler ( <i>Oporornis tolmiei</i> )	0.3 <sup>a</sup>	18.3 <sup>a</sup>	4.8 <sup>a</sup>	3.6 <sup>a</sup>	—	—	—	—	—	0.6 <sup>a</sup>	—	—	—	3.7 <sup>a</sup>
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	1.0 <sup>a</sup>	2.0 <sup>a</sup>	5.4 <sup>a</sup>	2.4 <sup>a</sup>	1.9 <sup>a</sup>	9.3 <sup>a</sup>	—	2.9 <sup>a</sup>	0.6 <sup>a</sup>	2.4 <sup>a</sup>	—	1.2 <sup>a</sup>	—	19.9 <sup>a</sup>
Red-faced Warbler ( <i>Cardellina rubrifrons</i> )	—	—	—	—	1.5	0.3	—	—	—	—	—	—	—	0.9
Painted Redstart ( <i>Myioborus pictus</i> )	—	—	—	—	17.1	14.0	—	—	—	—	—	—	—	0.5 <sup>a</sup>

TABLE 1. Continued.

Species	Desert flats		Desert wash		Creek bottom		Pine-oak		Pine-oak-juniper		Pine		Pine-fir	
	S	F	S	F	S	F	S	F	S	F	S	F	S	F
Olive Warbler ( <i>Peucedramus taeniatus</i> )	—	—	—	—	0.2 <sup>a</sup>	—	—	—	—	1.8	6.4	1.8	3.7	4.6
Censuses (n)	7	6	4	4	8	5	6	5	4	4	4	4	4	4
Total density	22.3	53.0	54.4	44.2	70.3	54.2	35.0	55.0	64.4	59.2	42.9	37.0	32.7	139.9
Species (n)	8	12	10	14	16	16	7	11	6	13	6	12	7	16
Species turnover <sup>b</sup>	50%		42%		19%		22%		37%		33%		39%	

<sup>a</sup> All individuals of this species in this location known to be transient.

<sup>b</sup> Calculated as (number of species unique to spring + number unique to fall)/(number of species present in spring + number present in fall).

TABLE 2. Values of each of 6 environmental variables recorded during spring (S) and fall (F) in each of the 7 habitat types.

Variable	Habitat type													
	Desert flat		Desert wash		Creek bottom		Pine-oak		Pine-oak-juniper		Pine		Pine-fir	
	S	F	S	F	S	F	S	F	S	F	S	F	S	F
VEGTOT	66	217	135	263	441	480	252	307	241	250	224	261	328	530
VEGONE	41	150	100	197	33	94	34	119	28	44	34	72	4	136
CANCOV	00	00	5	9	71	84	33	36	21	26	68	72	89	92
PSRICH	7	8	9	11	12	12	4	4	7	7	4	4	6	7
HEIGHT	0.7	0.7	0.8	0.8	11.6	12.1	7.0	7.0	6.4	6.7	11.3	12.0	18.9	19.0
ADJINS	66	78	113	97	243	67	40	175	55	33	9	16	10	217

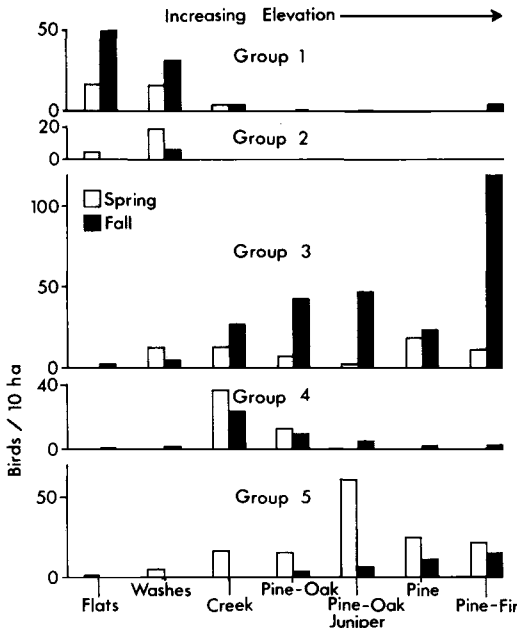


Fig. 3. Frequency histograms of the density of birds in each of 7 habitat types during spring and fall seasons. Bird species are subdivided into 5 groups, each representing a distinctive seasonal pattern of distribution and abundance. The members of each group are shown in Fig. 2.

