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HABITAT USE AND HABITAT OVERLAP OF RIPARIAN BIRDS IN THREE ELEVATIONAL ZONES[1]

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Abstract. I examined patterns of variance in habitat use and habitat overlap in 20 breeding bird species found along a riparian vegetational gradient in southeastern Wyoming to test whether habitat use in species differed (1) from availability of random habitat resources, (2) among elevational zones, and (3) between species that inhabited only one zone and species that occupied multiple zones. I sampled habitat features in bird territories and at random stations on 10 8.1-ha study grids distributed over an elevational gradient of 940 m. Principal components analysis was performed on both randomly sampled and territory-centered habitat data to examine the habitat use of each bird species in relation to the random centroid in n-dimensional habitat space. Using this transformed data set, I computed habitat size of each species, defined as degree of specialization in habitat use; species-habitat position, defined as use of common or scarce habitat; habitat overlap among species; and sum of variation in structure of the available habitat.

Habitat size was significantly smaller for bird species found in subalpine riparian shrublands than for those found in foothill woodlands, but this result was partly a reflection of variation among elevational zones in structural diversity of the available habitat. The null hypothesis that species used habitat as it occurred randomly was rejected for all three subalpine bird species examined, 6 of 10 dominant mid-elevation species, and 1 of 10 lowland species. Habitat overlap among species did not vary among zones, but habitats used by lowland species were closer to the random expectation than habitats used by mid-elevation or subalpine species. In general, species restricted in distribution to one zone had smaller habitat sizes than species occupying multiple zones, but some zone-dependent species were generalists within their zones.

Vegetation of lowland riparian habitats was structurally more complex than that of riparian habitats at higher elevations, and bird species richness and bird abundance were greatest in riparian lowlands. Because most lowland species were generalized in habitat use and occupied habitats that were similar among species, I concluded that bird species diversity was greater in lowlands than in mid-elevation and subalpine shrublands merely because woodlands were more heterogeneous. The large proportion of generalists in deciduous woodlands of the central Rocky Mountains may be explained by geographic dispersal patterns. Woodland species may have been historically prevented from dispersal by the ecological barrier of the Great Plains grasslands. Recent establishment of widespread riparian forest permitted colonization of woodland bird species, with generalists colonizing first.

Key words: bird species diversity; central Rocky Mountains; elevational zones; foothill woodlands; habitat complexity; habitat overlap; habitat specialization; habitat-niche size; riparian bird communities; southeastern Wyoming; spatial scale; subalpine shrublands.

INTRODUCTION

Numerous studies have demonstrated that complex habitats support more species than structurally simple habitats because more resource dimensions are available, and these can be exploited in more ways (MacArthur and MacArthur 1961, Pianka 1967, Recher 1969, Karr and Roth 1971, Rosenzweig 1973, Cody 1974, 1981). A popular paradigm used to explore strong correlations among vegetation structure, species diversity, and species coexistence patterns has been Hutchinson's (1958) spatial model of the niche (Anderson and Shugart 1974, Whitmore 1975, 1977, Inger and Colwell 1977, Sabo 1980, Sabo and Holmes 1983). Factors typically proposed to influence species diversity and community development include the abundance and variety of resources, the extent that species use these resources, and the degree that these resources are shared (MacArthur 1972). Under conditions of resource limitation and competition, species diversity should increase with increased diversity of available resources, increased niche overlap, reduced average niche size, or a combination of these (Pianka 1979). Because resource limitation and competition are dif-

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ficult to demonstrate in natural communities (Wiens 1984), these forces may not always explain trends in niche size and overlap.

I use the terms "niche size" and "niche overlap" in this paper with reference only to patterns of habitat occupancy. The partitioning of habitats is only one aspect of the niche structure of communities, and other kinds of resource partitioning, such as diet, nest site selection, and foraging position and technique, are important in a thorough analysis of niche patterns.

A complicating factor in the study of community structure and complexity is scale of observation. This is usually evident as spatial or temporal variation in the environment (Wiens 1973, 1981, Johnson 1980; but see Maurer 1985). Community boundaries can be defined at different levels of resolution because, as levels are changed, structures of complex communities change (Allen and Starr 1982, Allen et al. 1984). In this paper habitat relationships in communities of birds breeding in riparian habitats of southeastern Wyoming were viewed at two spatial scales. The first scale was the entire elevational continuum. Because habitat structure and complexity varied along the altitudinal gradient, I also studied avian communities in three elevational zones. Changes in the spatial distribution of trees, shrubs, and ground cover produced overall differences in habitat structure that could be classified using elevational limits (Finch 1986, 1989). Variation in habitat relationships at the zonal level was examined to determine if zonal differences in habitat structure and complexity affected niche size and overlap.

I previously showed that negative associations among bird species in this system were uncommon and could be explained by different habitat affinities, and that habitat variation alone explained spatial fluctuations in bird numbers (Finch 1987). Increased species richness in lowland cottonwood habitats was partially explained by an increased number of guilds and numbers of species per guild produced by increased habitat layering (Finch, 1989). Given this base, further insight into factors that regulate bird numbers and distribution may be provided by examination of bird–habitat relationships at different spatial scales. I asked the following questions: (1) What is the relationship between variability in species habitat use in different riparian zones and structural diversity of the available habitat? (2) Are the habitats used by lowland riparian birds more specialized than those of subalpine species, thus allowing greater species packing and consequently higher species diversity? (3) Is there a relationship between breadth of habitat use and geographic restriction? For example, does a species that occupies several riparian zones use more habitat structures than a species that is restricted to one zone? (4) If habitat use is examined at different spatial scales, how does this alter niche interpretations? (5) What processes best explain patterns of habitat use, habitat overlap, and species diversity among riparian bird species?

Methods

Study area

The investigation was performed in streamside habitats in, or within 16 km of, the Medicine Bow National Forest in Albany and Carbon Counties, southeastern Wyoming. Ten 8.1-ha study plots, staked and flagged as rectangular grids, were established along foothill and montane drainages over an elevational gradient ranging from 2050 to 2990 m (Finch 1987). The lower elevation (2050–2250 m) plots were dominated by narrowleaf cottonwood (*Populus angustifolia*) and both tree and shrub willows (*Salix* spp.), but at elevations >2285 m a mixture of shrub willow species covered a high proportion of the land surface area. In subalpine forests riparian habitats were composed of shrubby thickets of *S. planifolia* and *S. wolfii* interspersed with boggy meadows. Site selection criteria and vegetation composition of the study areas are described in greater detail in Finch (1987, 1988, 1989).

Sampling random and bird habitat

Habitat structure was sampled in July and August of 1982, 1983, and 1984, within the boundaries of bird territories, either near nest sites or at mapped locations of breeding birds (James 1971). Vegetation sampling at bird or nest locations has commonly been used to partition sets of habitat features selected by different bird species and individuals (Whitmore 1975, Roth 1979, Karr and Freemark 1983). Bird-centered sampling evaluates habitat relationships better than other traditional methods because it is more precise and efficient, and because data can be pooled at various spatial scales (e.g., individual study stand, series of stands in a local area, or all stands in a geographical region or set of regions) (Larson and Bock 1986).

