Positive associations among riparian bird species correspond to elevational changes in plant communities

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This paper is dedicated to the memory of Dr. George Menkens

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Bird count data were used to characterize patterns of abundance and distribution among 20 bird species occupying streamside habitats of the central Rocky Mountains. Cluster analysis classified bird assemblages from 10 study plots into three elevational zones that varied in bird species diversity. Monotonic declines in total bird densities over the elevational gradient corresponded to spatial fluctuations in population levels of a few numerically dominant species. Of 190 correlations in counts of species pairs, 48 were significant, a much greater proportion than that expected by chance. Only 12 of the 48 associations were negative, suggesting that current competition may be less important than other processes in structuring these communities. Five suites of the positively associating species were detected using cluster, correlational, and variance analyses. Aggregated species responded to habitat ecotones by simultaneously increasing or decreasing in abundance. Group composition was dependent on patterns of species distribution among elevational zones, and on whether species were specialists or generalists in habitat use. Abundances of 19 species were related to five habitat gradients created by principal components analysis of habitat structure. A reasonable explanation for positive covariance in bird abundance is that species responded similarly to limiting resources that were associated with elevational zones.

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Les résultats de dénombrements d'oiseaux ont été utilisé pour caractériser l'abondance et la répartition de 20 espèces d'oiseaux des zones riparienes dans le centre des Montagnes Rocheuses. Les résultats d'analyses de groupements ont permis de classifier les regroupements d'oiseaux de 10 carrés échantillons situés dans trois zones d'altitudes différentes, distinctes par la diversité des espèces d'oiseaux. La diminution simultanée des densités totales d'oiseaux le long du gradient altitudinal correspond aux fluctuations spatiales des densités de population de quelques espèces dominantes. De 190 corrélations constatées entre des paires d'espèces, 48 étaient significatives, une proportion beaucoup plus grande que celle qu'on pourrait prévoir dans le cas d'une répartition aléatoire. Seulement 12 des 48 corrélations étaient négatives, ce qui indique que la compétition du moment est probablement moins importante que les autres mécanismes qui structurent la communauté. Cinq ensembles d'espèces en association positive ont été identifiés par des analyses de groupements, des analyses des corrélations et des analyses de variance. Les espèces rassemblées réagissaient aux écotones en augmentant ou en diminuant simultanément leur abondance. La composition des groupes était fonction de la répartition des espèces dans les zones d'altitudes différentes et aussi des habitudes spécialistes ou généralistes face à l'habitat. L'abondance de 19 espèces a été examinée en fonction de cinq gradients d'habitats révélés par une analyse en composantes principales. La covariance positive entre les abondances peut s'expliquer par la réaction semblable de diverses espèces à des ressources limitantes associées à l'altitude.

[Traduit par la rédaction]

Introduction

Patterns in bird communities are frequently sought using species co-occurrence data. Though random patterns of species co-occurrence are reported in some bird assemblages (e.g., Connor and Simberloff 1979; Simberloff and Connor 1981; Wiens and Rotenberry 1981), nonrandom distributions have been distinguished in others (e.g., Alatalo 1982; Gilpin and Diamond 1982; Diamond and Gilpin 1982; Gutzwiller and Anderson 1988). Processes that regulate bird populations and that ultimately structure bird communities include competition for limiting resources, predation or brood parasitism, habitat variation and extent, and changes in other extrinsic factors like weather and climate (e.g., Dhondt and Eyckerman 1980; Rotenberry and Wiens 1980*a*, 1980*b*. Grant and Grant 1982; Dunning and Brown 1982; Ambuel and Temple 1983; Martin 1988*a*, 1988*b*). Underlying causes of community structure are often inferred from observed patterns of species coexistence, but competitive processes are difficult to detect using co-occurrence data (Rosenzweig et al. 1985; Hastings 1987; Cale et al. 1989).

Because positive species associations are more common than inverse relationships (Schluter 1984; Brawn et al. 1987; Mountainspring and Scott 1985), verifying and interpreting patterns of species aggregations should be as meaningful as detecting competitive interactions. In bird populations, many species positively covary in abundance when they track shared resources that vary in time or space (Dunning and Brown 1982; Hutto 1985; Gutzwiller and Anderson 1988). To predict abundance and quality of resources like food, nest sites, and cover, as well as likelihood of predation, competition, or reproductive success, birds presumably use habitat features as environmental cues (Hildén 1965; Cohen 1967; Nillson 1984). Bird communities are often organized along gradients of habitat structure (e.g., Karr and Roth 1971; Smith 1977; Roth 1979), and vegetational changes at ecotones or edges limit populations of some species (e.g., Wegner and Merriam 1979; Kroodsma 1984; Terborgh 1985; Yahner 1988). Examining numerical responses to habitat transitions in clusters of species may clarify overall patterns in species diversity and community composition (Kolasa 1989). Groups of species that respond as individual units to habitat changes are known as indicator guilds or response guilds (Verner 1984; Knopf et al. 1988). Identifying response guilds may have utilitarian value if trends in guild abundance reflect environmental changes due to

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resource-management practices (Severinghaus 1981; Verner 1984; but see Landres et al. 1988).

In this study, I distinguished habitat response guilds in riverbank bird communities by comparing patterns of species habitat occupancy with patterns of species co-occurrence. I used bird count data to characterize relationships in abundance and distribution among species and to identify species responses to vegetational gradients and habitat ecotones along an elevational gradient. Trends in counts of individual species and in pooled abundances of positively associating species were used to interpret changes in species diversity. I did not test for competitive interactions or infer causal mechanisms from patterns of species coexistence (see Cale et al. 1989), but after discounting implausible processes, I proposed factors that could produce observed patterns in bird assemblages.

I tested the general null hypotheses that (*i*) spatial fluctuations in counts of individual bird species were unrelated to zonal transitions in plant communities, (*ii*) abundances of pairs of bird species were not associated, (*iii*) counts of multiple species did not covary, (*iv*) species coexistence patterns were unrelated to trends in habitat structure, and (*v*) species composition in sets of covarying species were independent of patterns of species specialization in habitat use. Abundance data for 20 bird species from 10 streamside areas were used to test the hypotheses. Study areas were classified into three elevational zones based on differences in habitat structure (Finch 1987, 1989*a*). Habitat generalists and habitat specialists were identified beforehand by comparing structural variability in habitats used by each of the 20 species with variability in randomly sampled habitats (Finch 1989*a*).

Study areas

Study plots were established in riverine habitats in, or within 16 km of, the Medicine Bow National Forest of southeastern Wyoming. Ten 8.1-ha plots, staked and flagged as rectangular grids, were distributed over an elevational gradient ranging from 2050 to 2990 m. Study plots encompassed a continuum of riparian plant species and vegetational communities, but excluded edge and upland habitats.