3). They are basically desert species (ANOVA, habitat effect;  $F = 18.8$ ,  $P < 0.01$ ), their densities increase considerably from spring to fall (ANOVA, season effect;  $F = 11.7$ ,  $P < 0.01$ ), and they shift their habitat occupancy toward the desert flats in the fall (ANOVA, season  $\times$  habitat;  $F = 4.5$ ,  $P < 0.01$ ).

**Group 2.**—Bell's Vireo (*Vireo bellii*) and Lucy's Warbler (*Vermivora luciae*) comprise this group (Fig. 3), and their habitat distribution is characterized by restriction to desert habitats in both seasons (ANOVA, habitat effect;  $F = 16.5$ ,  $P < 0.01$ ). Their densities decrease significantly from spring to fall (ANOVA, season effect;  $F = 8.2$ ,  $P < 0.01$ ), and they shift from desert flats and washes in the spring to exclusive use of the desert-wash habitat in the fall (ANOVA, season  $\times$  habitat;  $F = 4.7$ ,  $P < 0.01$ ).

**Group 3.**—This group is composed of 9 species (Fig. 3) that are basically mid- to high-elevation birds (ANOVA, habitat effect;  $F = 5.2$ ,  $P < 0.01$ ) whose density increases significantly from spring to fall (ANOVA, season effect;  $F =$

16.4,  $P < 0.01$ ). These species shift markedly to the highest elevation forests in the fall (ANOVA, season  $\times$  habitat;  $F = 4.0$ ,  $P < 0.01$ ).

**Group 4.**—This is principally a mid-elevation group (ANOVA, habitat effect;  $F = 44.1$ ,  $P < 0.01$ ) composed of 4 species (Fig. 3) whose densities decrease significantly from spring to fall (ANOVA, season effect;  $F = 7.7$ ,  $P < 0.01$ ). They become significantly more broad in their habitat distribution from spring to fall (ANOVA, season  $\times$  habitat;  $F = 2.7$ ,  $P < 0.05$ ).

**Group 5.**—Ruby-crowned Kinglet (*Regulus calendula*) and Yellow-rumped Warbler (*Dendroica coronata*) comprise this group (Fig. 3), characterized by mid- to high-elevation birds (ANOVA, habitat effect;  $F = 6.3$ ,  $P < 0.01$ ) whose densities decrease significantly from spring to fall (ANOVA, season effect;  $F = 17.2$ ,  $P < 0.01$ ). They shift markedly from lower- to higher-elevation forests from spring to fall (ANOVA, season  $\times$  habitat;  $F = 3.6$ ,  $P < 0.01$ ).

Thus, one can identify groups of species that use the available range of habitats during the spring and fall in a fashion that is similar to one another but differs from members of other groups. In fact, one could use a higher level of similarity from the dendrogram to identify a greater number of species groups, each distributed in distinct fashion within and between seasons, but the characteristics and biological reality of such groups become more difficult to determine.

Aspects of vegetation structure that differed greatly among sites within a season were canopy cover and mean vegetation height, while between-season changes in vegetation density and insect density generally were pronounced within a given site (Table 2). In general, the densities of birds belonging to each of the 5 species groups were well correlated with at least 1 of the vegetation parameters (Table 3). The desert groups were negatively associated with measures of tall or dense vegetation, while the birds of higher-elevation habitats were positively associated with such measures. The index of insect abundance, with one exception, was not strongly correlated with the density of any single group of birds, but it was significantly positively correlated with combined insectivorous bird density (Table 3).