In this study, I sampled vegetation at the center of a cluster of observations, or territory, rather than at the location of the first bird seen, to reduce the bias associated with single detections of highly visible singing males. Locations of territories were determined by spot-mapping pairs of birds on each site from mid-May through early July of the three study years. 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 territorial pair.

Following the bird-census period, habitats were sampled at territory centers using the clusters of mapped observations as a guide to territory locations (Noon 1981). Vegetation samples were located in proportion to the abundance of each bird species on each study area. Habitat features were sampled at a total of 444 territories of 20 species distributed over the elevational continuum. Sample habitat data were pooled in each species across years to give estimates of habitat char-

TABLE 1. Structural variables used in analysis.

Mnemonic acronym	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 (James and Shugart 1970).
SHBA	Shrub basal area	Mean basal area (m^2) of nearest shrubs (≥1 m tall) in each quadrant (Mueller-Dombois and Ellenberg 1974).
SHCD	Shrub crown diameter	Mean diameter (cm) of nearest shrubs (≥1 m tall) in each quadrant.
SHHT	Shrub height	Mean height (m) of nearest shrubs (≥1 m tall) in each quadrant.
SHDIS	Shrub dispersion	Mean distance (m) to nearest shrubs (≥1 m tall) in each quadrant.
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 0.3–1 m height interval.
VFD3	Vertical foliage density in mid-canopy layer	Same as VFD1, but in 1–2 m height interval.
VFD4	Vertical foliage density in upper layer of understory	Same as VFD1, but in 2–9 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 (Wiens 1969).
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	Percent of surface that is bare, or covered with litter, measured with ocular tube (James and Shugart 1970).
GRASS	Grass–forb ground cover	Percent cover of grasses and forbs measured with ocular tube (James and Shugart 1970).
WATER	Water cover	Percent cover of water measured with ocular tube (James and Shugart 1970).
COVER	Woody vegetation cover	Percent cover of woody plants (<1 m tall), saplings, and downed logs measured with ocular tube (James and Shugart 1970).

acteristics within each of three elevational zones as well as over all 10 plots. Elevational zones were classified as follows: Zone 1 = three cottonwood–willow sites ranging from 2050 to 2250 m; Zone 2 = three mixed shrub-willow sites ranging from 2290 to 2530 m; Zone 3 = four *S. planifolia–S. wolfii* sites ranging from 2590 to 2990 m (Finch 1987, 1989). Zonal boundaries were determined by classifying the 10 study plots using cluster analysis of habitat structure (40 random samples per plot). Three clusters of plots were formed using the complete linkage procedure of amalgamating cases based on Euclidean distances between habitat structures (Program P2M of Biometrical Computer Programs, Dixon and Brown 1979). Plots were previously classified into the same three zones based on mean abundances of the 20 bird species considered in this study (Finch 1987), verifying that the elevational limits established by habitat structure were recognized by birds as well.

Forty random locations on the grid of each study plot were sampled in the same way as the territory-centered samples. Sites were chosen by selecting grid coordinates from a table of random numbers (Rohlf and Sokal 1969). Randomly sampled data were pooled to give estimates of habitat features of each plot, groups of plots within elevational zones, and all plots combined. I justified pooling random and territory-centered samples from different plots within each elevational zone and over all plots based on (1) cluster analysis of plot vegetation characteristics that revealed high similarities among plots within zones (this study), and (2) univariate nested-design analyses of variance (ANOVAs) that revealed habitat variability within plots similar to (or greater than) that among plots for both random (Finch 1987) and territory-centered samples (Finch 1988).

At each sampling location I measured 34 structural habitat variables following a point-centered quarter sampling procedure (Noon 1981). Habitat features were sampled by dividing each location into four quadrants oriented in the cardinal compass directions. Fifteen of the original variables were deleted from the final analyses because they were invariant, irrelevant ecologically, or highly correlated with other variables. Pearson product-moment correlations were used to assess relationships between habitat variables. Within pairs or groups of highly correlated variables I retained the variable that had the sampling distribution most close to normality. Descriptions and sampling techniques for the remaining 19 variables are presented in Table 1.

Data analysis

I used multivariate analysis of variance (MANOVA) on 19 habitat variables to assess whether habitat centroids differed among 20 bird species. Principal components analysis (PCA) with varimax rotation was used to examine the position of each bird species and the random habitat centroid in n-dimensional habitat space. All 400 random sites and 444 territory-centered samples were entered into the PCA. Components with eigenvalues >1 were used in further analyses. Scores in each resultant habitat factor were summed and averaged for each species and for the random group at three spatial scales: study plot, elevational zone, and all plots combined. Because of sample size limitations, only the last two scales were used in the territory-centered data.

The position of species centroids in n-dimensional space relative to a centroid representing randomly available habitat resources was defined as the habitat-niche position (Dueser and Shugart 1979, Reinert 1984, James and Lockerd 1986). Habitat position was calculated as the Euclidean distance between each species' centroid in principal components space and the random habitat centroid (Carnes and Slade 1982). A close position implies use of common habitat and a distant position means use of scarce habitat. A multidimensional measure of variability in habitat use by a species, defined as habitat size, was computed as the mean squared distances, $\Sigma d^2_{ij}/n_i$, of individual species scores from the centroid of that species. This measure reflects the amount of variation within species and is relatively unaffected by sample size or position of the origin of PCA axes (Carnes and Slade 1982). Smaller mean variances indicate greater specialization in habitat use by each species. An index to variability of available habitat was estimated in a similar manner as the amount of variation in habitat structure, computed as the mean squared distance of random scores from the random centroid. Statistical comparisons of habitat size were accomplished using F ratios of squared distances (Carnes and Slade 1982). Species with habitat sizes that differed significantly from the variance measured for randomly available habitat were considered specialists, while those with habitat sizes that did not differ were defined as generalists.

To determine if species that occupied only one of the three elevational zones were more specialized in habitat use than species that inhabited multiple zones, I used chi-square analysis to examine the relationship between numbers of each type of species with close (<0.9), middle (0.9–1.3), and distant (>1.3) habitat positions, and small (<2.5), moderate (2.5–3.5), and large (>3.5) habitat sizes. Cutoff values were based on equal increments in each class, computed by subtracting the smallest value of position or size from the largest, and dividing by three. The result was added to the lowest value of size or position to calculate the first cutoff. Mann-Whitney U tests were used to compare mean ($\pm$SD) habitat positions and habitat sizes of zone-dependent and zone-independent species.

At a narrower spatial scale, I used F ratios to compare habitat size of each species within each zone to the variability of random habitat at the same spatial scale. Variation in available habitat on each of the 10 plots was also computed using the 40 random samples per plot to detect correlational trends in habitat diversity with increase in elevation and distance from the master centroid of pooled random plots. Kruskal-Wallis one-way ANOVA was used to test for differences in habitat variability among zones averaged by plot.

Species-habitat overlap ($\hat{a}$) along each principal component axis was calculated using Maurer's (1982) formula, modified from Harner and Whitmore (1977):

$$\hat{a} = (2s_1s_2/s_1^2 + s_2^2)^{1/2}e^{-d^2/2(s_1^2+s_1^2)},$$

where d is the distance between species centroids, and s_1 and s_2 are the standard deviations of principal component scores for each species. Total overlap was computed as the product of overlap values for each axis (Maurer 1982). Four overlap matrices were created using two spatial scales: elevational zone and all plots pooled. Cluster analysis of total overlap values using the average linkage procedure of Program P1M of BMDP Biomedical Computer Programs (Dixon and Brown 1979) was applied to each matrix to hierarchically arrange multiple species based on degree of similarity of habitat use.

