

BIRD-HABITAT RELATIONSHIPS IN RIPARIAN
COMMUNITIES OF SOUTHEASTERN WYOMING

by

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Bird-habitat relationships along a riparian gradient in southeastern Wyoming were examined from 1982 to 1984. Breeding birds were spot-mapped on ten study grids established over an elevational cline of 933 m. Habitat analyses indicated significant trends of decreasing vegetational complexity from low to high elevations, with declines in number of habitat layers, and increased dominance of shrub willow. To evaluate avian responses to these changes in habitat structure, I used three analytical approaches.

In Chapter 1, I tested the null hypothesis of no association among bird species by contrasting number of significant correlations in species abundances across the elevational cline to that predicted by chance alone. The null hypothesis was rejected because 48 of 190 correlations were significant. Species abundance levels were significantly related to one or more principal components or habitat gradients. Once effects of habitat trends were removed using partial correlational analysis, the number of significant correlations in species' abundances substantially declined. I concluded that habitat variation alone sufficed to explain species associations and spatial fluctuations in bird numbers.

Effects of habitat changes on avian guild structure were explored in Chapter 2. Ground and lower-canopy foragers dominated all three zones, but upper-canopy, aerial, and bark foragers declined in abundance with ascending elevation. Highest guild similarities were between lowland cottonwood plots and mixed shrub willow areas. Trends in avian numbers were explained by relating guild occupancy patterns to presence or absence of habitat strata in each zone.

Patterns of habitat niche size and overlap were examined in Chapter 3. Habitat niche size in lowland species was enlarged compared to shrubland species because the structural resource base was broader, and woodland species were on average more flexible in habitat use. At the observational scale of the elevational cline, zone-restricted species displayed a narrower average niche size than zone-independent species, but at the resolution level of the zone, many of these species were eurytypic, exhibiting wide intra-zonal variability in habitat use. Viewing avian communities at two observational scales revealed patterns in niche relationships that were obscured at a single scale.

PREFACE

This dissertation examines the relationship between bird abundance patterns, habitat gradients, and habitat niche size and overlap of bird species in riparian vegetational communities of southeastern Wyoming. I chose to study riparian communities for a variety of reasons. Riparian habitats are rare, typically comprising less than 2% of the total land area in the western United States. In the central Rocky Mountains, about 80% of the region's avifauna breed or winter in cottonwood woodlands and 28% use riparian habitats exclusively. In addition, bird species richness and bird abundance are usually much higher in streamside habitats than in surrounding upland vegetation. Thus, a better understanding of avian habitat selection in riparian ecosystems is essential for protecting and managing these critical habitats. Data on bird numbers and species richness will aid the U.S. Forest Service in choosing avian indicator species and in developing Wildlife-Habitat Relationships Models for riparian habitats on National Forests.

The underlying reasons for high bird species diversity and patterns of species associations in riparian ecosystems can be assessed using hypotheses of current ecological interest. Because riparian communities are highly complex, accurate interpretations of community patterns are difficult. Yet many contemporary ecological theories are based on interpretations of simple ecosystems that are

limited in view and possibly misrepresentative of some natural communities. To broaden our understanding of community organization and development and to verify community niche theory, complex systems must be investigated also. With these goals in mind, I tested a variety of null hypotheses related to bird species diversity, species associations, niche size and overlap, and habitat structure in riparian ecosystems.

My thesis is divided into three chapters. In the first chapter, I used data from bird counts and habitat structure measurements to discover how and why bird populations vary in abundance across an elevational cline. In the second chapter, I investigated the relationship between dominance patterns of avian foraging guilds and habitat stratification in three riparian zones. The last chapter used a niche metrics approach to address the underlying reasons for variation in bird species diversity in riparian habitats.

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CHAPTER 1
COVARIATION OF BIRD SPECIES ALONG AN ELEVATIONAL CLINE
IN THE CENTRAL ROCKY MOUNTAINS

ABSTRACT.--Bird species associations and responses to habitat variation along a riparian elevational cline in southeastern Wyoming were examined between 1982 and 1984. Breeding birds were spot-mapped on ten 8.1-ha study grids established over an elevational range of 933 m. Low-elevation sites (2050 to 2250 m) contained a cottonwood overstory; mid-elevation (2300 to 2530 m) plant associations were comprised of mixed species of shrub-willow; and high-elevation sites (2600 to 3000 m) were dominated by shrub thickets of one dwarf willow species. To test the null hypothesis of no association among bird species, I compared abundance patterns of species pairs and contrasted the number of significant correlations to that predicted by chance alone. Patterns of association among suites of species were determined by organizing significant positive correlations into groups based on Euclidian distances between species abundances. To assess potential underlying reasons for patterns of species co-occurrence, I examined the relationship between species distributions and rank elevational zones, and then applied principal components analysis (PCA) to a series of habitat variables to detect major habitat trends. The relationship between bird species distributions and habitat gradients was then evaluated to determine if habitat variation was

responsible for variation in bird numbers. Once species-habitat associations were ascertained, species interactions were sought by performing a second test of species-species associations, controlling for shared habitat gradients and elevation using partial correlation analysis.

The null hypothesis of no association among bird species was rejected because 48 of 190 correlations of species abundances were significant, a much greater proportion than that expected by chance; 36 correlations were positive, and only 12 were negative. Five groups of covarying species were detected: 1) species occurring principally in lowland cottonwood habitats; 2) species nesting primarily in dense shrub foliage at middle elevations; 3) species reaching peak abundance in lowland woodlands, but occupying mid-elevation shrub habitats as well; 4) species reaching peak abundance in shrub willow habitats, but also found in shrub patches of lowland woodlands; and 5) species preferring subalpine shrub meadows. Nineteen of 20 bird species were significantly associated with specific habitat zones.

Five principal components (PC1-PC5), each representing a habitat gradient, were found using PCA on a set of 19 vegetation features. PC1 signified a gradient of decreasing canopy height and tree density related to increase in elevation; PC2 represented a shrub size continuum; PC3 was a gradient of shrub dispersion and cover; PC4 accounted for variation in mid-canopy foliage density; and PC5 characterized variation in ground cover and surface moisture. Abundance levels of 19 of 20 bird species were significantly related to one or more of

these gradients. Once the effects of these habitat and elevational trends were removed using partial correlational analysis, the number of significant correlations between species' abundances substantially declined. The null hypothesis of no association among species was accepted because habitat variation and elevation alone sufficed to explain spatial fluctuations in bird numbers. I concluded that pairs and suites of covarying species were positively associated because they shared the same habitat affinities, responding similarly to changes in riparian habitat structure.

INTRODUCTION

Community ecologists have long been interested in detecting patterns in the distribution and abundance of species, and discovering what underlying processes cause these patterns in species assemblages (Wiens 1983). Historically, plant ecologists viewed communities as random sets of noninteracting species, the abundance of each species regulated independently according to its own environmental requirements (Gleason 1926, Curtis 1959). With the rise of the MacArthurian school of thought in the 1950's and 1960's, a paradigm began to prevail that communities were highly ordered units of interacting species and that interspecific competition for similar resources was the predominant force structuring communities (e.g., MacArthur 1958, 1971, 1972; Cody 1974; Schoener 1974a; Diamond 1975, 1978). Advocates of the competition paradigm have often inferred that absence of competition in contemporary communities was a result of historical competition for resources that has ultimately led to current resource partitioning among species. Connell (1980) criticized this conclusion, which he labeled "the ghost of competition past," as illogically interpreting the absence of competition as proof of its existence. Like Connell (1980), Strong (1984) and Wiens (1984) regard this hypothesis as unsatisfactory because it is not falsifiable.