Correlations between the seasonal change in magnitude of each environmental variable and the seasonal change in bird density (Table 4) show that, of the variables measured, only the

TABLE 3. Pearson product-moment correlations between environmental variables and bird densities. Each correlation was calculated with data from the 69 censuses that were conducted in the 7 habitats and 2 seasons.<sup>a</sup>

Group <sup>b</sup>	VEGTOT	VEGONE	ADJINS	CANCOV	PSRICH	HEIGHT
1	-0.31**	0.55**	-0.03	-0.53**	0.22*	-0.56**
2	-0.39**	0.18	0.01	-0.39**	0.16	-0.41**
3	0.43**	0.19	0.29*	0.39**	-0.09	0.45**
4	0.59**	-0.23*	0.56**	0.44**	0.54**	0.32**
5	0.07	-0.39	-0.05	0.15	-0.12	0.24*
All species	0.44**	0.18	0.41**	0.28	0.15	0.32**

<sup>a</sup> \*  $P < 0.05$ , \*\*  $P < 0.01$ .

<sup>b</sup> Groups as defined in Fig. 2.

density of vegetation <1 m high ( $r = 0.93$ ,  $n = 7$ ) and the index of insect abundance ( $r = 0.92$ ,  $n = 7$ ) were able to account for the between-season change in bird density.

#### DISCUSSION

##### *Habitat distribution of migrants: proximate cues.*—

The significant seasonal shifts in habitat distribution of most migratory species are of interest because of the lack of visible change in many cues that have been suggested or implied to be important settling cues by authors of habitat-selection studies that were conducted during the breeding season (e.g. James 1971, Whitmore 1975).

Although some of the habitat variables predict the density of birds over all habitats and both seasons in this study as well (CANCOV, PSRICH, HEIGHT; Table 3), the same variables do not change seasonally within a habitat (Table 2). Therefore, these habitat variables are unlikely to be the proximate cues used by the birds for a settling response. The other three habitat variables (VEGTOT, VEGONE, ADJINS)

did change noticeably from spring to fall, apparently in response to the seasonal summer rainfall that is characteristic of southeastern Arizona (Fig. 4). Some of the birds could have been responding to the surge of vegetative growth near the ground, which was striking in the desert and pine-fir forest habitats and was well correlated with the increase in bird densities in those habitats from spring to fall (Table 4). Holmes et al. (1979) and Beedy (1981) commented that low, understory vegetation represents a unique foraging environment that, when present, is capable of attracting a distinct foraging guild.

Alternatively, the birds could have been responding to changes in food resources independent of vegetation changes, which is possible because VEGONE and ADJINS are not correlated ( $r = 0.37$ , NS), or to some combination of both variables. Balda et al. (1975) argued that shifts in food availability among habitats best accounted for seasonal shifts in habitat occupancy of transient Flammulated Owls (*Otus flammeolus*), although whether the authors meant to imply a direct response to food availability is uncertain. Austin (1970) also suspect-

TABLE 4. Pearson product-moment correlation coefficients between the magnitude of spring-to-fall change (factor by which spring value is multiplied to give fall value) in bird density and the magnitude of spring-to-fall change in each of the 6 environmental variables.<sup>a</sup> There is a single spring-to-fall calculation for each variable in each habitat ( $n = 7$ ).

Group <sup>b</sup>	VEGTOT	VEGONE	ADJINS	CANCOV	PSRICH	HEIGHT
1	0.42	0.90**	0.87**	-0.24	0.65	-0.52
2	0.89**	0.24	0.29	-0.41	-0.70*	0.22
3	-0.35	0.26	0.27	-0.18	-0.24	-0.01
4	-0.23	0.03	0.02	0.14	-0.06	0.21
5	0.34	0.72*	0.73*	-0.49	0.38	0.09
All species	0.32	0.93**	0.92**	-0.45	0.47	-0.48

<sup>a</sup> \*  $P < 0.05$ , \*\*  $P < 0.01$ .

<sup>b</sup> Groups as defined in Fig. 2.