All other analyses were performed using SPSS and SPSS^x programs (Nie et al. 1975, Hull and Nie 1981, SPSS 1986). Analysis of three data sets composed of raw, log-transformed, and a combination of reciprocal, square-root, and log-transformed variates (Kleinbaum and Kupper 1978) produced biologically similar results. Results of analyses of log-transformed data are reported because the data most closely adhered to statistical assumptions.

RESULTS

Habitat trends at overall spatial scale

An overall MANOVA for 19 variables and 20 species indicated that the habitat centroids significantly differed among bird species (Wilks' lambda = 0.170, $P < .001$). An overall PCA of 20 species plus random habitat produced five principal components with eigenvalues >1.0 (Table 2). One-way ANOVAs indicated that habitat centroids for the 20 species (see Table 3) differed significantly on each of five components (Table 2). Biological interpretations of each factor are based upon the habitat variables that are most highly correlated with that principal component (Table 2). The first component was most highly correlated with the following variables (listed in descending magnitude of correlation): tree density (TDEN), canopy height (CANHT), percent willow (WILLOW), vertical foliage

TABLE 2. Summary statistics of a principal components analysis of random and territory-centered habitat data, and matrix of correlations with varimax-rotated factors. High correlations between original variables and factors are underlined.

Statistic	Principal components				
	1	2	3	4	5
Eigenvalue	5.20	2.72	2.40	1.36	1.02
% of variance	27.40	14.30	12.60	7.10	5.30
Cumulative %	27.40	41.60	54.30	61.40	66.80
F ratio†	14.89****	4.18****	1.54**	3.89****	1.67**
		Correlation matrix‡			
CANHT	0.858	−0.187	0.213	0.104	0.008
TDEN	0.883	−0.230	−0.161	0.020	−0.074
SHBA	−0.272	−0.034	0.761	−0.044	0.019
SHCD	−0.073	−0.137	0.894	0.063	0.037
SHHT	0.099	0.020	0.675	0.320	0.076
SHDIS	0.064	−0.684	0.202	−0.186	0.002
VFD1	−0.138	0.219	0.164	−0.138	0.409
VFD2	−0.221	0.632	−0.042	−0.034	0.092
VFD3	−0.087	0.396	0.120	0.605	−0.004
VFD4	0.498	−0.100	0.101	0.628	−0.103
VFD5	0.623	−0.016	−0.085	0.041	0.014
CANCOV	0.610	−0.052	0.119	−0.609	0.005
COVER	−0.114	0.596	−0.038	−0.011	−0.167
WILLOW	−0.686	0.123	0.375	0.005	0.067
EVH	−0.136	0.743	0.081	0.015	0.084
FRUIT	−0.593	−0.268	−0.171	0.137	−0.113
BARE	0.491	−0.326	−0.067	0.109	−0.323
GRASS	−0.032	−0.118	−0.022	0.036	0.678
WATER	−0.166	0.045	0.158	−0.061	−0.139

† Results of ANOVA for 19 variables and 21 groups (20 species plus random group) testing for differences among mean species scores on each principal components axis (** $P < .01$, **** $P < .0001$).

‡ Acronyms of habitat variables are described in Table 1.

density of overstory (VFD5), canopy cover (CANCOV), percent fruiting shrubs (FRUIT), foliage density in upper understory (VFD4), and bare ground coverage (BARE). Component one represented a habitat gradient from wooded sites with densely foliated tree canopies, many fruiting shrubs, and open ground, to treeless sites densely covered by shrub willow. This axis distinguished species that used habitats dominated by cottonwoods heavily (e.g., Tree Swallow, House Wren, Warbling Vireo) from species using shrub willow areas (e.g., Lincoln's Sparrow, White-crowned Sparrow, Wilson's Warbler) (Fig. 1).

Variables correlated with the second factor were effective vegetation height (EVH), shrub dispersion (SHDIS), foliage density of small shrubs (VFD2), and woody vegetation cover (COVER). This factor described understory features varying from situations with low shrub-density and surface cover to thickly vegetated sites with high foliage-density in the shrub layer. This second axis clearly separated species using open, shrubless sites (e.g., Tree Swallow, Western Wood Pewee, and Mourning Dove) from species using dense shrub cover (e.g., Wilson's Warbler, Common Yellowthroat) (Fig. 1).

Factor three was highly correlated with shrub crown diameter (SHCD), shrub basal area (SHBA), and shrub height (SHHT). This component which represented a shrub size gradient from tall, spreading shrubs to small shrubs, separated species found at sites with tall shrubs (e.g., Dusky Flycatcher, MacGillivray's Warbler) from species using the opposite extreme (e.g., Western Wood Pewee, House Wren) (Fig. 1).

The fourth component had highest correlations with foliage density in mid- and upper understory layers (VFD3, VFD4) and canopy cover (CANCOV). This factor described a gradient from a dense, closed canopy to a sparsely foliated overstory (Fig. 2). This axis distinguished White-crowned Sparrow, Wilson's Warbler, Lincoln's Sparrow, and Western Wood Pewee from species selecting dense canopies (e.g., Dusky Flycatcher, Song Sparrow, Willow Flycatcher, Brown-headed Cowbird).

Component five had high positive correlations with grass–forb cover (GRASS) and foliage density in the surface layer (VFD1). This factor described ground surface features varying from a dense, herbaceous ground layer to sites with little surface vegetation (Fig. 2). Brewer's Blackbird, MacGillivray's Warbler, Gray Catbird, and Dusky Flycatcher were associated with herbaceous surfaces, whereas the Tree Swallow was found at sites with bare ground.