Noncompetitive coexistence of animals sharing common resources may actually be widespread (Birch 1979; Strong 1982, 1984; Wiens 1983,

1984; Lawton 1984; James and Boecklen 1984). Bird communities in nonequilibrium grassland and shrubsteppe habitats were shown to be characterized by a "decoupling" of ecological interactions (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981). Individuals exploited resources opportunistically in nonsaturated habitats, and population dynamics were influenced by density-independent agents such as weather and climate rather than by resource availability (Wiens 1984). In such nonequilibrium systems, patterns in the distribution and abundance of species were lacking or were loose and inconsistent. Wiens and Rotenberry (1981) noted that nonrandom community patterns were more difficult to observe at the local level than on a broad geographical scale because they were the grouped attributes of individual species' processes.

Despite such admonitions, it is unwise to infer from these findings that most communities are noninteractive or patternless, especially if temperate shrubsteppe habitats are atypical, as suggested by Schoener (1982). Although interspecific competition may not be as prevalent as was once thought (Wiens 1977), experimental studies convincingly show that many species do directly compete for resources (Connell 1983, Schoener 1983). In addition, nonrandom patterns produced by processes other than competition have been demonstrated repeatedly in a wide variety of communities (e.g., Birch 1979, Gatz 1979, 1981; Lawton and Strong 1981; Wilbur and Travis 1984). In vertebrate populations, a dominant process causing the aggregation of positively associating species is one of tracking

shared, fluctuating resources (Dunning and Brown 1982, Schluter 1984). Schluter (1984) has indicated that positive rather than negative species associations are the norm in animal communities.

Habitat occupancy patterns of multiple species along gradients of habitat structure are often examined to find positive or negative trends in bird species associations. Pairs or suites of bird species that covary in distribution and abundance may be exhibiting a common response to variation in habitat features. Such association (and disassociation) patterns caused by changes in habitat structure are readily observed along temperate altitudinal gradients (e.g., Abele and Noon 1976, Noon 1981a). Noon (1981a) invoked the idea of past competition to explain the habitat association patterns of five thrush species arrayed along an elevational montane cline in Vermont. Terborgh (1971, 1985) and Terborgh and Weske (1975) also concluded that competitive exclusion was the dominant process accounting for the altitudinal limits of Andean birds in Peru. In the Andean ecosystem, Terborgh (1985) convincingly demonstrated that habitat ecotones accounted for only one-sixth of species distributional boundaries. Terborgh suggested that competitive interactions were far less important in temperate mountains than in tropical ones.

To readdress the question of species association patterns in temperate ecosystems, I searched for patterns in avian distribution and abundance along a local riparian elevational continuum in the central Rocky Mountains, asking the following questions:

1) Do elevational zones define the boundaries of habitat types and bird assemblages?

2) Can general patterns in species richness and overall bird abundance be found that parallel elevational habitat changes?

3) Are the distributions and abundance levels of individual bird species limited by habitat ecotonal changes?

4) Do pairs, suites, or whole assemblages of bird species covary in their abundance and, if so, are such positive associations related to variation in habitat structure and elevational ecotones? Also, if habitat trends do not predict co-occurrence patterns, is an alternative hypothesis of biotic interaction among species supported?

5) If any bird species are negatively associated, can an explanation be found without invoking the "ghost of competition past"?

To answer these questions, I first tested the null hypothesis of no association among bird species along an altitudinal cline. To assess potential underlying reasons for species associations, I examined the relationship between species distributions and altitudinal habitat trends. If habitat variation is responsible for variation in bird numbers, then species co-occurrence patterns may be a secondary consequence of species-habitat association patterns. I therefore removed the effects of habitat; retested the null hypothesis of no association; and compared these results to my first test of no association.

STUDY AREA AND METHODS

Description of Study Sites.--Study sites were established in streamside habitats in (or within 16 km of) the Medicine Bow National Forest of southeastern Wyoming (Figure 1). Ten 8.1-ha study grids were distributed over a riparian elevational gradient of 933 m. Each grid was marked at 33.5-m intervals with wooden stakes painted fluorescent orange. Grid dimensions were adapted to the variable widths of the streams in the following interval block combinations: 4 X 18 (sites 2 and 7); 3 X 24 (sites 3, 4, 5, 9 and 10); 2 X 36 (site 6); and 6 X 12 (sites 1 and 8). Study areas encompassed a continuum of riparian plant species and vegetational communities and excluded edge habitats (Table 1).

At lower elevation sites (2050 to 2250 m), narrowleaf cottonwood (Populus angustifolia) dominated the upper canopy, with scattered plains cottonwood (P. sargentii), aspen (P. tremuloides), peachleaf willow (Salix amygdaloides), and cedar (Juniperus scopulorum). Understories at these sites were dominated by combinations of tree and bush willow species (Table 1).

Additional shrubs locally common or present at lower elevations and extending up to elevations of about 2600 m were thinleaf alder (Alnus tenuifolia), maple (Acer glabrum), birch (Betula fontinalis), river hawthorn (Crataegus rivularis), western snowberry (Symphoricarpus occidentalis), golden currant (Ribes aureum),

Figure 1. Locations of ten study plots (Pl-P10) in southeastern Wyoming. Refer to Table 1 for a description of study plots.