The lower-elevation (2050–2250 m) plots were located on wide foothill floodplains dominated by narrowleaf cottonwood (*Populus angustifolia*), and were surrounded by mixed grass prairie and large water corridors. Understories at lowland sites were composed of a variety of tree and bush willow species (*Salix* spp.). Mid-elevation (2290–2530 m) plots were established along mountain creeks and were typically bordered by sagebrush (*Atriplex tridentata*), grassland, and lodgepole pine (*Pinus contorta*) forest. Cottonwoods disappeared and aspen (*P. tremuloides*) occurred in small isolated groves within bush willow communities. New dominant willow speices were added to communities, and other willows were locally present (*S. barclayi*, *S. ligulifolia*, and *S. candida*). At high elevations (2590–3000 m), *S. planifolia* was found in monocultures or mixed with *S. wolfii*. These subalpine willow parks were interspersed with wet or boggy meadows and surrounded by mixed stands of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*).

Methods

Sampling bird populations and habitats

Birds were spot-mapped on each study plot from mid-May through early July of 1982, 1983, and 1984. Each study plot was visited a minimum of eight times each year, and each visit lasted from 2 to 4 h. Three observers, each assigned to a set of three or four plots, recorded all birds seen or heard each year on maps of each study grid. A minimum of three grouped observations on each map defined a territory. Edge clusters were counted as belonging to the plot if more than half of the observations were recorded within or on the plot boundaries. Birds recorded once or twice were considered to be visitors and were not included in the analyses. Abundance of each territorial species and of all species combined is reported as the number of territories observed on an 8.1-ha area. Abundance of Brown-headed Cowbirds was estimated from spot-map observations and brood parasitism data and is reported as numbers of male–female units for comparison with other species. Species richness is the number of species known to be nesting on a study plot, based on territorial data and results of nest searches.

To improve the accuracy of spot-map counts, intensive 2-h nest searches were conducted immediately following each mapping visit and on alternate days. Nest searches improved the probability of (*i*) distinguishing multiple avian pairs in a cluster of mapped observations, (*ii*) determining the status of edge territories, and (*iii*) distinguishing between nesting birds and floaters. Approximately 50 h were spent in nest search effort per plot per year. To increase the chances of detecting floating birds and surreptitious territorial pairs, I also netted and color-banded birds on each plot in 1984, using ten 2.1 × 10.7 m nets, each with a mesh size of 1.3 cm. Nets were monitored on each plot from 06:00 to 19:00 for 5 consecutive days. Netting and banding data were used to substantiate the presence of pairs in cases where mapping results were inconclusive.

Habitat structure was sampled in July and August of 1982 at 40 random locations on each of the 10 bird-count grids ($n = 400$ samples). Sampling sites were chosen by selecting grid coordinates from a table of random numbers. At each sampling location I measured 34 structural habitat variables by means of a point-centered quarter sampling procedure (Finch 1989*a*). Habitat features were sampled by dividing each location into four quadrants oriented in the cardinal compass directions. Invariant and redundant variables were deleted, reducing the data set to 19 variables for statistical analyses. Pearson product-moment correlations were used to determine relationships between habitat variables. Within pairs of highly correlated variables I retained the variable that had the sampling distribution closest to normality. Descriptions and sampling methodologies for the remaining 19 variables are presented in Table 1. To improve normality and adhere to statistical assumptions, all tests used log-transformed data. Values are reported for backtransformed data for ease of interpretation.

Data analysis

Bird assemblages and zone variation

I applied Pearson correlations to compare numbers of breeding species and numbers of territories with plot elevation. To determine if distributional patterns of bird species corresponded to zones of habitat structure, a cluster analysis was performed on a species × plot (20 × 10) matrix of mean abundances. Groups of plots were formed using the UPGMA procedure (average linkage between groups) of amalgamating cases, based on the arithmetic average of Euclidean distances between pairs of abundances in different clusters. To determine the "correct" number of clusters, I applied Mojena's stopping rule No. 1 (cited in Aldenderfer and Blashfield 1984), which specifies that the number of clusters prior to a prominent jump in the fusion coefficient is the probable solution. The results of this rule were tested using Wishart's application of the *t*-statistic (cited in Aldenderfer and Blashfield 1984). The number of clusters was corroborated by examination of an icicle plot of cluster solutions (Norusis 1988).

Twenty migratory species were included in analyses. Bird species were excluded if they did not nest or defend territories within study areas; if their rarity resulted in unreliable counts (e.g., species at the boundaries of their ranges); if their taxonomic dissimilarity generated trivial comparisons (e.g., duck versus warbler); or if their associations with riparian habitats were spurious (e.g., species whose occurrences depended exclusively on the presence or absence of upland habitats). Because counts of migratory species differed among plots ($P < 0.05$) but not among study years ($P > 0.05$) (Finch 1989*b*), plot abundances were averaged across years for use in all computations. Lack of significant year-to-year fluctuations in abundance has previously been reported in western migrants but is less common in permanent

TABLE 1. Structural variables used in analysis

Variable		Sampling method
CANHT	Canopy height	Mean height (m) of nearest trees (or shrubs if no trees in sample) in each quadrant
TDEN	Tree density	Number of trees >3 cm DBH in 100 m^2
CANCOV	Canopy cover	Canopy closure (%) measured with ocular tube
SHBA	Shrub basal area	Mean basal area (m^2) of nearest shrubs (≥1 m tall) in each quadrant
SCHD	Shrub crown diameter	Diameter (cm) at breast height of nearest shrubs (≥1 m tall) in each quadrant
SHHT	Shrub height	Mean height (m) of nearest shrubs in each quadrant
SHDIS	Shrub dispersion	Mean distance (m) to nearest shrub (≥1 m tall)
VFD1	Vertical foliage density in grass–forb layer	Mean number of vegetation contacts falling against vertical rod in <0.3-m height interval
VFD2	Vertical foliage density in small shrub layer	Same as VFD1, but in 0.3- to 1-m height interval
VFD3	Vertical foliage density in midcanopy layer	Same as VFD1, but in 1- to 2-m height interval
VFD4	Vertical foliage density in upper layer of understory	Same as VFD1, but in 2- to 9-m height interval
VFD5	Vertical foliage density in overstory layer	Same as VFD1, but in >9-m height interval
EVH	Effective vegetation height	Height at which a 20 cm wide board is >90% obscured by vegetation at a distance of 5 m
WILLOW	Percent willow	Proportion of shrub species in distance sample that are willows
FRUIT	Percent fruiting shrubs	Proportion of shrub species in distance sample that bear drupes
BARE	Percent bare ground	Percentage of surface that is bare or covered with litter, measured with ocular tube
GRASS	Grass–forb ground cover	Percent cover of grasses and forbs measured with ocular tube
WATER	Water cover	Percent cover of water measured with ocular tube
COVER	Woody vegetation cover	Percent cover of woody plants (<1 m tall), saplings, and downed logs measured with ocular tube

NOTE: DBH, diameter at breast height.

residents exposed to harsh overwintering conditions (Raphael and White 1984; Hejl and Beedy 1986).

Habitat structures were categorized into three elevational zones (Finch 1989*a*): (1) three cottonwood–willow sites ranging from 2050 to 2250 m; (2) three sites with mixed shrub willow ranging from 2290 to 2530 m; (3) four subalpine willow sites ranging from 2590 to 2990 m. To verify habitat variation among zones, a nested-design analysis of variance was performed on 19 habitat attributes to determine and adjust for the effects of plot variation within elevational zones before evaluating zone variation. Using plots as replicates within zones, I used multivariate analysis of variance (MANOVA) to determine if zones differed in overall habitat structure. To determine if patterns of species distribution were related to breaks in plant communities, I assessed overall and pairwise differences in mean counts among zones by means of one-way analysis of variance (ANOVA) and least significant differences (LSD) test.