The habitats used by each species are represented by

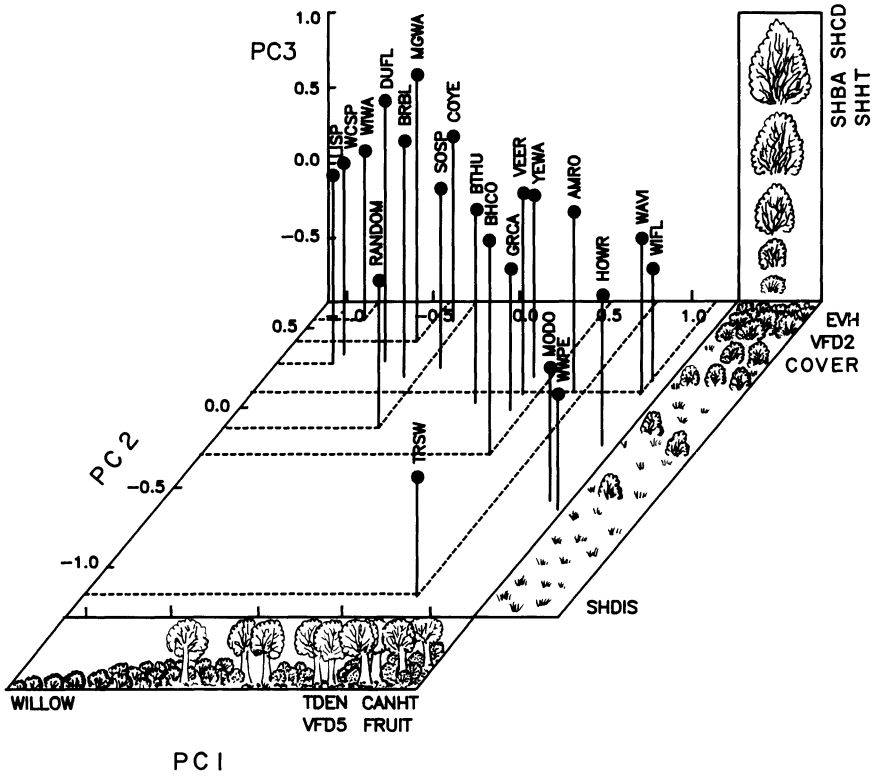

FIG. 1. Positions of species and random centroids relative to the first three principal axes with pictorial interpretation of associated habitat gradients. See Table 1 for descriptions of habitat acronyms: see Appendix for species acronyms.

a combination of all five habitat dimensions derived from PCA. I interpreted general patterns of habitat use among the 20 species by examining multifactor habitat centroids and mean habitat vectors for each species.[2] The random habitat centroid was positioned at approximately the origin of the PCA, with mean factor scores approaching zero on all five axes. The random centroid therefore served as a reference point for evaluating positions of species' centroids in multidimensional space. Species using habitats with taller and denser canopies and more trees than the average random habitat site (CANHT = 4.0 m, CANCOV = 22.9%, TDEN = 10.8 trees/100 m^2) were Mourning Dove, Western Wood Pewee, Willow Flycatcher, Tree Swallow, House Wren, Veery, American Robin, and Warbling Vireo. In these habitats, bare ground comprised up to 50% of the surface area in any bird territory in contrast to 14.3% at the average random site, and shrub cover was always less than the random average (COVER = 34.4%). Maximum values of bare ground coverage and shrub dispersion were attained on Tree Swallow sites (BARE = 59.4%, SHDIS = 13 m). Species that used habitats with few trees (TDEN < 10 trees/100 m^2), dense shub cover (SHDIS < 2.0 m), high percentage of willow species (WILLOW > 70%), and high shrub foliage density (VFD2 > 1.0 contacts) were Dusky Flycatcher, MacGillivray's Warbler, Common Yellowthroat, Wilson's Warbler, Song Sparrow, Lincoln's Sparrow, and White-crowned Sparrow. Sites occupied by MacGillivray's Warbler, Common Yellowthroat, Song Sparrow, Brewer's Blackbird, and Brown-headed Cowbird were characteristically moist (WATER > 5.5%), and thickly foliated in the high shrub layer (VFD3 > 0.6 hits). In addition, Brewer's Blackbird, Dusky Flycatcher, MacGillivray's Warbler, and Gray Catbird occupied locations that were densely covered by grasses and forbs (GRASS > 65%).

Overall habitat size and habitat overlap

The habitat position of each species at the widest spatial scale (all elevations) was computed (Table 3) as the distance to the random habitat centroid for all plots in principal components space (Carnes and Slade 1982). Species located near the random centroid used widespread, readily available habitat resources, whereas species positioned far from the random centroid used scarce habitat resources. Species closest to the random

[2] See ESA Supplementary Publication Service Document No. 8902 for three pages of supplementary material, which provides means ± standard errors of original variables and five principal components for 20 species. For a copy of this document, contact the author or order from the Ecological Society of America, 328 East State Street, Ithaca, New York 14850-4318 USA.

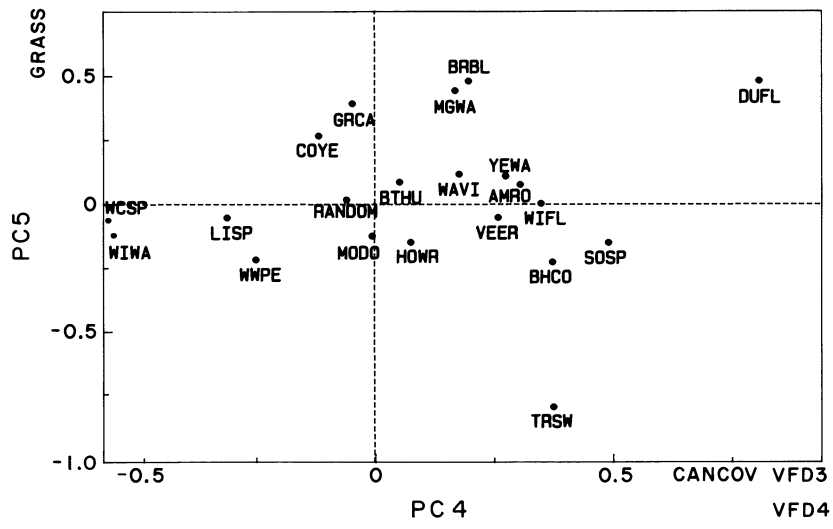

FIG. 2. Positions of species and random centroids relative to the fourth and fifth principal components axes. See Table 1 for descriptions of habitat acronyms; see Appendix for species acronyms.

centroid (habitat position < 0.9) were Brewer's Blackbird, Broad-tailed Hummingbird, Gray Catbird, Veery, Song Sparrow, Yellow Warbler, Lincoln's Sparrow, and Brown-headed Cowbird. These widespread species were distributed over multiple elevational zones. Yellow Warbler, Lincoln's Sparrow, and Song Sparrow were numerically dominant species as well (Finch, 1989). Species positioned farthest from the random centroid (habitat position > 1.3) were Tree Swallow, Western Wood Pewee, Willow Flycatcher, House Wren, and Dusky Flycatcher. Of these species, pewees used cottonwood woodlands exclusively; Willow Flycatchers selected shrub sites in cottonwood or mixed willow habitats bordered by mixed grass prairie; Dusky Flycatchers were found only on shrub plots bordered by coniferous forest; and swallows and wrens were abundant in habitats where cavity nests were present.

Specialization in habitat use by each species is represented by the variance of observations around the species' centroid (Carnes and Slade 1982). Two-tailed F tests were used to compare species' habitat sizes to the variance of the random habitat sample. Habitat sizes for 9 bird species differed significantly from the random expectation, while those for the remaining 11 species did not (Table 3). Wilson's Warbler exhibited the narrowest range of habitat use, followed closely by MacGillivray's Warbler, White-crowned Sparrow, Common Yellowthroat, Dusky Flycatcher and Lincoln's Sparrow, all with significant habitat sizes of 2.04 or smaller. Species using an intermediate range of habitats included Brewer's Blackbird, Gray Catbird, and Yellow Warbler. High variability in habitat use was exhibited by Tree Swallow, Brown-headed Cowbird, House Wren, Song Sparrow, Mourning Dove, Willow Flycatcher, Broad-tailed Hummingbird, Western Wood Pewee, American Robin, Veery, and Warbling Vireo. Estimates of habitat use that varied more than the random sample (Brown-headed Cowbird, Tree Swallow) were probably an effect of sampling error and were not considered biologically meaningful if they did not differ statistically from the random sample.