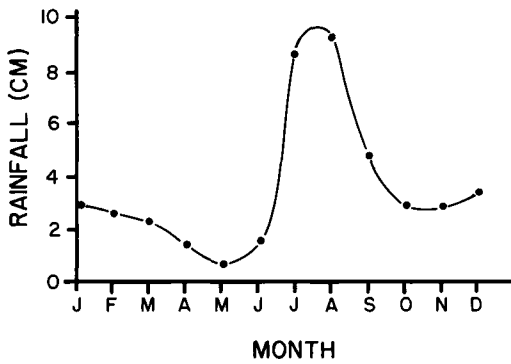


Fig. 4. The yearly pattern of rainfall for south-eastern Arizona, as illustrated by 33 yr of data from Portal, Arizona (Green and Sellers 1964).

ed that changes in food availability could account for seasonal shifts in habitat use by the warblers of southern Nevada, but he added that the temperature extremes in the lowlands during fall, rather than a decrease in food availability *per se*, could act to prevent use of such areas by physiologically intolerant species.

*Habitat distribution of migrants: ultimate factors.*—According to a recent school of thought, as long as it does not limit bird populations, food will be “loosely” exploited and will not be an important factor determining bird species presence and abundance. This idea has led to the development of the “checkerboard” model (Rotenberry and Wiens 1980a, Wiens 1981), in which an unfilled checkerboard represents an unsaturated breeding habitat and a subsection of the board represents one’s study plot. From year to year (or place to place within a year) variations in the kinds and abundances of species is very much a stochastic process, determined with about as much certainty by the composition and abundance of checkers within a subset of the checkerboard after the board has been given a vigorous shake. Thus, according to this model, one would not expect a close correspondence between bird population densities and current food resource levels—they would be independent (Fig. 5B). One would expect a close correspondence between bird and food abundance only during an ecological “crunch” (Wiens 1977) year, when food resource levels are unusually low relative to bird density (Fig. 5A). At the other extreme is the possibility that, even though food may not be limiting, competition still may exert a significant influence on bird community structure.

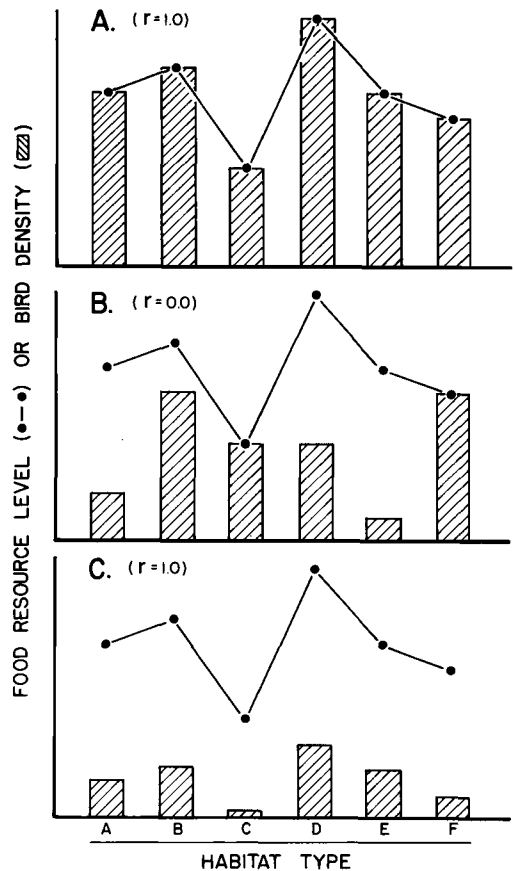


Fig. 5. Graphical representation of the possible relationships between the abundance of a predator (histograms) and its prey (connected dots) across a series of habitat types. (A) The numbers of predators may be limited by prey availability in each habitat, in which case there would be a close correspondence between predator and prey densities. (B) Food may not limit predator populations in most habitats, in which case competition for food will not occur and there will be a poor correspondence between predator and prey densities. (C) Food may not limit predator populations in most habitats, but competition through the economics of foraging will produce a close correspondence between predator and prey densities.

This idea follows directly from optimal foraging theory (Krebs et al. 1983), which assumes that competition is not an all-or-none phenomenon and that, although the strength of competition for food will vary with the degree to which it is limited, food is always limited to some extent and the economics of foraging will demand that birds distribute themselves non-

randomly in space. This results in a close match between food resource production and bird abundance, no matter what the absolute level of food availability (Fig. 5C).