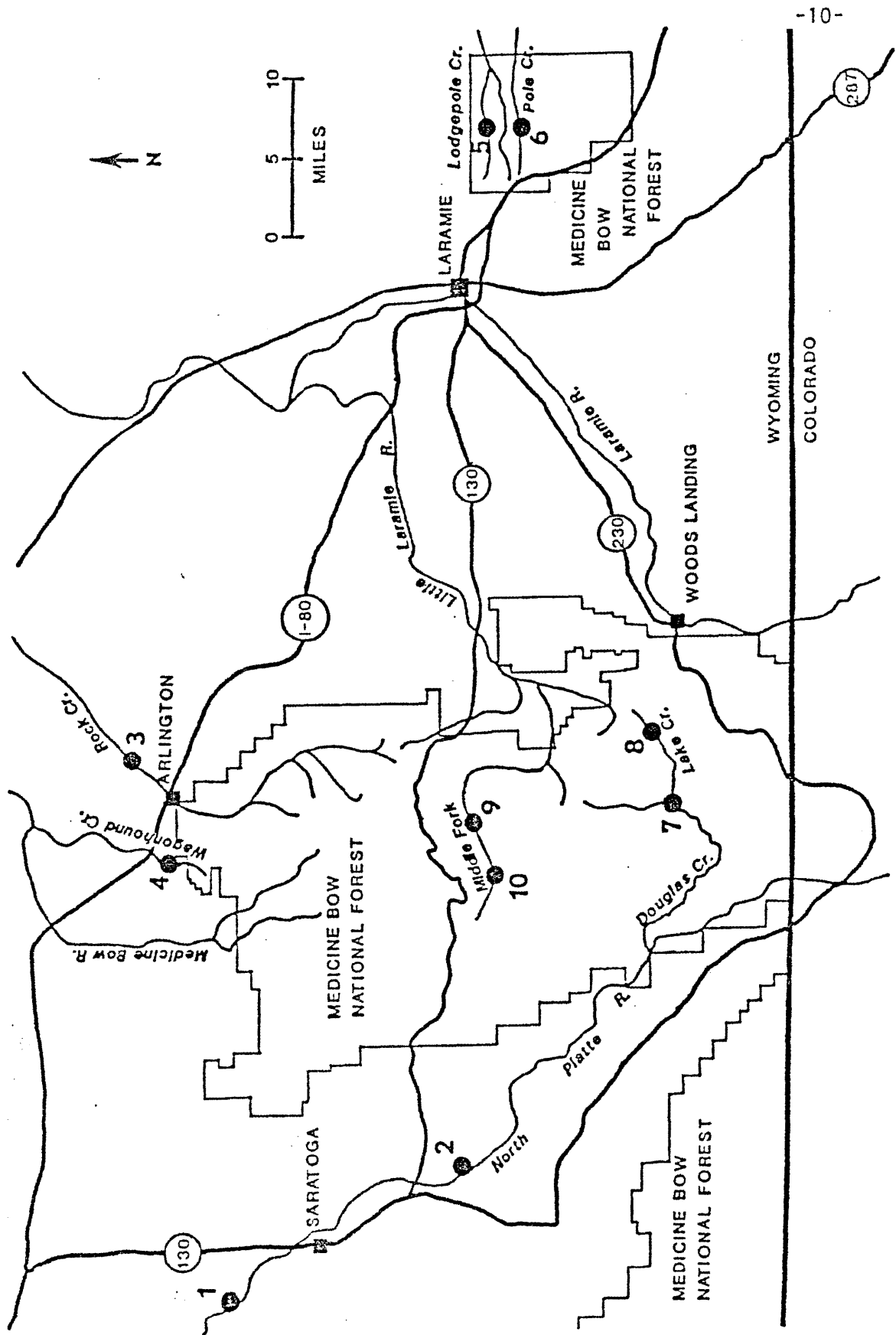


Table 1. Description of dominant overstory and understory vegetation in study areas.

Site no.	Drainage	Elevation (m) ²	Dominant vegetation	
			Overstory	Understory
1	Poote Camp, N. Platte River	2054	<u>Populus angustifolia</u>	<u>Betula fontinalis</u> , <u>Salix exigua</u> , <u>S. lasiandra</u> , <u>S. ligulifolia</u>
2	Treasure Island, N. Platte River	2097	<u>P. angustifolia</u>	<u>Betula fontinalis</u> , <u>S. exigua</u> , <u>S. interior</u> , <u>S. bebbiana</u> , <u>S. lasiandra</u>
3	Rock Creek	2256	<u>P. angustifolia</u> <u>P. tremuloides</u>	<u>S. bebbiana</u> , <u>S. monticola</u> , <u>S. drummondiana</u>
4	Wagonhound Creek	2286	<u>Populus spp. (scattered)</u> <u>Betula fontinalis</u> , <u>Alnus</u> <u>tenuifolia</u> , <u>S. bebbiana</u> , <u>S. exigua</u> , <u>S. boothi</u>	<u>Calamagrostis canadensis</u> , <u>Carex</u> , spp.
5	N. Fork, Middle, Lodgepole Creek	2470	<u>P. tremuloides (isolated</u> <u>clusters)</u> , <u>S. geveryana</u> , <u>S. boothi</u> , <u>S. ligulifolia</u> , <u>S. planifolia</u>	<u>C. canadensis</u> , <u>Carex</u> spp.
6	Pole Creek	2530	<u>P. tremuloides (scattered)</u> , <u>S. geveryana</u> , <u>S. lasiandra</u> , <u>S. barclayi</u>	<u>C. canadensis</u> , <u>Carex</u> spp.
7	Douglas Creek	2591	<u>S. planifolia</u> , <u>S. wolfii</u>	Boggy meadow, <u>Deschampsia</u> <u>cespitosa</u> , <u>Carex</u> spp.
8	Lake Creek	2789	<u>S. planifolia</u> , <u>S. wolfii</u>	Boggy meadow, <u>Deschampsia</u> <u>cespitosa</u> , <u>Carex</u> spp.
9	Middle Fork, Little Laramie R.	2930	<u>Picea engelmanni</u> (encroaching)	Wet meadow, <u>Deschampsia</u> <u>cespitosa</u> , <u>Carex</u> spp.
10	Middle Fork, Little Laramie R.	2987	<u>S. planifolia</u>	Wet meadow, <u>Deschampsia</u> <u>cespitosa</u> , <u>Carex</u> spp.

gooseberry (Ribes spp.), common chokecherry (Prunus virginiana), serviceberry (Amelanchier alnifolia), cinquefoil (Potentilla gracilis, P. fruticosa), wild rose (Rosa woodsii, R. acicularis), red raspberry (Rubus idaeus), and red-osier dogwood (Cornus stolonifera).

Short-grass prairie interspersed with sagebrush (Artemisia spp.) bordered lower elevation communities.

Mid-elevation drainages (2290 to 2530 m) were typically bordered by sagebrush (A. tridentata), grassland, and lodgepole pine (Pinus contorta) forest. Cottonwoods disappeared and aspen occurred in small isolated patches within bush willow communities. New dominant willow species were added to communities (Table 1) and there were local occurrences of Salix barclayi, S. ligulifolia, and S. candida.

At high elevations (2590 to 3000 m), S. planifolia was found in monocultures or mixed with S. wolfii. The subalpine parks formed by these species were associated with wet or boggy meadows surrounded by mixed stands of Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa). A more detailed account of plant species distributions in the Medicine Bow Mountains can be found in Nelson (1974). Distributional patterns of central Rocky Mountain willow species are described in Knopf and Cannon (1982) and Cannon and Knopf (1984). I used the taxonomic keys of Argus (1957) and Nelson (1974) to identify closely related willow species.

Sampling Avian Populations.--Avian populations were counted on the ten study grids using the International standard of the spot-map method (Robbins 1970) during the breeding seasons (May to July) of

1982, 1983, and 1984. 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 visitors and were not included in the analyses. Each study plot was visited 8 to 15 times each year, and each visit lasted from 2 to 4 hrs. Abundance of each species and of all species combined is reported as the number of territorial pairs observed on an 8.1-ha area. Species richness is the number of species known to be nesting on a study site based on nest searches and territorial data.

To improve the accuracy of spot-map counts, intensive two-hour nest searches were randomly walked immediately following each mapping visit, as well as on alternate days. Nest searches improved the probability of 1) distinguishing multiple avian pairs in a cluster of mapped observations, 2) determining the status of edge territories, and 3) distinguishing between nesting birds and floaters. Approximately 50 hours 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 m x 10.7 m nets, each with a mesh size of 1.3 cm. Nets were monitored on each site from 600 hrs to 1900 hrs for five sequential days. Netting and banding information was used to substantiate the presence of pairs in cases where mapping information was inconclusive (Verner 1985).

Habitat Sampling.--Vegetation structure was sampled in 1982 at 40 randomly selected grid intersections within the boundaries of each

avian-censusing plot. At each location, 34 habitat characteristics were measured following a point-centered quarter sampling procedure recommended by Noon (1981b) for habitats dominated by shrubs. Redundant, invariant, or unimportant variables were deleted, reducing the data set to 19 variables for statistical analysis (see Data Analysis section for further variable selection criteria). Table 2 presents descriptions, acronyms, and sampling methodology of these 19 variables. To improve normality and adhere to statistical assumptions, all statistical tests used log-transformed data. Values are reported for raw data for ease of interpretation.

Data Analysis.--For each species, annual differences in bird abundance (territorial pairs/8.1 ha) were analyzed using one-way ANOVA. Anova was performed on the factor YEAR (1982, 1983, 1984) using three to four sites in each elevational zone. Twenty species were chosen for these analyses based on 1) their high and relative dominance in one or more habitats, and 2) confidence in the reliability of population counts, based on spot-mapping, nest searches and banding. Because annual differences in abundance were not significant for any of these species ($p > 0.05$), averages of yearly plot abundances were used in all subsequent computations. Two cluster analyses were performed on mean abundances of the 20 species to 1) classify plots into habitat zones based on species distributional patterns, and 2) detect suites of associated species. Clusters of plots or species were formed using the complete linkage procedure of amalgamating cases

Table 2. Structural variables used in analysis.