There was no consistent relationship between habitat position and habitat size of species at the scale of all pooled plots ($r = 0.14$, $t = 0.60$, $P > .05$) (Fig. 3). For example, Lincoln's Sparrow used only the common shrubland types (small size, close position) whereas Tree Swallow, House Wren, and Mourning Dove were flexible within the scarcer woodland habitats (large size, far position). I considered species that chose narrow ranges of scarce habitat (small significant size < 2.0, far position > 1.0) to be the most specialized users of the overall riparian spectrum. This pattern was evident in three species that occupied one zone only (zone-dependent): Wilson's Warbler, MacGillivray's Warbler, and Dusky Flycatcher (Fig. 3). Song Sparrow, Brown-headed Cowbird, American Robin, and Veery demonstrated widest use of commonly available habitat (large nonsignificant size >3.5, close position <1.0) and were zone-independent.

Cluster analysis of the matrix of total overlap values computed at the spatial scale of the entire riparian continuum produced a hierarchical arrangement of overlaps among species (Fig. 4). The greatest overlap occurred in Wilson's Warbler, White-crowned Sparrow, and Lincoln's Sparrow, species that dominated subalpine shrub habitats. MacGillivray's Warbler and Common Yellowthroat, species found principally in mixed-shrub habitats, also overlapped with the subalpine group. Eight species that reached peak abundance in woodlands also showed high overlap in habitat use. This group was composed of Mourning Dove, House Wren, Western Wood Pewee, Willow Flycatch-

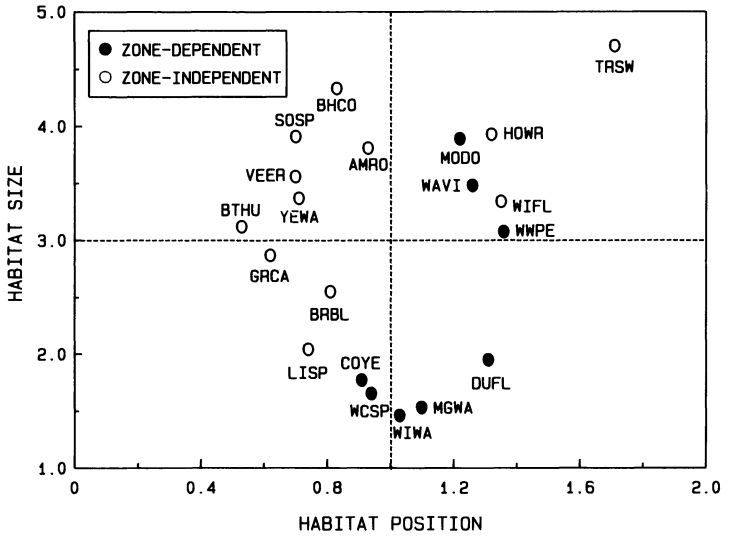

FIG. 3. Relationship between habitat size and habitat position in zone-dependent and zone-independent riparian birds. Dashed lines approximate midpoints of distributions. See Appendix for species acronyms.

er, Warbling Vireo, and American Robin. Eight species that occupied mixed-shrub habitats, or shrub patches within woodlands, formed a third group. Within this group, Yellow Warbler, Veery, and Broad-tailed Hummingbird formed a tight cluster which was linked to Brown-headed Cowbird at a greater distance. I found cowbird eggs in the nests of Yellow Warblers and Veeries, so high habitat overlap is not surprising. Dusky Flycatcher and Gray Catbird also overlapped extensively, as did Brewer's Blackbird and Song Sparrow. Finally, the Tree Swallow showed lowest overlap with any group of species, probably because of its unique combination of aerial-foraging and cavity-nesting habits.

Zonal variation in habitat size

Variability in habitat use by individual species can partially be explained by a trend in variability of the study plots. I applied Carnes and Slade's (1982) estimator of habitat variability to random habitat sampled at each of 10 study plots, and found increasing structural variability with decrease in elevation ($r = -0.62$, $t = 2.24$, $P < .05$). Therefore the habitat use of a riparian species is limited by the reduced habitat complexity present at high elevations. To adjust for differences in habitat structures among elevations I calculated habitat sizes of species by elevational zone and statistically compared these to the habitat sizes of random samples in each zone. The same five axes were used, but species and random scores were summed by zone, rather than across all 10 plots. Because fewer species occupied each zone, fewer species were sampled at this narrower spatial scale. Because of insufficient sample sizes within zones, Gray Catbird and Brown-headed Cowbird were excluded from this analysis, while some species were examined in only one zone even though they occupied multiple zones.

In the low-elevation cottonwood zone, only 1 of 11 species (Willow Flycatcher) used a narrow range of the

TABLE 3. Habitat position (distance from centroid of a random sample representing mean available habitat to species centroids), habitat size (mean squared distances of observations from species centroid), and zone dependency patterns of 20 bird species.

Species	*n*	Habitat position	Habitat size‡	Zone dependency§
Random	400	0.00	3.97	
Wilson's Warbler	28	1.02	1.47***	yes
MacGillivray's Warbler	10	1.10	1.53***	yes
White-crowned Sparrow	24	0.94	1.65***	yes
Common Yellowthroat	12	0.91	1.77***	yes
Dusky Flycatcher	7	1.31	1.95**	yes
Lincoln's Sparrow	60	0.74	2.04***	no
Brewer's Blackbird	17	0.81	2.55†	no
Gray Catbird	9	0.62	2.87**	no
Western Wood Pewee	15	1.37	3.04	yes
Broad-tailed Hummingbird	16	0.53	3.12	no
Willow Flycatcher	11	1.35	3.34	no
Yellow Warbler	60	0.71	3.37†	no
Warbling Vireo	16	1.26	3.48	yes
Veery	21	0.70	3.56	no
American Robin	41	0.93	3.81	no
Mourning Dove	11	1.22	3.89	yes
Song Sparrow	40	0.70	3.91	no
House Wren	30	1.32	3.93	no
Brown-headed Cowbird	8	0.83	4.33	no
Tree Swallow	8	1.71	4.70	no

‡ Species with habitat sizes that are significantly different (two-tailed F test) from habitat size of the random sample are marked as follows: † $P < .1$, ** $P < .01$, *** $P < .001$).

§ Species that occur in only one of the three elevational zones are defined as zone-dependent and are rated "yes."