Species–species associations

To detect groups of covarying species, a plot species matrix of bird abundances was entered into a cluster analysis (single linkage method). To pinpoint major sources of variation in total bird densities, I regressed pooled species abundances in groups of covarying species with total abundance by means of stepwise multiple regression. The coefficient of determination, R^2, was computed to measure goodness of fit of the linear model, and ANOVA was used to test the hypothesis of no linear relationship. Linear regression was an appropriate model because standardized residuals were unrelated to predicted values based on examination of scatterplots, and because outliers were absent. I calculated simple correlations to determine if overall abundance fluctuated with counts of specific species. To determine if numerically dominant species influenced trends in total density, effects of their population fluctuations were removed by computing partial correlation coefficients (r_p) between residual total abundance and elevation.

Relationships between pairs of species were assessed using Pearson correlation coefficients. I compared confidence limits of observed percentages of significant correlations with those expected by chance to test the null hypothesis of no association between pairs of species. Patterns of association among sets of species were confirmed by organizing significant positive correlations of species pairs into the groups assigned by cluster analysis of species abundances. χ^2 analysis was used to test the null hypothesis that the proportion of positive correlations for all possible pairs in species groups was equal to that calculated for all 190 species pairs. I used contingency tables to test whether species composition in cluster groups was independent of avifaunal composition by zone. The numbers of species shared between each zone and cluster were entered in the analysis.

To test the null hypotheses that species in clusters do not covary

among plots, I used the variance test suggested by Schluter (1984). The index of species association in plots is $W = NV$, where N is the number of plots and V the ratio of the estimated variance in total number of individuals per sample (species pooled by cluster) and the sum of the variances of individual species densities. A value greater or less than 1 indicates that species abundances covary positively or negatively across plots, respectively. I followed McCulloch's (1985, eq. 6) recommendation to use the F-ratio for determining the critical values for rejecting the null hypothesis of no association.

Species–habitat associations

I applied principal components analysis with varimax rotation to the matrix of 400 samples × 19 habitat variables to determine trends in plant community structure. High correlations of habitat variables with the principal component (PC) scores from the reduced set of PCs were used to interpret each component. To determine if abundances of different bird species varied with specific habitat axes, simple correlations were calculated between the factor scores of each component (eigenvalues >1.0) averaged by plot, i.e., 40 random vegetation samples per plot, and the plot abundances of each of the 20 species.

Species that use a broad array of habitat resources may differ in abundance and distribution from habitat specialists (Brown 1984; Bock 1987). I previously described the 20 species along this elevational gradient as specialists or generalists on the basis of variability in habitat use (Finch 1989*a*). In this study I used χ^2 analysis to determine if the frequency distributions of specialists and generalists differed by cluster groups of covarying species.

Results

Bird species diversity and habitat zones

A total of 100 bird species was observed during the 3-year study period. Forty species were found nesting or defending territories within study plot boundaries; 24 species foraged or rested occasionally (e.g., raptors) or frequently (shorebirds, gulls, waterfowl, swallows) in the study areas; 30 species were migrants or edge visitors from upland habitats; and 6 species were considered unusual in southeastern Wyoming. Of the nesting species, 5 were ducks, rails, and sandpipers, which were too dissimilar in taxon, morphology, and behavior to be compared with other community members, and 15 were rare, supplying insufficient population samples (≤2 territories/10 plots per year) for trend analysis.

Species richness and bird abundance per plot varied from a high of 20 nesting species and 114 nesting pairs at lower elevations to a low of 3 nesting species and 23 pairs at high elevations (Fig. 1). Plot elevation accounted for 80% of the variation in mean species richness (of 100 observed species) ($r = 0.89$, $P < 0.001$) and 78% of the variation in total bird abundance ($r = 0.88$, $P < 0.001$). Species richness and bird abundance fluctuated markedly and in synchrony at two zonal breaks along the elevational continuum (Fig. 1). Reduction and ultimate loss of a tree overstory separated mid-elevation shrublands from foothill habitats, and reduction in shrub diversity and increase in woody ground cover explained the break between montane shrublands and subalpine parks (Table 2). In all, nine habitat features varied among zones after within-zone variation was adjusted for by means of nested-design ANOVA (Table 2). MANOVA indicated that zones differed in overall patterns of vegetation structure (Wilks' $\lambda = 3.4 \times 10^6$, $P < 0.01$).

Zonal differences in bird species richness and bird abundances were related to patterns of species responses to these two ecotonal breaks in plant communities. Cluster analysis of the species × plot matrix of bird densities suggested three clusters, each composed of three to four study plots in which

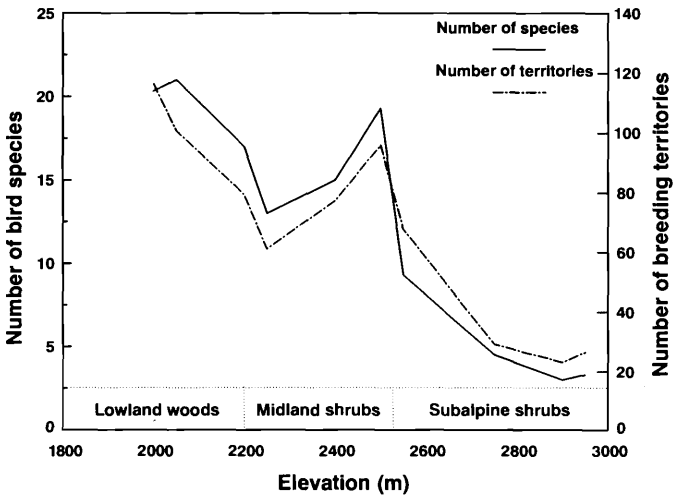

FIG. 1. Trends in numbers of bird species and numbers of territories across a riparian elevational gradient.

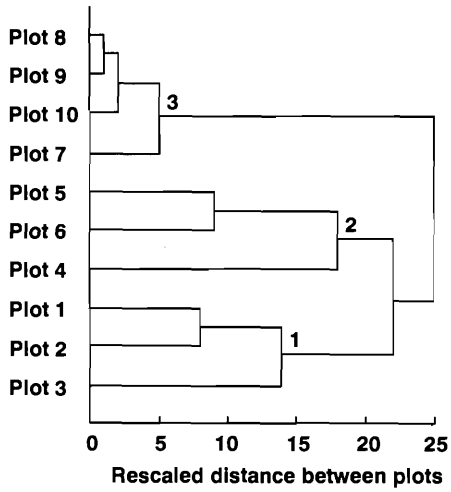

FIG. 2. Cluster analysis of 10 study plots based on Euclidian distances (rescaled from 1 to 25) between abundances of 20 common bird species. Plots are numbered in elevational order from 1 through 10. Bird assemblages in three riparian zones were classified as follows: 1, lowland woods; 2, mid-elevation shrublands, 3, subalpine shrublands.

species composition and numbers of birds were similar (Fig. 2). Cases (plots) splintered off individually, starting with the four-cluster solution. A three-cluster solution was confirmed using Mojena's stopping rule (Wishart's test: $t = 3.78$, df = 8, $P < 0.01$). The bird assemblages at the 10 plots clustered into the same three elevational zones that were identified beforehand and confirmed by tests of zonal variation in habitat structure.