Mnemonic acronym	Variable	Sampling method
CANH	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 quadrant.
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 in each quadrant (Mueller-Dombois and Ellenberg 1974).
SHCD	Shrub crown diameter	Diameter (cm) at breast height of nearest shrubs 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 interval.
VFD2	Vertical foliage density in small shrub layer	Same as VFD1, but in 0.3 - 1 m interval.
VFD3	Vertical foliage density in mid-canopy layer	Same as VFD1, but in 1-2 m interval.
VFD4	Vertical foliage density in upper layer of understory	Same as VFD1, but in 2-9 m interval.
VFD5	Vertical foliage density in overstory layer	Same as VFD1, but in > 9-m 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).
WILL	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	Bare ground coverage	Percent cover of bare ground 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).
WAT	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).

based on Euclidian distances between abundances (Program P2M of BMDP Biomedical Computer Programs Dixon and Brown 1979).

Relationships between pairs of species were assessed using Pearson product-moment correlation coefficients. Significant patterns of association among sets of species were detected by organizing significant positive correlations into preassigned groups based on Euclidian distances between species abundances. Then, by comparing confidence limits of observed percentages of significant correlations with that expected by chance, overall patterns of significance could be seen (Sokal and Rohlf 1969). A chi-square test ($\alpha = 0.05$) was performed to determine if the distribution of positive correlations was less heterogeneous within species groups than between the two sets of correlations.

A variance test suggested by Schluter (1984) was used to test the null hypothesis that the 20 species do not covary among plots. The index of species association in samples is the ratio, $V = S_T^2 / \sum \sigma_i^2$, where S_T^2 is the estimated variance in total species number, and $\sum \sigma_i^2$ is the sum of the variances of individual species densities. The expected value of V under H_0 is 1. A value greater or less than 1 indicates that species covary positively or negatively in abundance in samples. To test the null hypothesis, the association index V was modified to $W = N \cdot V$, where W = index of species association in plots, N = number of plots, and V = index in samples. 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.

For a sample (N) of 10 plots and a density (M) of 20 species and $\alpha = 0.10$, the probability is 0.90 that W will lie between the critical limits $5 \leq W \leq 16$.

An important underlying factor that may cause direct or inverse relationships in distribution and abundance of species is similarity or dissimilarity in habitat preferences. To examine the relationship among species distributions and habitat variation, habitat zones were first assigned rank index values according to high, middle or low elevational positions. To detect trends in species abundance across zones, Kendall's rank correlation coefficient was computed using the elevation-habitat index and the abundance of each species.

Significant positive correlations indicated that a species was strongly associated with high-elevation plots, whereas high negative correlations indicated association with lower elevation zones. Pairwise comparisons of abundances between habitat zones were used to pinpoint specific zone affinities of each species.

A nested design analysis of variance was performed on 19 vegetation attributes to determine and adjust for the effects of site variation within elevational zones, before evaluating zone variation. Wilks' lambda statistic was used to report multivariate differences within and among zones, and univariate F-tests were used to assess variation in specific habitat variables. Habitat variables were selected if at least one simple regression between abundance of a bird species and the vegetation attribute was significant. If two habitat

variables were highly correlated ($r^2 > 0.8$), the variable with the lower correlation with bird abundance was deleted.

I applied principal components analysis (PCA) to the set of 19 habitat variables to evaluate the association between bird populations and riparian habitat gradients. High correlations of habitat variables with the factor scores from the reduced set of principal components were used to interpret each component. Partial correlations between the mean factor scores of significant components (eigenvalues > 1.0) and the abundances of selected species were then calculated to assess the relationship between each gradient and each species. Once significant species-habitat associations were ascertained, a second test of species-species associations was conducted, this time controlling for shared habitat gradients and elevation using partial correlation analysis. Removing the influence of habitat and elevation improved the probability of detecting relationships resulting from species interactions.

Student's t distribution was used to test the significance of product-moment, Kendall's rank, and partial correlations. The SPSS statistical package was used to perform all calculations except cluster analysis (Nie et al. 1975, Hull and Nie 1981).

RESULTS

Bird Associations and Suites of Covarying Species.--A total of 100 bird species were observed during the three-year study period. Forty species were found nesting or defending territories within study

plot boundaries; another 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 other habitats; and six species were considered unusual to southeastern Wyoming. Of the nesting species, five were ducks, rails, and sandpipers which were too dissimilar in taxon, morphology, and behavior to be compared to other community members, and 15 species were uncommon, supplying insufficient population samples for trend analysis. Twenty nesting species with sufficient population sizes and accurate counts were examined in detail (Table 3).

Mean yearly species richness (based on 100 bird species) and total bird abundance both showed high inverse correlations with plot elevation ($\underline{r}^2 = 0.80$; $\underline{P} < 0.001$, and $\underline{r}^2 = 0.78$, $\underline{P} < 0.001$, respectively). Mean 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 three nesting species and 23 pairs at high elevations (Figure 2).

Using product-moment correlations to detect associations among the 20 species, 48 (25.3%) of 190 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 $\alpha = 0.05$ probability level. Confidence limits of the observed percentage of significant correlations (19.2-31.6%) did not overlap with confidence limits of the expected percentage (6.2-15.0%), so the difference between observed and expected was significant. Thus, I

Table 3. Number ($\pm$ S.E.) of territorial pairs per 8.1 ha of 20 bird species censused at ten study sites. Values are three-year means of breeding season densities in 1982, 1983 and 1984.