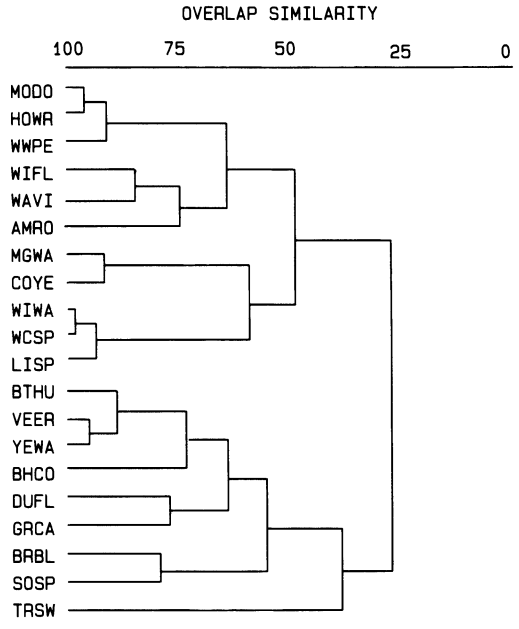

FIG. 4. Dendrogram of habitat-niche overlaps in 20 bird species (full names given in Appendix). Overlaps are based on data gathered across the entire elevational gradient. The overlap index describes similarity in habitat use among species, with an index value of 100 indicating identical habitat use and a value of 0 meaning no similarity in habitat occupancy patterns.

available habitat (Table 4). In the zone of mixed shrub-by willows, 6 of 10 species (Lincoln's Sparrow, Dusky Flycatcher, Broad-tailed Hummingbird, MacGillivray's Warbler, Common Yellowthroat, and Yellow Warbler) used specialized habitats, and in the subalpine willow zone all three species had specialized habitats. Average habitat size of bird species also differed significantly among the three zones (Kruskal-Wallis test, $H = 12.6$, $P = .002$).

Zonal variation in habitat overlap

I used overlap values as measures of shared PC score distributions and applied cluster analysis to each zone overlap matrix. In the cottonwood–willow zone a group of species composed of the American Robin, Western Wood Pewee, Mourning Dove, House Wren, and Yellow Warbler showed considerable habitat overlap ($\hat{a} > 0.80$) (Fig. 5A). This cluster was closely allied to the random sample, with the robin showing highest similarity in habitat distribution to the random sample. Similarity in habitat use was also high in the Veery and Warbling Vireo, but the Song Sparrow, Willow Flycatcher, and Tree Swallow showed little overlap with any species, instead forming linkages only after all lower order amalgamations had been made.

Habitats were shared in a different manner in the mixed shrub-willow zone, where two major clusters of species were formed (Fig. 5B). Neither group showed the random habitat use found by some of the species occupying the cottonwood zone. Likewise, the subalpine willow species overlapped more among themselves than with the random sample (Fig. 5C). Mean ($\pm$SD) overlap values for randomly sampled habitats and habitats selected by species were 0.81 ± 0.15 for Zone 1, 0.60 ± 0.13 for Zone 2, and 0.73 ± 0.04 for Zone 3. Mean overlaps between habitats available and those used differed significantly among zones (F ratio

TABLE 4. Habitat sizes of bird species among three elevational zones in Wyoming: cottonwood–willow (Zone 1), mixed shrub-willow (Zone 2), and subalpine willow (Zone 3).‡

Species§	Zone 1		Zone 2		Zone 3	
	N	Size	*N*	Size	*N*	Size
Random	120	3.31	120	3.10	160	2.58
Mourning Dove	11	3.89				
Broad-tailed Hummingbird	6	2.30	10	2.14†		
Western Wood Pewee	15	3.04				
Willow Flycatcher	8	1.98†				
Dusky Flycatcher			7	1.95†		
Tree Swallow	7	4.39				
House Wren	27	3.54				
Veery	10	2.83	11	2.49		
American Robin	29	3.39	12	2.44		
Warbling Vireo	13	2.79				
Yellow Warbler	30	2.77	30	2.30†		
MacGillivray's Warbler			10	1.53***		
Common Yellowthroat			12	1.77†		
Wilson's Warbler					28	1.47***
Song Sparrow	12	3.66	28	3.23		
Lincoln's Sparrow			20	1.71***	39	1.59***
White-crowned Sparrow					24	1.65**
Brewer's Blackbird			14	2.22		

‡ Two-tailed F tests († $P < .10$, ** $P < .01$, *** $P < .001$) were used to compare species habitat sizes to random habitat sizes within each zone.

§ Gray Catbird and Brown-headed Cowbird (Table 3) are excluded from analyses of zones because of insufficient sample sizes within zones.

TABLE 5. Numbers of zone-dependent and zone-independent species (out of 20) with habitat centroids near to (<0.9), intermediate (0.9–1.3) and far from (>1.3) that of the random habitat, and small (<2.5), intermediate (2.5–3.5), and large (>3.5) habitat sizes.

	Zone-dependent		Zone-independent	
	No.	(%)	No.	(%)
Habitat position				
Near	0		8	(40)
Middle	6	(30)	1	(5)
Far	2	(10)	3	(15)
Habitat size				
Small	5	(25)	1	(5)
Middle	2	(10)	5	(25)
Large	1	(5)	6	(30)

= 6.78, $P < .01$). In contrast, mean habitat overlap between species did not vary among zones (F ratio = 2.54, $P > .05$). Mean (±SD) overlaps between species were 0.65 ± 0.2 in Zone 1, 0.68 ± 0.12 in Zone 2, and 0.85 ± 0.07 in Zone 3. To summarize, Zone 1 species as a whole appeared to use habitats randomly, whereas species in Zones 2 and 3 showed similar use of specialized habitats.

Comparisons of zone-dependent and zone-independent species

Based on whether habitat size for a species differed significantly from random size in a zone, only 1 of 11 woodland species chose a restricted range of structural features, 6 of 10 mixed shrub-willow species did so, and all three subalpine species were specialized. Mean habitat sizes of species in mixed shrub-willow and subalpine willow differed from random habitat by 27 and 39%, respectively, in contrast to a 4% difference between species and random habitat in the woodland zone. Habitats in the two shrub-willow zones contained more zone-restricted species than foothill cottonwood communities. If the habitat features required are not distributed evenly within a zone, then more shrubland species may be restricted in distribution, using specialized patches available only within the zone. Only 3 of the 11 woodland species were found in only one zone (Mourning Dove, Western Wood Pewee, and Warbling Vireo), and none of these species used habitat differently from random use. These species used wooded sites with high canopy cover and high canopy height, suggesting that the tree itself was the habitat feature selected.

In contrast, two of the three subalpine species (Wilson's Warbler and White-crowned Sparrow) occupied only one zone and both used vegetation non-randomly. These species selected sites covered by dense willow, and avoided areas with herbaceous or bare surfaces (Finch 1988). Wilson's Warbler and White-crowned Sparrow may be restricted to the subalpine zone because they prefer high visibility, lower shrubs, greater moisture, and/or fewer bird species. Within that zone they select thick shrub thickets.

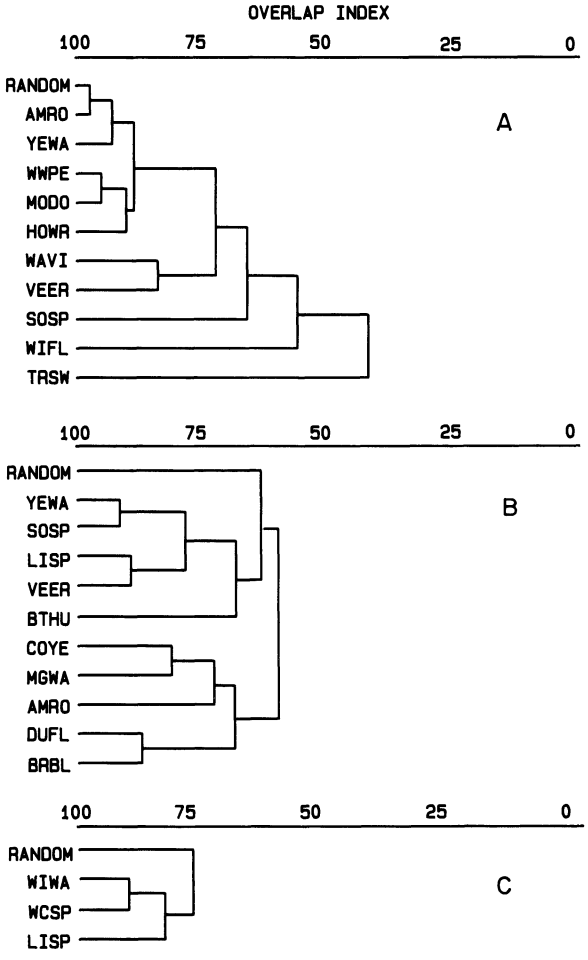

FIG. 5. Dendrograms of species-habitat overlaps in three riparian zones. See Fig. 4 for interpretation of index values; see Appendix for a description of species acronyms. A: species common to cottonwood lowlands (Zone 1); B: mixed shrub-willow (Zone 2) species; C: subalpine willow (Zone 3) species.