Species responses to habitat breaks

Of 20 selected species, the abundance levels of 15 varied among zones ($P < 0.05$) (Table 3). Pairwise differences in counts of four additional species were identified using LSD tests. Mean counts of American Robin, Yellow Warbler, and Song Sparrow were dissimilar in all pairwise comparisons between zones (Table 3), with highest numbers of robins and warblers in lowland areas and peak numbers of sparrows in the intermediate zone. The Mourning Dove, Western Wood-Pewee, and House Wren, species observed primarily in

TABLE 2. Results of nested-design ANOVA testing the effects of site variation within elevational zones, and zone variation of 19 selected vegetation features

Habitat feature[a]	Elevational zone			Significance level[b]	
	Low	Middle	High	Plot within ZONE effect	ZONE effect
CANHT (m)	8.9±0.3	2.1±0.1	1.5±0.1	***	**
TDEN (no./100 m^2)	49.0±6.0	5.0±0.1	1.0±0.0	***	***
SHBA (m^2)	0.2±0.0	0.4±0.1	0.2±0.0	***	ns
SHCD (cm)	131.0±7.5	154.9±7.9	116.4±6.3	***	ns
SHHT (m)	2.0±0.1	2.1±0.1	1.5±0.1	***	ns
SHDIS (m)	5.7±0.6	5.1±0.7	4.2±0.3	***	ns
VFD1 (no. of hits)	2.0±0.1	2.8±0.2	2.9±0.1	***	ns
VFD2 (no. of hits)	0.5±0.1	1.3±0.1	1.7±0.1	***	ns
VFD3 (no. of hits)	0.2±0.0	0.8±0.1	0.3±0.1	***	ns
VFD4 (no. of hits)	1.0±0.1	0.5±0.1	0.0±0.0	ns	***
VFD5 (no. of hits)	0.5±0.1	0.0±0.0	0.0±0.0	ns	***
CANCOV (%)	54.8±3.3	20.1±2.7	1.0±6.0	ns	***
COVER (%)	13.5±1.7	24.3±2.5	57.6±4.2	***	*
WILLOW(%)	25.7±2.8	78.6±2.5	90.7±1.8	***	**
EVH (m)	0.3±0.0	0.5±0.1	0.6±0.0	***	ns
FRUIT (%)	54.5±3.2	14.1±2.0	9.1±1.8	***	*
BARE (%)	34.7±3.0	6.4±1.4	4.9±1.1	***	*
GRASS (%)	51.1±3.1	65.5±3.0	42.7±5.1	***	ns
WATER (%)	1.3±0.8	3.9±1.4	4.5±1.1	***	ns

NOTE: Values for variation within elevational zones are given as mean ± SE.
[a]For definitions of habitat features see Table 1.
[b]Based on nested-design MANOVA evaluating differences among sites and zones.
*, $P < 0.1$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

TABLE 3. Significant differences in counts of 20 bird species across three habitat zones, based on results of ANOVA and pairwise comparison tests

		P	Comparisons
Mourning Dove (MODO)	*Zenaida macroura*	0.017	*ac*
Broad-tailed Hummingbird (BTHU)	*Selasphorus platycercus*	0.001	*ab*
Western Wood-Pewee (WWPE)	*Contopus sordidulus*	0.066	*ac*
Willow Flycatcher (WIFL)	*Empidonax traillii*	0.082	*bc*
Dusky Flycatcher (DUFL)	*Empidonax oberholseri*	0.111	*b*
Tree Swallow (TRSW)	*Tachycineta bicolor*	0.161	*c*
House Wren (HOWR)	*Troglodytes aedon*	0.000	*ac*
Veery (VEER)	*Catharus fuscescens*	0.079	*bc*
American Robin (AMRO)	*Turdus migratorius*	0.001	*abc*
Gray Catbird (GRCA)	*Dumetella carolinensis*	0.234	
Warbling Vireo (WAVI)	*Vireo gilvus*	0.020	*bc*
Yellow Warbler (YEWA)	*Dendroica petechia*	0.000	*abc*
MacGillivray's Warbler (MGWA)	*Oporonis tolmiei*	0.001	*ab*
Common Yellowthroat (COYE)	*Geothylpis trichas*	0.118	*ab*
Wilson's Warbler (WIWA)	*Wilsonia pusilla*	0.034	*bc*
Song Sparrow (SOSP)	*Melospiza melodia*	0.000	*abc*
Lincoln's Sparrow (LISP)	*Melospiza lincolnii*	0.030	*c*
White-crowned Sparrow (WCSP)	*Zonotrichia leucophrys*	0.005	*bc*
Brewer's Blackbird (BRBL)	*Euphagus cyanocephalus*	0.150	*b*
Brown-headed Cowbird (BHCO)	*Molothrus ater*	0.000	*bc*

NOTE: Pairwise comparisons were computed using the least significant difference range test. Significant differences ($P < 0.05$) between two elevational zones are indicated as follows: *a*, zone 1 vs. zone 2; *b*, zone 2 vs. zone 3; *c*, zone 1 vs. zone 3.

lowland woods, differed in abundance between the lowland and middle zones, and between the lowland and highland zones. Most frequent in mid-elevation areas, the Broad-tailed Hummingbird, MacGillivray's Warbler, Common Yellowthroat, Dusky Flycatcher, and Brewer's Blackbird varied in abundance between the middle zone and other zone(s). The Willow Flycatcher, Warbling Vireo, Veery, Brown-headed Cowbird, and Tree Swallow, species absent from subalpine sites, had disparate counts between the subalpine zone and one or more lower zones. Common inhabitants of highland areas, the Wilson's Warbler, White-crowned Sparrow, and Lincoln's Sparrow also differed in abundance between subalpine habitats