Species ^a	1	2	3	4	5	6	7	8	9	10
Hemionid										
Mourning Dove (MDOV)	6.00 $\pm$ 0.01	3.66 $\pm$ 0.65	0.67 $\pm$ 0.34							
Zenaida macroura										
Broad-tailed Hummingbird (BTBH)		2.67 $\pm$ 0.34	2.33 $\pm$ 0.66	6.00 $\pm$ 1.00	6.00 $\pm$ 0.00	4.33 $\pm$ 0.88	0.67 $\pm$ 1.15			
Selasphorus platycercus										
Western Wood Pewee (WWPE)	5.00 $\pm$ 0.58	3.33 $\pm$ 0.88								
Contopus sordidulus										
Willow Flycatcher (WIFL)	2.00 $\pm$ 0.58	3.00 $\pm$ 1.16	0.67 $\pm$ 0.65	3.67 $\pm$ 0.65						
Empidonax traillii										
Dusky Flycatcher (DUFY)	0.67 $\pm$ 0.65	0.67 $\pm$ 0.65	1.00 $\pm$ 0.01		3.00 $\pm$ 1.53	3.67 $\pm$ 1.20				
Empidonax oberholseri										
Tree Swallow (TRES)	7.67 $\pm$ 1.20	2.33 $\pm$ 1.46	0.67 $\pm$ 0.66			2.67 $\pm$ 1.20				
Tachycineta bicolor										
House Wren (HWRN)	15.67 $\pm$ 0.34	13.00 $\pm$ 1.53	8.00 $\pm$ 0.58	1.33 $\pm$ 0.88		0.33 $\pm$ 0.34				
Troglodytes aedon										
Veery (VEER)	1.00 $\pm$ 0.00	2.33 $\pm$ 0.34	7.33 $\pm$ 0.88	4.67 $\pm$ 0.66	4.00 $\pm$ 1.16	0.67 $\pm$ 0.34				
Catherpes fuscescens										
American Robin (AMRO)	18.67 $\pm$ 4.71	12.67 $\pm$ 1.20	9.67 $\pm$ 1.20	5.00 $\pm$ 1.16	7.67 $\pm$ 0.66	8.33 $\pm$ 0.34	1.00 $\pm$ 0.58			
Turdus migratorius										
Gray Catbird (GRAY)	0.33 $\pm$ 0.34	2.33 $\pm$ 0.34		3.00 $\pm$ 0.58	0.33 $\pm$ 0.34					
Dumetella carolinensis										
Warbling Vireo (VIRE)	1.67 $\pm$ 0.66	4.00 $\pm$ 0.58	5.33 $\pm$ 0.88		2.00 $\pm$ 0.00	3.33 $\pm$ 0.88				
Vireo gilvus										
Yellow Warbler (YELL)	29.33 $\pm$ 2.19	33.00 $\pm$ 2.31	28.33 $\pm$ 1.86	18.00 $\pm$ 0.58	11.67 $\pm$ 1.20	16.00 $\pm$ 4.90				
Dendroica aestiva										
MacGillivray's Warbler (MGWA)				2.67 $\pm$ 0.66	3.67 $\pm$ 0.88	0.33 $\pm$ 0.34				
Spinus tolmiei										
Common Yellowthroat (COYE)					2.00 $\pm$ 0.00	4.00 $\pm$ 1.00	1.00 $\pm$ 0.00			
Wilson's Warbler (WILW)								19.00 $\pm$ 2.65	5.50 $\pm$ 0.50	6.0 $\pm$ 0.58
Song Sparrow (SONS)	3.33 $\pm$ 0.34	5.67 $\pm$ 0.66	2.67 $\pm$ 0.88	8.67 $\pm$ 1.77	10.33 $\pm$ 2.85	9.00 $\pm$ 3.06	3.00 $\pm$ 0.58			
Melospiza melodia										
Lincoln's Sparrow (LISP)			1.00 $\pm$ 0.00		12.00 $\pm$ 4.59	13.33 $\pm$ 2.19	27.33 $\pm$ 3.49	17.00 $\pm$ 0.00	13.33 $\pm$ 1.67	9.33 $\pm$ 0.34
Melospiza lincolni										
White-crowned Sparrow (WCSP)						0.33 $\pm$ 0.34	8.00 $\pm$ 1.53	4.00 $\pm$ 1.00	4.0 $\pm$ 0.58	10.00 $\pm$ 1.16
Zonotrichia leucophrys										
Brewer's Blackbird (BRBL)			1.00 $\pm$ 1.00		5.33 $\pm$ 0.34	12.67 $\pm$ 1.34				
Eumegascops cinerea										
Brown-headed Cowbird (BRCO)	1.67 $\pm$ 0.68	2.33 $\pm$ 1.46	2.00 $\pm$ 1.00	2.00 $\pm$ 0.58	1.67 $\pm$ 0.34	0.67 $\pm$ 0.66				
Polioptila alix										

^a Study sites are arranged by elevational order (see Table 1).

^b Scientific names and taxonomic order follow the recommendations of the A.O.U. Committee on Classification and Nomenclature (1982).

Figure 2. Trends in bird species richness and overall bird abundance across a riparian elevational gradient.

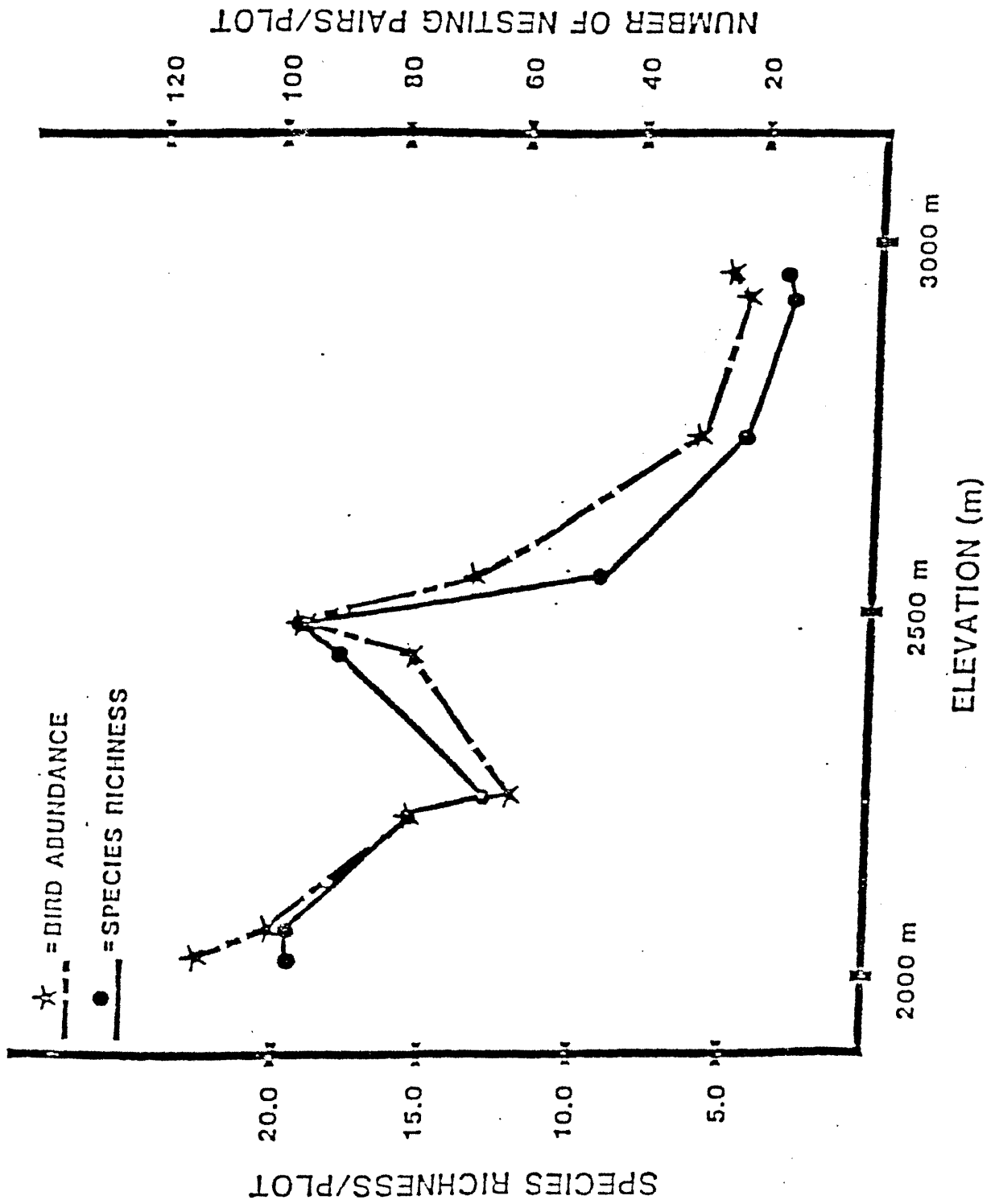


Table 4. Results of cluster and Pearson product-moment correlation analyses specifying groups of species that covary in abundance across census plots. Species groups denoted by block areas in table and group identification numbers were produced.