At the largest elevational scale, the effects of zone restriction on niche patterns were clearer. When habitat-niche characteristics were compared between 8 zone-dependent species and 12 zone-independent species using data pooled over all plots (Table 3), significant differences in mean habitat position (Mann-Whitney $U = 23$, $P = .057$) and habitat size (Mann-Whitney $U = 17$, $P = .016$) were revealed. Species that occupied more than one zone had mean (±SD) habitat positions (0.91 ± 0.36) that were closer to the random centroid than zone-restricted species (1.14 ± 0.17) and larger mean habitat sizes (3.46 ± 0.75) than zone-dependent species (2.35 ± 0.97). A greater number of zone-dependent species also had intermediate or far habitat positions, implying use of scarcer habitat ($\chi^2 = 11.4$, $P < .01$), and smaller habitat sizes ($\chi^2 = 7.0$, $P < .05$) than did zone-independent species (Table 5),

TABLE 6. Summary of community attributes of riparian breeding birds in southeastern Wyoming based on findings from Finch (1986, 1987, 1989), and this study. Results are reported at two spatial scales: overall gradient and elevational zone.

		Elevational zone		
	Overall gradient	Cottonwood–willow	Mixed shrub-willow	Subalpine willow
Habitat base	—*	Complex	Moderate	Simple
Species richness†	45	35	28	12
Number of pairs per 8.1 ha‡	—*	98.8 ± 19.08	78.1 ± 18.25	36.4 ± 22.14
Number of guilds	6	6	5	3
Mean random : species overlap	—*	0.81 ± 0.15	0.60 ± 0.13	0.73 ± 0.04
Mean species : species overlap	0.40 ± 0.26	0.65 ± 0.20	0.68 ± 0.12	0.85 ± 0.07
Random habitat size (A)§	3.97	3.31	3.10	2.58
Mean species' habitat size (B)§	3.02 ± 0.99	3.19 ± 0.77	2.26 ± 0.71	1.57 ± 0.09
Difference between A and B (%)	24	4	27	39
Average species	—*	Generalist	Moderate	Specialist

* — = not applicable.
† Total number of breeding species counted in each zone and across the entire gradient.
‡ Pair abundance was first averaged across plots within each year and zone, then averaged across the three years.
§ Random habitat size is the variance of random station scores from the random centroid, whereas mean species habitat size is the average of the variances of breeding-territory scores from each species centroid.

further corroborating major differences in habitat use between these groups.

Because some zone-independent species had smaller habitat sizes within a particular zone (e.g., Zone 1: Willow Flycatcher; Zone 2: Broad-tailed Hummingbird, Yellow Warbler, Lincoln's Sparrow) than did zone-restricted species (e.g., Zone 1: Warbling Vireo, Western Wood Pewee, Mourning Dove) (Table 4), differences in habitat size were not as evident at the zone level of resolution. Such zone-independent species specialized on habitat patches within zones even though they had a wide distribution. In addition, habitat sizes of some zone-independent species (Yellow Warbler and Brewer's Blackbird) differed from size of the total resource base but not from size of a zonal base. Changing the scale of observation resulted in a different view of the system. As Allen and Starr (1982) argue, there is no reason to expect that any scale of observation is more important or valid than other levels. The key to understanding complex community patterns is to examine systems at several different scales.

Other effects of spatial scale

Habitat use was less similar among all 20 species at the scale of the entire elevational gradient (mean species: species overlap = 0.40) than at the zone level (Table 6). Variability in random samples and in territory-centered samples was also generally greater at the scale of the gradient than at the zone level (see Table 6: mean habitat size of species), as expected given the wider range of habitat structures. More species and more guilds were also encompassed using the wider scale (Table 6).

DISCUSSION

In this study, I examined avian habitat use during the breeding season at the spatial scales of the altitudinal gradient and the elevational zone. Characteristics of the studied communities are summarized in Table 6. I used indices of habitat-niche size and habitat overlap to test a variety of hypotheses. Because the mean species-habitat size was significantly smaller in subalpine birds than in foothill birds, I rejected the null hypothesis of no difference in habitat use among zones. However, since random habitat size was also smaller in subalpine habitats than in cottonwood habitats, I suggest that species-habitat size is limited by habitat diversity within each zone.

The null hypothesis that species-niche size is equal to the size of the habitat resource base was not rejected for most of the cottonwood–willow species examined, but was rejected for all of the subalpine species and 6 of the 10 mixed-willow species. I conclude that, on average, lowland species were generalized in habitat choice, subalpine species were specialized, and mid-elevation species were intermediate.

Mean overlaps among species did not vary among zones, suggesting that zonal variation in species diversity was not accomplished through variation in sharing of habitat space. Overlap between occupied habitats and randomly sampled habitats did vary among zones (null hypothesis rejected), indicating that species used available habitats differently among zones. Cottonwood–willow species were more likely to use habitat randomly whereas subalpine species used habitat selectively avoiding open meadows while selecting shrub thickets.

On average, zone-dependent species had smaller habitat sizes than zone-independent species, but some zone-dependent species were generalists within their zones. Over the whole gradient, 5 of the 8 zone-dependent species were specialists, while only 4 of 12 zone-independent species were specialists. The null hypothesis of no difference in species-habitat size and size of the resource base was not rejected for three zone-dependent lowland species: Western Wood Pewee,

Warbling Vireo, and Mourning Dove. Although each of these species occupied only one riparian zone in this study, they are also commonly found in woodlands far from streams (Finch and Reynolds 1988). If zone-dependency in these species only applies to riparian habitats, then their nonspecialized use of streamside woodlands may be explained by their widespread use of other (nonriparian) habitats.