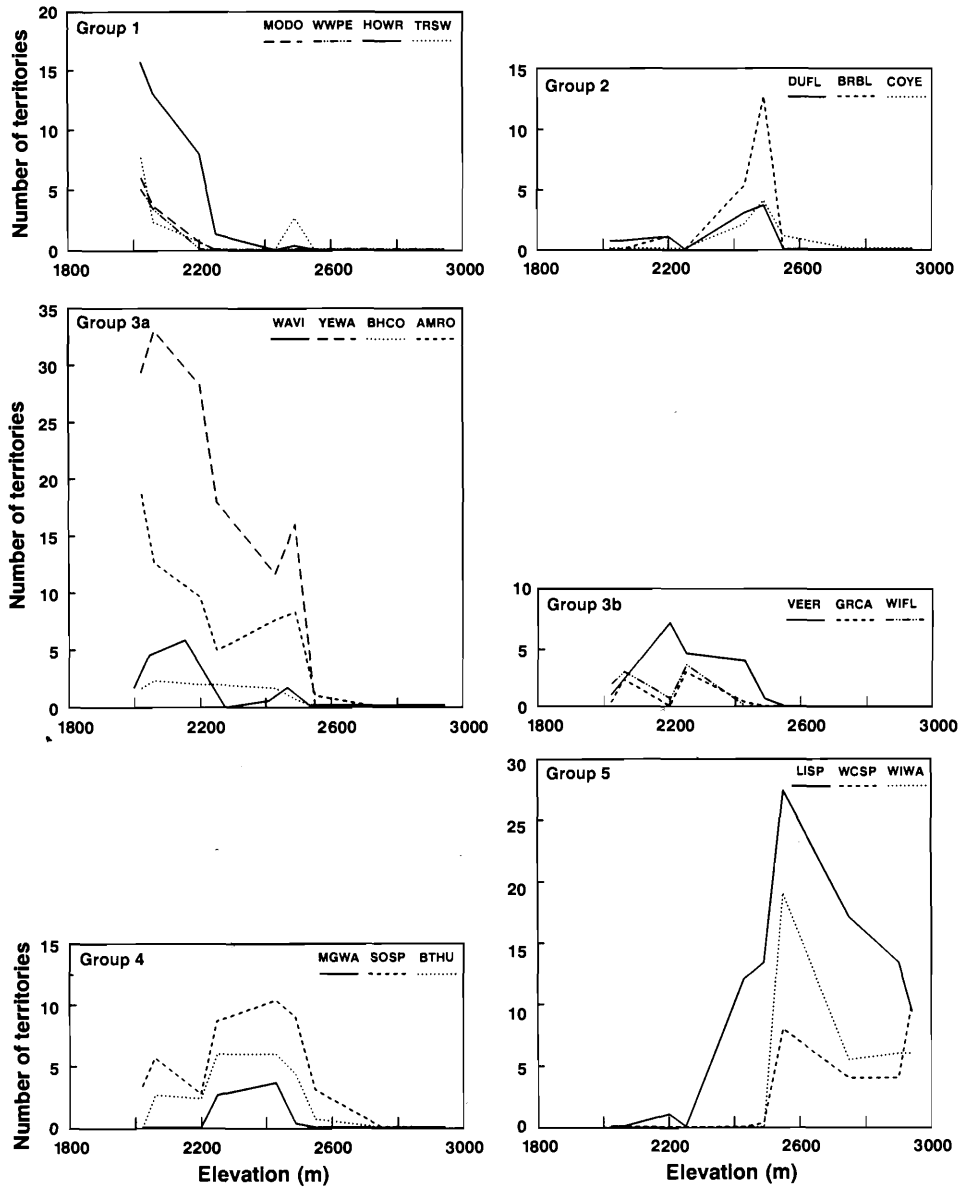

FIG. 3. Population levels of 20 bird species at 10 study plots positioned along an elevational grade. Trends in five groups of covarying species are depicted. Species in group 3 were divided into *a* and *b* to simplify the illustration. See Table 3 for explanation of abbreviations of species names.

and lower zones. Only the Gray Catbird exhibited no strong preference for any one elevational zone, being equally distributed at low densities across the lower and middle zones.

Groups of species associations

Five groups of co-occurring species were generated using cluster analysis of 20 species. Group composition was dependent on patterns of species distributions among zones ($\chi^2 = 17.8$, df = 8, $P = 0.023$), and on whether species were specialists or generalists in habitat use ($\chi^2 = 11.53$, df = 4, $P = 0.021$).

Group 1 comprised the Mourning Dove, Western Wood-Pewee, House Wren, and Tree Swallow, habitat generalists that inhabited riparian woodlands. Loss of these species corresponded to decline in density of overstory trees with increase in elevation (Fig. 3). Variation in abundance of all bird species was positively correlated with decreased density in this group ($r = 0.74$, $P = 0.014$) and with population reductions in each of the four species ($P < 0.05$, but $P > 0.01$).

Group 2 was composed of the Dusky Flycatcher, Brewer's Blackbird, and Common Yellowthroat, species previously identified as habitat specialists because their use of habitats differed from the availability of random habitat resources (Finch 1989*a*). These species nested primarily in mid-elevation habitats with dense shrub foliage, reaching peak abundance on the highest plot of the mid-elevation zone (Fig. 3). Group 4 also contained species that reached maximum abundance in mixed shrub habitats, but these species were also found in foothill woodlands (Fig. 3). The Song Sparrow was a habitat generalist, MacGillivray's Warbler was a specialist, and the Broad-tailed Hummingbird had mixed strategies (Finch 1989*a*). Variation in the abundance of all bird species was not related to pooled densities of species in group 2 ($r = 0.39$, $P = 0.269$) or group 4 ($r = 0.43$, $P = 0.212$), or to abundances of any individual species within these groups ($P > 0.05$).

The seven species comprising group 3 were Willow Flycatcher, Yellow Warbler, Brown-headed Cowbird, American Robin, Veery, Gray Catbird, and Warbling Vireo. These

TABLE 4. Five groups of covarying bird species classified by cluster analysis, and correlations of abundances that differed between pairs of species

Group	Species[a]																			
1	MODO		+	+	+					+		+								
1	WWPE	1		+	+					+		+								
1	HOWR	1	1		+					+		+						−		
1	TRSW	1	1	3								+								
2	DUFL	4	4	6	4		+	+								+				
2	BRBL	6	6	8	6	1		+												
2	COYE	5	5	7	4	1	1													
3	WIFL	2	2	4	2	3	6	4		+	+			+				−	−	
3	YEWA	3	4	5	4	4	7	7	1		+	+	+		+			−	−	−
3	BHCO	3	3	4	3	2	5	4	1	1		+	+	+	+		+	−	−	−
3	AMRO	2	3	4	2	3	6	5	2	2	1							−	−	
3	VEER	5	5	6	6	4	6	5	2	3	1	4							−	
3	GRCA	2	2	5	4	3	6	4	1	2	1	2	1							
3	WAVI	3	3	5	3	1	5	3	3	1	1	1	2	4						
4	MGWA	5	5	7	5	3	4	2	3	5	2	5	3	2	4		+	+		
4	SOSP	6	6	7	6	1	5	2	2	6	1	5	4	1	4	2		+		
4	BTHU	6	6	7	6	1	5	2	3	6	2	5	3	2	4	1	1			
5	LISP	8	8	8	8	7	6	4	8	8	8	8	8	8	8	7	8	8		+	+
5	WCSP	7	6	8	7	6	7	6	6	8	7	8	7	6	7	6	8	7	5		+
5	WIWA	8	7	8	8	7	8	7	7	8	8	8	8	7	8	7	8	8	5	2	

NOTE: Positive (+) and negative (−) correlations ($P < 0.05$) between species abundances are indicated in the upper half of the table. Numbers in the lower half of the table are rank values of Euclidian distances between species. The value 1 indicates greatest similarity and 8 indicates least similarity. Actual distances for each ranking are as follows: 1, <2.28; 2, 2.28–2.67; 3, 2.67–3.20; 4, 3.20–3.73; 5, 3.73–4.47; 6, 4.47–5.92; 7, 5.92–6.93; 8, >6.93.