Group	Species acronyms	MODO	WPE	HOWR	TRSW	DUFL	BRBL	COYE	WIFL	YEMA	BHCO	AMRO	VEER	GRCA	WAVI	MGWA	SOSP	BTHU	LISP	WCSP	WIWA
1	MODO		+	+	+					+											
1	WPE	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	YEMA	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	

^a Significant ($P < 0.05$) positive and negative correlations between species abundances are indicated with "+" and "-", respectively in the upper half of the table. Two-tailed t tests were used to evaluate significance.
^b The numbers in lower half of the table are rank values for Euclidian distances between species with the value 1 indicating greatest similarity and the value 8 indicating lowest similarity. For each ranking actual distances are 1 = < 2.28; 2 = 2.28 to 2.67; 3 = 2.67 to 3.20; 4 = 3.20 to 3.73; 5 = 3.73 to 4.47; 6 = 4.47 to 5.92; 7 = 5.92 to 6.93; 8 = > 6.93.

rejected the null hypothesis that pairs of bird species were not associated. Twelve significant correlations (6.3%) were negative, and 36 (19.0%) were positive. Positive correlations suggested similarities in habitat preferences between species. For example, mourning dove, western wood pewee, house wren, and tree swallow occurred primarily in cottonwood stands. Wrens and swallows nested in tree cavities, and doves and wood pewees always built nests in tall trees rather than shrubs. Thus, all paired correlations among these four species were positive.

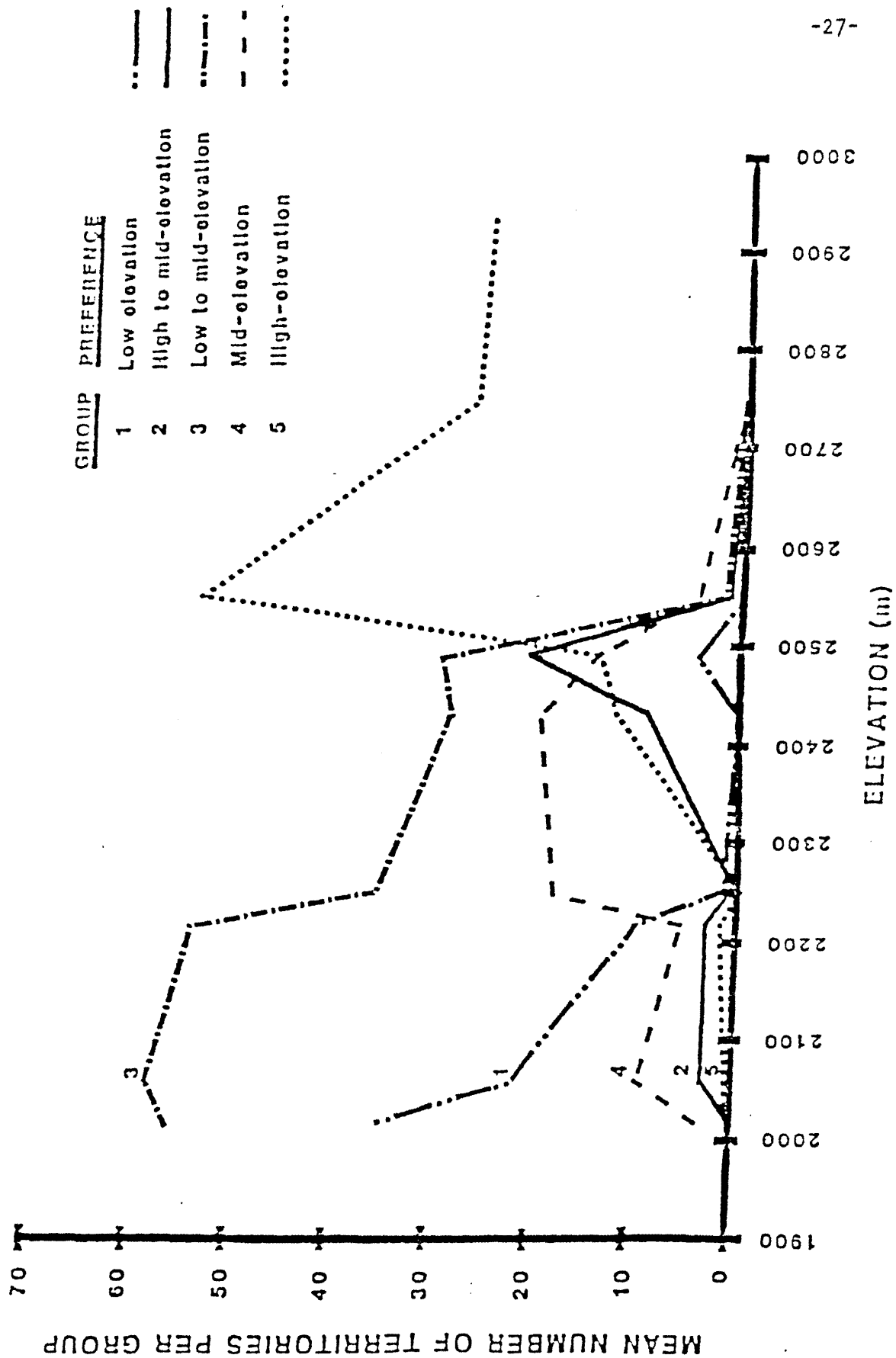
Five groups of covarying species were generated using cluster analysis (Table 4). When significant correlations of species abundances were arranged by Euclidian distance, it was evident that species pairs within each cluster were positively correlated in most cases (Table 4). The distribution of positive correlations in the species by species matrix was highly heterogeneous primarily because the number of positive correlations within species groups was much greater than that expected by chance ($\chi^2 = 159.5 > \chi^2_{0.05,1} = 3.84$). The significance of this test implies that these groups of co-occurring species are statistically consistent, but it does not imply interaction among species because species may respond in common to changes in resources or climate along the elevational gradient.

Group 1 was composed of the tree-dwelling species described above. Group 2 was composed of dusky flycatcher, Brewer's blackbird, and common yellowthroat. These species nested primarily in mid-elevation habitats with dense shrub foliage. Group 3 was comprised of willow

flycatcher, yellow warbler, brown-headed cowbird, American robin, veery, gray catbird, and warbling vireo, species that reached peak abundance in low-elevation cottonwood habitats, but that occurred in mid-elevation shrub habitats as well. The fourth group contained species that reached peak abundance in shrub-willow habitats but were also found in shrub patches of cottonwood habitats. Lincoln's sparrow, white-crowned sparrow and Wilson's warbler, members of the last group, were more abundant in subalpine habitats with dwarf shrub willow and grass meadows. When abundance levels of these five groups are plotted with elevation, peaks and trends are easily tracked (Figure 3).

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 habitats that were structurally simple, whereas species in Group 3 nested in tall shrubs or trees and employed a variety of flycatching, foliage-gleaning, and ground-foraging strategies. The negative correlations were, therefore, readily explained by differences in nesting and foraging habitats. Disparity in habitat choice also explains the negative relationship between cavity-nesting house wrens and ground-nesting Lincoln's sparrows. Unlike other members of Group 5, however, Lincoln's sparrows were

Figure 3. Trends in bird abundance within groups of covarying species.
Group determination and composition are given in Table 4.



common on all shrub-willow plots regardless of elevational position. The substantial increase in population size of this species in depauperate subalpine communities (Table 3) suggests that resource competition may have limited its abundance in lower elevation habitats. Although I considered competitive release as a possibility in this sparrow, foraging technique and foraging and nesting substrate are unlikely to overlap greatly with its negatively associated species (see guild classifications, DeGraaf et al. 1985). It is also unlikely that Lincoln's sparrows avoided settling in habitats with the nest parasitic cowbird because on sites where the two species co-occurred, no cowbird eggs or nestlings were found in 18 Lincoln's sparrow nests. All Lincoln's sparrow nests, regardless of site elevation, were found on the ground under very small shrubs (< 0.5 m tall), or tall grass. Thus, increased availability of its preferred nest substrate in high-elevation dwarf willow habitats is the best explanation for its population "release."