Species diversity, habitat use, and habitat complexity

Using my test results, i.e., habitat sizes, habitat overlaps, I then asked questions about the relationship between species diversity and habitat use. When resources are heterogeneous and widely available, species diversity should be high compared to communities with fewer resources (MacArthur and MacArthur 1961, Pianka 1979). This prediction was supported when measures of habitat structure and species diversity were compared among zones. Cottonwood lowlands were structurally and floristically more complex than riparian shrub communities. This was reflected by the larger mean values for structural variability (size) of randomly sampled habitats (Table 6). Species richness, overall bird abundance, and the number of foraging guilds were substantially higher (Finch 1986, 1987; Table 6) in foothill woodlands. Zonal differences in bird species diversity were not readily explained by differences in mean species-niche size or habitat overlap, contrary to some ideas (Schoener 1974*a*, *b*, Diamond 1975, Roughgarden 1976). Mean species-habitat size in cottonwood communities was only 4% smaller than mean random size in that zone, and few species had habitat sizes that differed significantly from random, suggesting that the woodland species assemblage contained a large generalist component. Considering also that habitat overlap between random sites and sites used by birds was higher in Zone 1 than in Zones 2 and 3, I conclude that many woodland species examined in this study were distributed in lowland habitats in a close-to-random manner. Mean habitat overlap among co-occurring woodland species was high (Overlap Index = 65%), but similar to those in the two shrub-willow zones. Thus species packing in the most complex habitat was not accomplished by either compression in habitat size of species (Schoener 1974*b*) or increased habitat overlap among species.

Given that (1) most species in Zone 1 made wide use of the available habitat structure, (2) mean habitat size of Zone 1 species was greater than in treeless shrub habitats, and (3) species-habitat overlaps in Zone 1 were no higher (or lower) than in shrublands, it seems likely that species diversity in narrowleaf cottonwood habitat was greater merely because the structural resource base is broader. Habitat resources were not clearly partitioned in this situation, and therefore competition for limiting habitat resources was probably not a major influence on avian community development. I suggest that narrowleaf cottonwood communities in southeastern Wyoming are not saturated, but lack specialist species dominant in eastern, southwestern, and coastal riparian systems (e.g., Carothers et al. 1974, Gaines 1974, Johnson and Jones 1977, Hehnke and Stone 1978). It should be remembered that the species sampled in this study were common or abundant, and that rare, possibly specialized species did not contribute any weight in the analyses.

These results agree with Knopf's (1986) that riparian woodland avifaunas of the central Rocky Mountains are composed primarily of ecological generalists with continental distributions, or of species at the east or west edges of their ranges. Knopf (1986) found that 67% of the dominant species in Colorado floodplain forest were continental, 8% western, 21% eastern, 0% central, and 4% introduced. Although species composition on my sites was less diverse than that on Knopf's, I found that 5 (14.3%) of the 35 woodland species counted on my study sites had western affinities, 3 (8.5%) had eastern, 1 (2.9%) had central, and the remaining 26 (74.3%) were continental generalists (see Finch 1989, for list of all species counted). Continental species are presumably adapted to a variety of environmental conditions and vegetational types, and it comes as no surprise that large habitat sizes were computed for a high proportion of cosmopolitan species in my woodland areas. Mengel (1970) suggested that the Great Plains grasslands served as an ecological barrier between avifaunas of eastern and western North America. Wider establishment of riparian forests since the turn of the century has apparently permitted recent colonization of woodland birds that were historically prevented from dispersal by the Great Plains (Knopf 1986). Early photographs and paintings, as well as records and journals of explorers and frontiersmen, indicate that plains cottonwood (*P. deltoides* var. *occidentalis*) traditionally occurred only in local patches in the Great Plains (Williams 1978, Skinner 1986). Planting of shelterbelt woodlands, and damming and irrigation practices have allowed cottonwoods to flourish in areas that were too dry and unsuitable before European settlement (Droze 1977, Williams 1978, Skinner 1986). Establishment of prairie riparian forests provided flight corridors for avian colonization of the central Rockies (Knopf 1985), including settlement of narrowleaf cottonwood habitats of the foothills and mountains. The first invasion of woodland birds consisted of cosmopolitan species able to adapt to new environmental conditions, presumably because of the generalized nature of their habitat use.

Ricklefs (1987) recommended that ecologists broaden their concepts of community processes by incorporating regional data related to geographic dispersal and species formation into analyses of ecological patterns at the local level. Dispersal and speciation add new species to communities, building up local diversity

(Ricklefs 1987). As diversity increases, the ecological niche is presumably compressed until it reaches a threshold size at which level other species are excluded (MacArthur and Levins 1967). At this saturation point local diversity can be explained in terms of niche size and the limiting similarity of coexisting species (MacArthur and Levins 1967). In nonsaturated environments, limits to niche size and number of coexisting species have not been reached, and therefore a historical, regional perspective involving species dispersal patterns, speciation rates, and evolutionary time is needed to resolve questions of local diversity (MacArthur 1965, Ricklefs 1987). An understanding of niche patterns and local diversity in riparian communities is improved by adopting a regional approach. My interpretation that avifaunas in narrowleaf cottonwood habitats of southeastern Wyoming are nonsaturated because niche sizes were not compressed is supported by the idea that the Great Plains serves as a historical geographical limit to dispersal of riparian birds. Local diversity in riparian woodland avifaunas in the central Rockies may therefore increase in time through processes of speciation, immigration, specialization, and consequent compression in niche size.

Conclusion

Constraints placed on species-habitat selection and community structure by spatial variation in the environment appeared to operate at different spatial scales. Spatial variation in vegetation at the level of resolution of the overall altitudinal gradient led to spatial differences in avian species composition, species richness, bird abundance, and number of guilds. In this paper, I used the amount of vegetational variation along the elevational gradient as an index to habitat resource complexity and abundance. A pyramid of habitat resources was demonstrated, with habitats at lower elevations having a broad and complex resource base and habitats at high elevations having a narrow and simple base. Viewed at this wide observational scale, individual species preferred specific segments of the habitat gradient as indicated by abundance patterns (Finch 1987, 1988, 1989). These segments corresponded to habitat zones influenced by elevation. Most zone-independent species were found to be habitat generalists at this overview level of resolution, whereas more zone-dependent species were identified as habitat specialists. These conclusions are supported by comparisons of average habitat size, position, and overlap and frequency distributions of zone-dependent and zone-independent species.

At the smaller observational scale of the elevational zone, new patterns of niche size and overlap emerged. Constraints on species assemblages included within-zone spatial variation in habitat structure and possibly physical proximity of other individuals and species within the zone. A different assortment of specialists and generalists appeared when within-zone measures of habitat size and overlap were considered. For example, some species that were habitat specialists at the wide observational scale were generalists within a zone (Yellow Warbler in Zone 1, Brewer's Blackbird in Zone 2), and vice versa (Willow Flycatcher in Zone 1, Broad-tailed Hummingbird in Zone 2). Some zone-dependent species remained habitat specialists regardless of scale (Wilson's Warbler, White-crowned Sparrow, Common Yellowthroat, Dusky Flycatcher, MacGillivray's Warbler), as did one zone-independent species (Lincoln's Sparrow).

Changing the scale of observation affected the range of variation that could be measured. In larger comparisons (i.e., total gradient), a greater diversity of species and habitat characteristics could be sampled. As the level of comparison was reduced (i.e., to the finer scale of zone), the range of variation correspondingly shrank. Thus, viewing communities at different levels of resolution identified patterns in habitat–species relationships that were obscure or incomplete at a single scale. As Maurer (1985) has argued, emphasis on a single observational scale reduces the ability of the observer to detect patterns or components of community response that are only clearly visible at other scales. The use of multiple observational scales should considerably enhance our understanding of complex ecological systems.

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