The majority of bird species that passed through southeastern Arizona during migration was distributed significantly differently over the available habitat types in both spring and fall. One can, however, identify groups of these insectivorous species whose seasonal patterns of density and distribution are similar to one another but very dissimilar to members of other such groups. Despite these differences among groups, when considered together, the combined densities of the small, insectivorous bird species match insect densities across habitats within a season (Table 3) and across seasons within a habitat (Table 4) remarkably well. In other words, there are groups of species that respond more or less independently of one another, but when taken together provide a good fit to food resource production. Such a correlation would not be expected according to null models that assume independence between food availability and bird density. The distinction between the predictions that necessarily follow from competition-based, and alternative, null hypotheses cannot be overemphasized. If food resource-based competition is absent, then one would not expect a correlation between food resource availability and numbers of consumers over a variety of sites; instead, all birds would be expected either to go to the same site (i.e. where food is most readily available) because use of food by one individual would not decrease its availability to another, or to distribute themselves randomly with respect to food availability (null model). It is important to appreciate that a null model does not predict, for example, 10 times more birds in a site that has 10 times more food than another site; that would be the case only if the area were 10 times larger.

Alternative hypotheses that do generate predictions consistent with my results include the following: (1) A non-competition-based hypothesis that the populations of both predator (birds) and prey (arthropods) were affected similarly, but independently, by the same mortality factors (e.g. weather). This is most unlikely because the migratory birds are present for a matter of days, and the physical conditions that affect arthropod populations in Arizona undoubtedly are not the same conditions

that affect the migratory birds while they are farther north in summer or south in winter. (2) A non-competition-based hypothesis that birds settle in the best habitat (in terms of food availability) until some non-food-related resource (e.g. space) becomes scarce and forces new arrivals to settle in the next best habitat (based on food availability) until it too becomes marginal (in terms of some non-food resource), and so on. On the basis of food availability, the suitability of each habitat (site) would be identical for all birds in this case, but we would not expect a correlation between food levels and bird densities because the relative levels of the non-food-related resources (such as space) would not be expected to be exactly the same as the relative food levels among sites. (3) The non-competition-based hypothesis that each bird species is responding to the presence of a specific prey type. The significant correlation between food availability and bird abundance shown here may exist only because the diversity of prey is itself correlated with my measure of food availability. At this point I have no way to test whether a correlation exists between prey species diversity and my measure of food abundance, but I can test another prediction that necessarily follows from this hypothesis, i.e. that bird species richness is correlated with my measure of food availability. This prediction follows because a diversity of kinds of food would, according to this hypothesis, allow a diversity of bird species to occur in the habitat. Indeed, the correlation is significant ( $n = 14$ ,  $r = 0.61$ ,  $P < 0.05$ ), and such an explanation seems plausible on this basis. It remains for future research to determine whether high seasonal turnover in insect species underlies the high seasonal turnover in bird species within a site, as would also be predicted by this hypothesis. (4) The competition-based hypothesis that "crunch" conditions existed during each year and season that I was present in Arizona. This is unlikely, however, because each of the years was normal in terms of rainfall (Cody 1981: Table 1). Finally, (5) the competition-based hypothesis that food availability determines, in an ultimate sense, the distribution and abundance of the insectivorous bird species during migratory passage. Because the combination of all bird groups provided the best fit to resource availability, this hypothesis would necessitate the presence of interspecific, as well as intra-specific, competition to explain the organiza-

tion of bird communities at these times of the year.