The index of species association, W , computed for all 20 bird species was 41.3 ($N \cdot V = 10 \cdot 4.13$) which fell outside the critical limits. Despite the occurrence of negative associations among 12 pairs of species, I concluded that as a whole, this bird assemblage covaried in a significant positive direction. I therefore rejected the null hypothesis of no community association. Positive association may be a shared response to interaction processes such as mutualism, competition, or predation (Schluter 1984) or it may be a non-interactive tracking response to variation in resources such as

food or habitat structure. The following analysis will shed some light on the habitat occupancy patterns of co-occurring species in an effort to ascertain the underlying reasons for species associations.

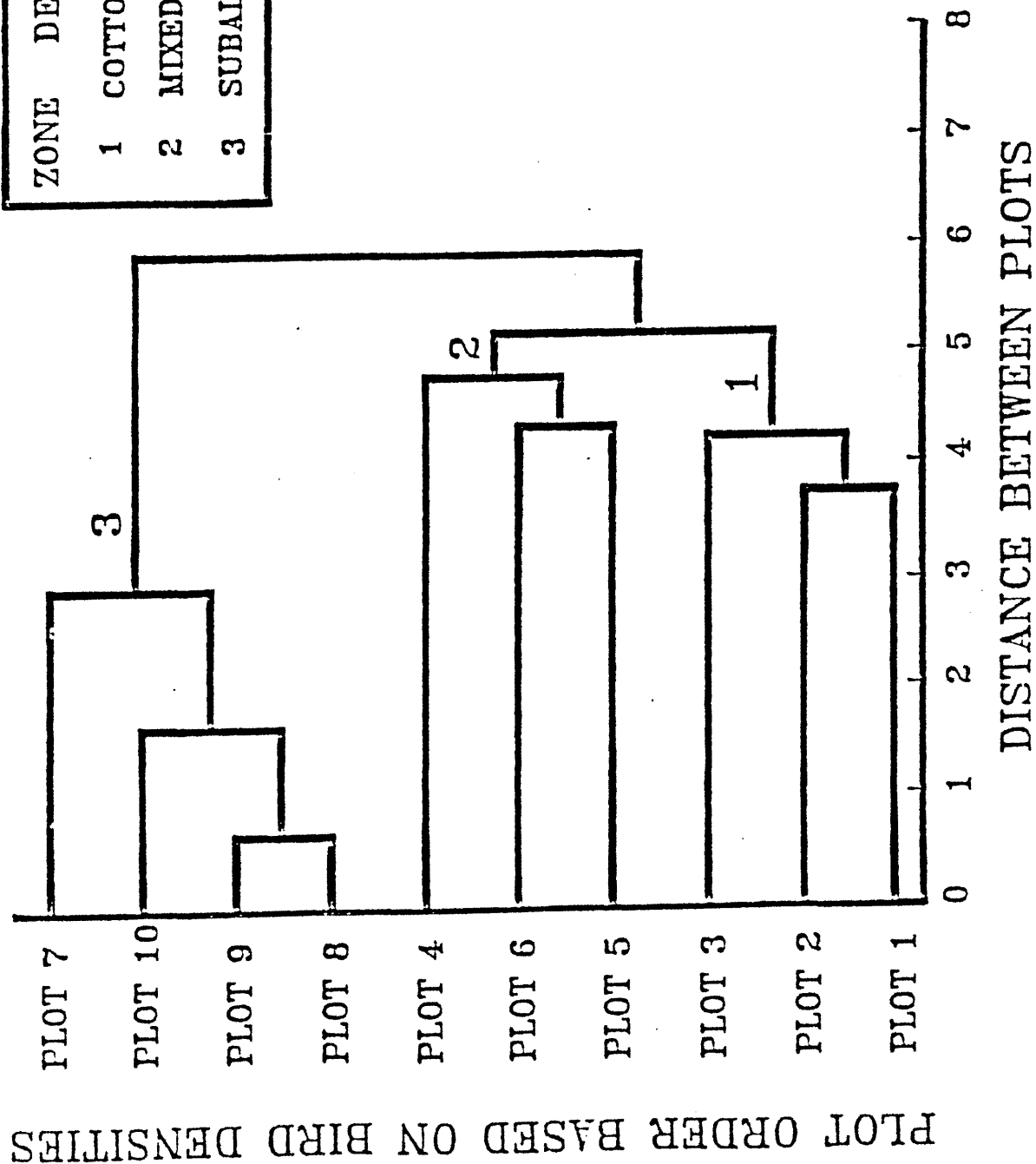
Relationships Between Elevational Zones and Bird Populations.--

Cluster analysis of the species by plot matrix of bird densities revealed three clusters, each composed of 3 to 4 study sites in which species composition and numbers of birds were similar (Figure 4). Bird assemblages clustered into three distinct elevational zones, presumably manifesting three bird communities. I assigned each of these zones an index value of one to three based on rank elevational order.

To test the hypothesis that these bird assemblages are organized into three communities in response to underlying vegetational differences, I first applied nested design multivariate analysis of variance to the set of 19 vegetation features using the cluster index as a categorical factor grouping sites into elevational zones. The overall MANOVA for three zones with three to four sites within each zone indicated that there were highly significant differences in vegetation among sites within zones (Wilks' $\lambda = 0.02$, $\underline{P} < 0.0001$) as well as among zones (Wilks' $\lambda = 3.4 \times 10^{-6}$, $\underline{P} < 0.01$). Univariate F-tests showed that vegetation within zones varied greatly in 16 of 19 variables ($\underline{P} < 0.001$), with only canopy cover and vertical foliage density in the upper two canopy layers (VFD4 and VFD5) showing no significant differences (Table 5). Once the within-zone variation was accounted for, the effects of ZONE emerged. Nine habitat features

Figure 4. Cluster analysis of study plots based on euclidian distances among abundances of 20 common bird species. Three habitat zones were determined as follows: 1 = low-elevation cottonwood-willow, 2 = mid-elevation shrub willow, 3 = high-elevation dwarf willow.

ZONE	DESCRIPTION
1	COTTONWOOD-WILLOW
2	MIXED SHRUB WILLOW
3	SUBALPINE WILLOW



varied significantly among zones (Table 5). These variables were related to increase in elevation in the following ways: 1) reduction and ultimate loss of a tree overstory (CANHT, TDEN, VFD4, VFD5, CANCOV), 2) reduction in shrub diversity (WILL, FRUIT), and 3) increase in woody ground cover (COVER, BARE) (Table 5). For example, TDEN (primarily cottonwoods) decreased from 4.67/100 m² in Zone 1 to 0.03/100 m² in Zone 3, and CANCOV declined from 54.8% to 1.0% (Table 5). The proportion of willow (Salix spp.) in the shrub samples increased from 26% to 91% from Zone 1 to Zone 3 with a corresponding decline in the proportion of fruiting shrubs (Table 5). Along with a COVER increase from 13.5% in Zone 1 to 57.6% in Zone 3 the percentage of bare ground declined from 34.7% to 4.9%, indicating that subalpine ground was densely covered by vegetation. Because the three elevational habitat zones were initially distinguished by avian abundance patterns, it seems probable that these vegetational changes among zones provided a means for structuring bird communities based on species habitat preferences.