[a]For explanation of abbreviations of species names see Table 3.

species crossed zonal boundaries, being most abundant in lowland woods but also common in mid-elevation shrublands (Fig. 3), with the exception of the Warbling Vireo, whose distribution in shrublands was limited to isolated aspen bosks. Most species within this group were generalists in habitat use, but the Gray Catbird was a specialist, and the Yellow Warbler and Willow Flycatcher varied in extent of specialization, depending on observational scale and zone (Finch 1989*a*). In a stepwise regression of abundances of all groups with total bird density, only group 3 was selected. Decline in its pooled bird counts explained 71% of the reduction in total bird numbers over the elevational grade ($R^2 = 0.71$, $P = 0.002$). Total numbers were most highly correlated with densities of two numerically dominant species, the American Robin ($r = 0.92$, $P < 0.001$) and Yellow Warbler ($r = 0.83$, $P = 0.003$). Significant relationships between total abundance and elevation disappeared after population effects of either robins ($r_p = -0.19$, $P = 0.605$) or Yellow Warblers ($r_p = -0.21$, $P = 0.588$) were removed.

Lincoln's Sparrow, White-crowned Sparrow, and Wilson's Warbler, habitat specialists belonging to the fifth cluster group, were most abundant in subalpine habitats with dwarf shrub willow and boggy meadows. Lincoln's Sparrow, the only species in this group to traverse zones, numerically dominated subalpine riparian avifaunas and was also present in mid-elevation and lowland zones (Fig. 3). Overall bird abundance was not correlated significantly with changes in counts of individual species in group 5 ($P > 0.05$), or with pooled grouped densities ($r = 0.55$, $P = 0.098$).

Using Pearson correlations to detect associations among pairs of species, 48 of 190 (25.3%) correlations between abundances of species pairs were found to be significant (Table 4). Only 10 of 190 correlations were expected to be significant by chance alone at the α level of 0.05. Confidence limits of the observed percentage of significant correlations (19.2–31.6%) did not overlap those of the expected percentage (6.2–15.0%), so the difference between observed and expected was significant. Of 48 significant correlations, 12 (25%) were negative and 36 (75%) were positive.

When significant correlations of species abundances were arranged in the pattern produced by cluster analysis, it was evident that most species pairs within each cluster were positively correlated (Table 4). The proportion of positive correlations within species groups was much greater than that calculated for all possible species pairs ($\chi^2 = 43.15$, df = 1, $P < 0.0001$). The index of species association, W, exceeded the upper critical limits for all five clusters, indicating that multiple species in each aggregation covaried in significant positive directions (Table 5). Fluctuations in counts of Yellow Warbler and American Robin were also positively correlated with trends in group 1 species, but mean Euclidian distance was greater (i.e., trends were less similar) in this aggregation than within group 1 ($t = 4.26$, df = 11, $P < 0.005$).

A group of negatively associated species was also identified in the arrangement of correlations by distance (Table 4). Specifically, abundances of species in group 3 were inversely correlated with abundances of species in group 5. With the exception of Lincoln's Sparrow, the distributions of species in group 5 rarely if ever overlapped those in group 3. Species in group 5 foraged and nested on or near the ground and selected plots with habitats that were structurally simple, whereas species in group 3 selected plots with tall shrubs or trees and employed a variety of fly-catching, foliage-gleaning, and ground-foraging strategies. Disparity in macrohabitat choice

TABLE 5. Variance values used in association tests, indexes of species associations (W),[a] and upper critical values ($\alpha = 0.05$) for testing the null hypothesis that species do not covary in each of five cluster groups

Group	No. of species	S_T^2	$\Sigma\sigma_i^2$	W	Upper critical limit	Null hypothesis
1	4	145.3	50.8	28.6	17.2	Rejected
2	3	45.4	20.8	21.8	16.3	Rejected
3	7	609.4	233.3	26.1	17.9	Rejected
4	3	57.6	23.6	24.4	16.3	Rejected
5	3	1094.9	134.2	91.2	16.3	Rejected

[a]$W = N(S_T^2/\Sigma\sigma_i^2)$, where S_T^2 is the observed variance in the total number of individuals per plot, $\Sigma\sigma_i^2$ is the sum of variances of individual species densities, and N is the number of plots (Schluter 1984).

TABLE 6. Principal components analysis of 19 vegetation variables, resulting in five significant components describing trends in habitat structure across study plots

Principal component	Eigenvalue	Percentage of variance	Interpretation of trend toward positive extreme
1	4.8	25.2	Lower elevation, higher canopy height and tree density; open, diverse shrub understory with less willow
2	2.7	14.2	Greater shrub size
3	2.3	12.0	Greater shrub density and cover, and greater foliage density of low understory
4	1.5	7.8	Greater foliage density at midcanopy
5	1.1	5.9	Higher herbaceous foliage density and ground cover, dryer sites

also explains the negative relationship between cavity-nesting House Wrens (group 1) and shrub-associated Lincoln's Sparrows (group 5). The 12 negative correlations between species were therefore related to macrohabitat differences in occupancy patterns.

Relationships between habitat gradients and bird populations

Five principal components (PC1–PC5) explained 65.1% of the structural variation in randomly sampled habitat (Table 6). The mean plot scores for PC1 were inversely correlated with elevation ($r = -0.90$, $P < 0.01$). PC1 represented a gradient of decreasing canopy height and tree density with increase in elevation (Table 6). Abundances of eight species, all members of cluster groups 1 and 3, were positively associated with PC1 (Table 7), indicating greater affinity for lowland plots with high tree density. Counts of species in group 5 were inversely correlated with PC1.

No species counts were significantly correlated with PC2, a gradient in shrub size. Counts of American Robin, Brown-headed Cowbird, and Yellow Warbler, and of all four species in group 1, were inversely related in distribution to PC3, a shrub density and cover gradient. Negative correlation with PC3 indicated affinity for plots with more open understory. In contrast, the distributions of Wilson's Warbler, Lincoln's Sparrow, and White-crowned sparrows were positively correlated with increasing shrub density and foliage density of low understory.

PC4 was positively correlated with spatial fluctuations in abundance of nine species that belonged to groups 2, 3, and 4 (Table 7). Positive correlation with PC4 signified greater dependence on plots with high foliage density at midcanopy or shrub height. The Gray Catbird, the only species with population levels that did not vary along any habitat gradient, loaded highest on PC4. Species in group 5 were inversely related to PC4.

Species more abundant at dryer plots with increased ground cover were positively correlated with PC5. Three of these species, the Dusky Flycatcher, Brewer's Blackbird, and Warbling Vireo, occupy a variety of upland habitats far from streams, and thus their distributions may be independent of the availability of water or resources associated with moisture. In contrast, the Common Yellowthroat, a close affiliate of marshes and beaver ponds on dryer plots, may load high on PC5 because it forages and nests in dense low cover.