By what mechanism would birds be able to achieve close matches to food resource levels through competitive adjustments, as would be necessitated by the fifth hypothesis above? According to the "crunch" hypothesis (Wiens 1977), under most environmental conditions it would be rare, if not impossible, for the kinds and densities of species to be able to match resource availability at any particular point in time because the individuals present at that point in time are the survivors or descendants of survivors that were able to "squeeze" through very different environmental conditions at some time in the past (Wiens 1977, Emlen 1981, Emlen and DeJong 1981). However, this view assumes that food levels vary unpredictably and that "... low-fecundity taxa such as many birds and mammals may be quite limited in their capacity to generate population growth sufficient to track variation in food resource levels at all closely" (Wiens 1977: 593). Whether or not the statistically significant but otherwise weak matches between food levels and bird densities demonstrated herein are closer than expected on the basis of the crunch hypothesis is not really clear. Nonetheless, the hypothesis plays down the importance of flexibility in foraging behavior (Alatalo 1980, Hutto 1981), which might enable birds to shift their habitat occupancy or densities within habitats to match current relative food-resource conditions, such as some woodpecker species seem to do within a year following a fire (Blackford 1955, Bock and Lynch 1970, Theberge 1976) or ducks may do from year to year (Nudds 1983). Terrill and Ohmart (1984) also describe a facultative migratory movement pattern of the Yellow-rumped Warbler that apparently is related to food availability.

The habitat shifts reported herein that correspond with shifts in food availability may result from birds being able to "test" several locations before settling in any one for their typical 4-6-day (unpubl. banding records) stopover period. Such resource tracking may be somewhat unique in that adjustments that "fine-tune" bird community composition to resource production may be much easier to accomplish during migration than during other times of the year. It also is possible that, although the relative food levels among habitats change dramatically between seasons, such change is

highly predictable and the migrants have been "programmed" to shift their habitat use accordingly. In either case, food availability could be of ultimate importance in producing such a close correspondence between the distribution and abundance of birds and their prey.

These results suggest the possibility that season-to-season or year-to-year differences in bird species composition and densities on a given plot (even breeding-season study plots) may be largely the result of nonrandom food assessment processes such as facultative settlement and migration (Serventy 1971, Ward 1971, Fretwell 1972, Sinclair 1978, Pulliam and Parker 1979, Wiens and Rotenberry 1981, Smith 1982) or "flyover" mechanisms (Nudds 1983). By this I do not mean to suggest that food-based competitive interactions are equally intense at all times and places. Rather, because competition is not an all-or-none phenomenon, the level of competitive interactions that does exist (mediated either directly or indirectly through relative food abundances among or within sites) may be responsible for much of the change that occurs in community structure from one place or time to another. More definitive explanations for the observed shifts in habitat use by these migratory birds must await testing of additional predictions that follow from the plausible alternative hypotheses presented above.

#### ACKNOWLEDGMENTS

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## 100 Years Ago in The Auk

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From "General Notes" (1885 Auk 2: 113-114):

"**Albinism.**—My attention was drawn to a note in the 'Oölogist' for April last, in which the writer gives his experience in albinism and asks for an explanation of these freaks of nature. In order to air my experience, and at the same time to give a probable cause, which I would like, for the sake of possible verification, other observers to look for in the future, is the object of the present note.

"True albinism is of course congenital, and is a condition in which the normal pigmentary matter is deficient in the system of the individual affected; in such cases the eyes are pink, and the skin with its appendages are white or nearly so. In the case of partial albinos, however, it is difficult; their condition can probably be explained by some circumstances occurring after birth which will account for the change in the color of the skin, such for instance as the case given by the writer in the 'Oölogist,' in which the skin had been injured on the back of a Swift, and next year the patch of white feathers indicated the situation of the injury. The same thing is

familiar in the case of the horse whose back or shoulder is galled by the harness; white patches appear, owing to lowered vitality of the injured part. These cases are familiar, but I wish to give possibly another cause acting in the same way, only more general. It is this. When a boy I shot among others a black squirrel peculiarly marked, it having a perfectly white tail, with some white about the head; on making a post mortem I discovered through a rent in the intestines a tape-worm about 20 feet in length. Did not wonder then that his head was gray. A few years after a partially white Red-winged Blackbird (*Agelaius phoeniceus*) was taken, which also contained two or three taenia; next a partial albino Mallard; then a Robin (*Turdus migratorius*) with a white head and mottled back and breast. All were mounted, and are now in my collection. Each of these had two or more tape-worms in their intestines. I am aware that birds, especially some species, are particularly obnoxious to tape-worms, and the above may have been merely coincidences; still it has been observed sufficiently often to make the fact suspicious as a cause of albinism.—G. A. M'CALLUM, *Dunnville, Ont.*"