Discussion

Species diversity and community changes

Numerical changes in bird populations at the group or guild level explained overall changes in species richness and bird abundance along habitat gradients. Monotonic declines in pooled bird densities over the elevational grade paralleled spatial fluctuations in population levels of two numerically dominant species, American Robin and Yellow Warbler. Once their population effects were partialled out, the relationship between overall bird abundance and elevation disappeared. The American Robin and Yellow Warbler belonged to a cluster of covarying species that crossed zonal boundaries and were identified in an earlier study as habitat generalists. Changes in bird abundance in this dominant group explained 71% of the variation in total bird densities.

In addition, community changes in numbers of bird species at the boundaries of elevational zones corresponded to addi-

TABLE 7. Correlations of bird abundance with five habitat gradients[a]

Species	Group label	Habitat gradient defined by PCA[c] 1	2	3	4	5
MODO	1	0.86***	−0.08	−0.52*	−0.12	−0.18
WWPE	1	0.79**	−0.11	−0.53*	−0.14	−0.23
HOWR	1	0.96***	−0.02	−0.47*	−0.02	−0.08
TRSW	1	0.62*	0.13	−0.57*	0.05	−0.16
DUFL	2	0.04	0.28	−0.41	0.60*	0.71**
BRBL	2	−0.23	0.35	−0.24	0.61*	0.49*
COYE	2	−0.34	0.42	−0.14	0.49*	0.52*
WIFL	3	0.57*	−0.09	−0.21	0.49*	−0.37
YEWA	3	0.89***	0.11	−0.48*	0.42	0.11
BHCO	3	0.65*	0.19	−0.53*	0.53*	0.14
AMRO	3	0.83**	0.19	−0.64*	0.27	0.10
VEER	3	0.42	0.25	−0.12	0.49*	0.23
GRCA	3	0.31	−0.22	−0.18	0.40	−0.32
WAVI	3	0.68*	0.35	−0.39	0.41	0.55*
MGWA	4	−0.35	0.17	−0.26	0.52*	0.15
SOSP	4	0.03	0.29	−0.27	0.72**	0.30
BTHU	4	−0.08	0.21	−0.17	0.73**	0.27
LISP	5	−0.71**	0.30	0.55*	−0.49*	0.24
WCSP	5	−0.52*	−0.27	0.49*	−0.47*	−0.32
WIWA	5	−0.43*	0.10	0.77**	−0.64*	−0.16

NOTE: For explanation of abbreviations of species names see Table 3. For descriptions of gradients see Table 5. Significance levels are based on t-tests of correlations and are as follows: *, $P < 0.1$; **, $P < 0.01$; ***, $P < 0.001$.

tions or omissions of sets of species with similar habitat affliations. Low-elevation woodlands had high species richness because multiple sets of covarying species merged together to form the overall bird assemblage, but in subalpine vegetation, species with similar habitat affinities formed an isolated group. Guild responses to three zones of habitat structure resulted in the formation of three bird communities identified by cluster analysis of plot assemblages.

The composition of the avifauna at any given position along the elevational gradient was dependent on the availability of suitable habitat strata (Finch 1989*b*). At high elevations, habitats were simple, supplying suitable resources for only a few species (Finch 1989*a*). Generally, shrublands contained fewer bird species than woodlands because tree-affiliated species were absent from treeless habitats, whereas woodlands contained both shrubs and trees. Similar relationships between habitat complexity and bird species diversity have often been reported (e.g., MacArthur and MacArthur 1961; Karr and Roth 1971; Cody 1974), but few studies relate changes in bird community structure along steep environmental gradients to numerical shifts in habitat response guilds. Examining changes in guild composition and abundance was likewise effective in interpreting bird community response to vegetation succession (Raphael et al. 1987), drought-induced habitat changes (Smith 1982), and grazing effects (Knopf et al. 1988).

Patterns of species co-occurrence and habitat structure

Of 190 possible associations between species pairs, 25.3% were significant, a much greater proportion than that expected by chance alone. Thus, I rejected the null hypothesis of no association between pairs of species. Seventy-five percent of the significant correlations were positive rather than negative, indicating that distributions of many pairs of species were similar. I also rejected the null hypothesis that counts of multiple species were not associated, because species in clusters covaried in significant positive directions. One explanation for positive correlations is that the best-adapted sets of species comprise communities (Cody 1966) and that current resource partitioning or "ecological fitting" (Janzen 1985) of coexisting species resulted from historical competition for resources (Schoener 1974; Diamond 1975, 1978; Brown and Zeng 1989). Experimental and observational studies convincingly show that many species do directly compete for resources (Connell 1983; Schoener 1983; Alatalo et al. 1986). Nonetheless, because the absence of current competition neither proves nor disproves its past existence (Connell 1980; Jackson 1981), tests of contemporary processes may better clarify nonrandom community patterns.

In this study, negative associations primarily occurred between species inhabiting different vegetation types. Two species having exclusive distributions should rarely compete for resources. Even on plots where such distributions overlapped, competition appeared unlikely, owing to interspecific disparities in foraging and nesting habits, morphology, and taxon. When variation in counts associated with habitat gradients was removed using partial correlational analysis, the number of significant interspecific correlations (eight species pairs) agreed with the random expectation (Finch 1987), suggesting that patterns of habitat selection explained species coexistence patterns (Mountainspring and Scott 1985; Gutzwiller and Anderson 1988; but see Rosenzweig et al. 1985). In a study of five thrush species arrayed along an elevational gradient in Vermont, negative associations among species also corresponded to habitat ecotonal changes (Noon 1981). As these species were similar in morphology, diet, foraging method, and nesting habits, Noon (1981) interpreted differences in habitat selection patterns as evidence for past competition. Terborgh (1971, 1985) and Terborgh and Weske (1975) concluded that competitive exclusion was the dominant process accounting for the altitudinal limits of Andean birds in

Peru. Habitat ecotones accounted for only one-sixth of species distributional boundaries in the Andean ecosytem (Terborgh 1985.

Though I have used bird-count data to identify suites of species that covaried in abundance, I believe that this data set is insufficient for discerning or discounting interspecific competition. Competition is difficult to ascertain using species co-occurrence data because it does not generate very large negative associations, and those that are produced are statistically difficult to detect (Hastings 1987). Furthermore, regression coefficients that presumably express interspecific interactions may be statistical artifacts of differences between census variances in pairs of rare and common species (Rosenzweig et al. 1985; but see Pimm 1985). Using simulated data, Cale et al. (1989) concluded that competition could not be inferred from abundance data because it was usually masked by pattern that was indistinguishable from random assembly. Application of the wrong observational scale confounds the problem. Though use of the macrohabitat level is effective in determining population trends of coexisting species (Morris 1987), a finer level of resolution may be more suitable for detecting competition. Similarities in species habitat use at the zonal level of resolution differed from those found at the scale of the elevational gradient (Finch 1989*a*). Moreover, at the local level of study area, House Wrens and Tree Swallows were observed to compete directly for artificial nests in foothill woodlands (Finch 1990). House Wrens excluded Tree Swallows from nest sites by destroying their eggs and nests, forcing them to nest elsewhere (see also Belles-Isles and Picman 1986). Yet counts of these two species were positively associated using a correlational approach. Though asymmetrical competition may depress populations of a subordinate species at the local level (e.g., Sherry and Holmes 1988), two competing species may appear to "share" habitats at the macroecological level because their populations adjust similarly to major environmental changes.

Nevertheless, coexisting organisms do often share common resources without competing (Strong 1982, 1984; Wiens 1984; Lawton 1984; Brawn et al. 1987). Positive rather than negative associations may actually be the norm in some animal communities (Schluter 1984). Interactive coexistence in birds may result when one species depends on another for secondary nest sites (e.g., delayed commensalism in cavity-nesting species, sensu Gutzwiller and Anderson 1988), or food, or when both species benefit (rare in birds). The natural histories of the 20 species that I examined precluded any possibility of interspecific relationships based on commensalism, predator–prey interactions, or mutualism. Thus, these processes are readily discounted as underlying factors producing observed patterns of aggregating species.

The role of nest predation in determining bird species distributions and coexistence patterns also merits further attention (Martin 1988*a*). If the search efficiency of nest predators is increased in habitats with high nest densities, bird species that select similar nest sites may reduce habitat overlap to lessen the probability of nest destruction (Martin 1988*a*, 1988*b*). Without experimental data on predation rates and nest-site use, I cannot rule out the possibility that nest predation in riparian habitats was a process that favored positive covariation of some bird species that partitioned nest sites. Nevertheless, because the nests of many guild members were found at similar heights and in similar vegetation within the same study areas (e.g., group 3: Willow Flycatcher, Yellow Warbler, Veery, robin; group 4: MacGillivray's Warbler, Song Sparrow, Broad-tailed Hummingbird) (unpublished data), the nest predation hypothesis is unlikely to account for species covariation in all five guilds.

Alternatively, positively associating species may aggregate if they track shared, fluctuating resources (Dunning and Brown 1982; Schluter 1984; Hutto 1985). In this study, five suites of covarying species were described using cluster, correlational, and variance analyses of species abundances. Patterns of species covariance corresponded to patterns of species habitat occupancy. Counts of species within each group simultaneously increased or decreased along gradients of habitat structure and elevation. Major breaks in habitat structure resulted from the recession of cottonwoods from montane stream banks and from the loss of shrub diversity from subalpine parks (Finch 1989*b*). In general, each group of co-occurring species responded uniquely to these abrupt transitions in habitat structure by either appearing or disappearing as a whole unit or by concurrently fluctuating in abundance. The classical definition of a guild is a group of species that use the same kinds of resources in a similar manner (Root 1967). In this study, habitat response guilds were identified from patterns of species covariance, even though some guild species differed in taxon, nesting behavior, and foraging strategy.

Because processes other than ecological fitting were less plausible, a reasonable explanation for positive covariation in bird abundance is that species responded similarly to habitat resources that were limited by biotic and abiotic factors associated with elevational zone. This does not conflict with the idea that interspecific competition may also have played a prior role in shaping bird communities. However, historical processes that result in ecological fitting of bird assemblages to available resources cannot be easily tested, whereas significant relationships with habitat gradients were confirmed. The following trends were obvious and support my interpretation. Species that nested in cavities or nested, perched, and foraged in overstory canopies disappeared in synchrony when trees were lost, presumably because nest sites, perches, or foraging substrates were no longer available. The densities of species that nested in or beneath small shrubs rose simultaneously in high-elevation treeless habitats dominated by small shrub thickets, possibly in response to increased numbers of potential nest sites. Species that foraged, nested, and perched within dense foliage of tall shrubs peaked in abundance at mid-elevation sites containing complex shrub communities. Because such species typically concealed nests and resting places in dense shrub foliage, increased availability of hiding sites and nesting cover may explain increased bird abundance. Widespread species occupying lowland and middle zones formed a group that declined in abundance when shrubs replaced trees as dominant plants. The overall loss of vertical habitat for spacing of nests and territorial pairs may explain such decreases in abundances of generalists.

Though these overall patterns were not surprising, the commonalities among certain guild members were more difficult to interpret. For example, the distribution of the wide-ranging Mourning Dove may be correlated with counts of species that nest in tree cavities (House Wren, Tree Swallow) and canopies (Western Wood-Pewee) solely because dove foraging habitats were adjacent to riparian woodlands or because low elevation rather than riparian habitat was the selected attribute. As Brewer's Blackbirds typically nested along edges rather than in the interior of riparian habitats, its specialized occupancy pattern may be defined by specific edge conditions, i.e., the mixing of riparian and adjacent grass–shrub communities.

Rather than tracking the distribution of habitats, the parasitic Brown-headed Cowbird may track the distribution of its hosts (e.g., Yellow Warbler, Willow Flycatcher, Veery). In addition, if populations are sampled on a wider spatial scale than that encompassed by riparian systems, overall densities of species associated with a broad range of vegetation types (e.g., Broad-tailed Hummingbird, American Robin) may be only loosely responsive to changes in availability of riparian resources.

Another perplexing pattern was the rarity of ground-nesting species in foothill woodlands. Though over-bank flooding of rivers is a periodic disturbance in lowland riparian communities, it is mostly absent at higher elevations in the central Rocky Mountains (Olson and Knopf 1988). Ground surfaces on my lowland study areas were submerged by floodwaters from late April through June of some study years (see Finch 1991 for a description of flood conditions in neighboring areas). Reductions in populations of ground-nesting species like Lincoln's and Song Sparrows may be related to avoidance of flood conditions which could cause breeding delays or nesting failure.

In contrast to the numerous species associations that I detected in riparian habitats, patterns of distribution and abundance of bird species occupying shrub-steppe habitats of simple structure were lacking or were loose and inconsistent (Rotenberry and Wiens 1980*a*, 1980*b*; Wiens and Rotenberry 1981). Wiens and Rotenberry failed to detect a pattern on the local level but did find a pattern on a broad geographical scale, which suggests that local shrub-steppe habitats were too invarient to reveal consistent associations. Similarly, Maurer (1985) suggested that communities appeared individualistic, in part, because the adaptational units of species may be much larger than local study areas. Finding a pattern in species–habitat associations may, therefore, simply be a matter of expanding the number of different vegetation types sampled to ensure a representative diversity of species-specific habitats. As in this study, patterns in species associations were readily discerned along relatively sharp elevational inclines (Terborgh 1971, 1985; Able and Noon 1976; Noon and Able 1978; Knopf 1985), owing to rapid spatial turnover in species and habitats.

In summary, breaks in vegetational gradients associated with elevation provided a means of structuring communities of streamside birds. If I had used a finer level of resolution (e.g., within a single plot or zone), macrohabitat transitions would have been inconspicuous, and patterns in species—habitat associations (if present) would be attributable to heterogeneity in microhabitat resources (e.g., Dueser and Shugart 1978; Price 1978) or other local factors. Macrohabitat differences in species distributions may sometimes be mistakenly ascribed to microhabitat selection (Morris 1984), in part because macrohabitats consolidate microhabitat information (Morris 1987). Clearly, interpretations of natural phenomena depend on the choice of observational scale (Allen and Starr 1982; Rudd et al. 1984; Maurer 1985). My results support the idea that suites of species adjust to different hierarchical levels detected at different spatial scales. Though specialists clustered together at the subdivision of the elevational zone, most generalists crossed zonal boundaries, grouping together at a wider level of observation.

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