Closer examination of population distributions of individual species across zones revealed marked trends in elevationally defined habitat preferences. Of 20 species considered, the abundance levels of ten showed significant negative correlation with the elevational index (Table 6). Negative correlations imply strongest association with low-elevation cottonwood-willow habitats. Mourning dove, house wren, American robin, veery, warbling vireo, yellow warbler, and brown-headed cowbird were highly associated with cottonwood-willow

Table 5. Mean ($\pm$ S.E.) values of 19 selected vegetation features and results of nested design analysis of variance testing the effects of site variation within habitat zones and zone variation of vegetation features.

Habitat feature	Cottonwood-willow		Shrub willow		Subalpine willow		Significance level ^b	
							Site within ZONE effect	ZONE effect
CANHT (m)	8.93 $\pm$ 0.3		2.08 $\pm$ 0.1		1.47 $\pm$ 0.1		***	**
TDEN (No./100 m ²)	~~4.61 $\pm$ 0.1~~ ^{59.94}		~~0.53 $\pm$ 0.1~~		~~0.03 $\pm$ 0.0~~		***	***
SHBA (m ²)	0.15 $\pm$ 0.02		0.44 $\pm$ 0.08		0.24 $\pm$ 0.03		***	n.s.
SHCD (cm)	130.95 $\pm$ 7.5		154.94 $\pm$ 7.9		116.39 $\pm$ 6.3		***	n.s.
SHHT (m)	2.01 $\pm$ 0.1		2.08 $\pm$ 0.1		1.47 $\pm$ 0.1		***	n.s.
SHDIS (m)	5.71 $\pm$ 0.6		5.08 $\pm$ 0.7		4.19 $\pm$ 0.3		***	n.s.
VFD1 (#hits)	1.98 $\pm$ 0.1		2.81 $\pm$ 0.2		2.91 $\pm$ 0.1		***	n.s.
VFD2 (#hits)	0.54 $\pm$ 0.1		1.30 $\pm$ 0.1		1.72 $\pm$ 0.1		***	n.s.
VFD3 (#hits)	0.23 $\pm$ 0.0		0.84 $\pm$ 0.1		0.33 $\pm$ 0.1		***	n.s.
VFD4 (#hits)	1.00 $\pm$ 0.1		0.51 $\pm$ 0.1		0.02 $\pm$ 0.0		n.s.	***
VFD5 (#hits)	0.45 $\pm$ 0.1		0.01 $\pm$ 0.0		0.00 $\pm$ 0.0		n.s.	***
CANCOV (%)	54.75 $\pm$ 3.3		20.12 $\pm$ 2.7		1.01 $\pm$ 6.0		n.s.	***
COVER (%)	13.50 $\pm$ 1.7		24.33 $\pm$ 2.5		57.56 $\pm$ 4.2		***	*
WILL (%)	25.76 $\pm$ 2.8		78.60 $\pm$ 2.5		90.74 $\pm$ 1.8		***	**
EVH (m)	0.30 $\pm$ 0.0		0.49 $\pm$ 0.1		0.64 $\pm$ 0.0		***	n.s.
FRUIT (%)	54.45 $\pm$ 3.2		14.11 $\pm$ 2.0		9.11 $\pm$ 1.8		***	*
BARE (%)	34.66 $\pm$ 3.0		6.43 $\pm$ 1.4		4.93 $\pm$ 1.1		***	*
GRASS (%)	51.13 $\pm$ 3.1		65.52 $\pm$ 3.0		42.72 $\pm$ 5.1		***	n.s.
WATER (%)	1.34 $\pm$ 0.8		3.86 $\pm$ 1.4		4.51 $\pm$ 1.1		***	n.s.

^a Definitions of habitat features are given in Table 2.

^b Based on nested design MANOVA evaluating differences among sites and zones. Significance levels are * p < 0.1; ** p < 0.01; *** p < 0.001; n.s. = not significant.

Table 6. Tests of significance for trends in bird abundance of 20 species across three habitat zones. Kendall's rank correlation demonstrates trend directions in elevational zone associations; and ANOVA with pairwise comparisons indicates differences in mean abundance among elevational zones.

Species Mnemonic ^a	Kendall's Rank Correlation ^b		ANOVA ^c	
	Coefficient	p	p	Comparisons
MODO	0.75	**	0.017	ac
BTHU	-0.28		0.001	ab
WIFL	-0.67	*	0.082	bc
DUFL	-0.38		0.111	b
WWPE	-0.59	*	0.066	ac
TRSW	-0.67	*	0.161	c
HOWR	-0.87	**	0.000	ac
GRCA	-0.48		0.234	
AMRO	-0.90	***	0.001	abc
VEER	-0.68	**	0.079	bc
WAVI	-0.76	**	0.020	bc
YEWA	-0.92	***	0.000	abc
MGWA	-0.11		0.001	ab
COYE	0.07		0.118	ab
WIWA	0.80	**	0.034	bc
BRBL	-0.25		0.150	b
BHCO	-0.87	**	0.000	bc
WCSP	0.81	**	0.005	bc
LISP	0.65	*	0.030	c
SOSP	-0.37		0.000	abc

^aCommon and scientific names of bird species are given in Table 3.

^bThe significance of each correlation coefficient was assessed using a one-tailed *t* test. A significant positive correlation indicates stronger association with subalpine willow habitats; a significant negative correlation indicates stronger association with low-elevation cottonwood-willow habitats. Species with nonsignificant correlations are either invariant in abundance across habitat zones (ANOVA reveals no significance) or prefer mid-elevation shrub willow ("ac" combination in pairwise comparisons). Significance levels are **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

^cF-ratio was used to test if bird abundance varied among three habitat zones. Pairwise comparisons were computed with least significant difference range test. Significant differences (*p* < 0.05) between two habitat types are represented by the following symbols or combinations thereof: a = Zone 1 vs Zone 2, b = Zone 2 vs Zone 3, c = Zone 1 vs Zone 3.

habitats $P < 0.001$), as were willow flycatcher, western wood pewee, and tree swallow ($P < 0.05$). Significant positive correlations, as in Wilson's warbler, white-crowned sparrow, and Lincoln's sparrow, indicated peak abundance in subalpine willow habitats. The abundance distributions of seven species were not significantly correlated with the rank elevational index. However, of these species five varied significantly using pairwise comparisons of abundance levels in three elevational zones (Table 6). Broad-tailed hummingbird, MacGillivray's warbler, and common yellowthroat occurred most frequently in mid-elevation shrub-willow habitat. Thus abundance levels for these species differed significantly between Zones 1 and 2, and 2 and 3, but not between 1 and 3 (Table 6) because 1 and 3 were alike in having few occurrences. Likewise dusky flycatcher and Brewer's blackbird reached peak abundance in Zone 2 but because these species secondarily occurred in Zone 1, only Zone 2 (peak abundance) and Zone 3 (zero abundance) levels differed greatly enough to be significant (Table 6). Song sparrow abundance also peaked in Zone 2 but levels differed significantly among all comparisons (Table 6). Only gray catbird exhibited no strong preference for any one elevational zone, being equally distributed at low densities across Zones 1 and 2 (note that this species never occurred in Zone 3).

Effects of Habitat Gradients on Bird Populations.--To understand the habitat preferences of individual species more clearly, I evaluated the results of principal components analysis of the habitat variables and then used the mean component scores for each study site

to assess possible causes for variations in avian abundance. Five principal components were significant (eigenvalues > 1.0), explaining 65.1% of the variation in habitat structure (Table 7). The mean site scores for principal component one (PC1) were highly inversely correlated with elevation ($\underline{r} = -0.80$, $\underline{P} < 0.01$). PC1 represented a gradient of decreasing canopy height and tree density explained by increase in elevation (Table 7). The understory shrub vegetation also changed, becoming a closed monotypic community at high elevations. PC1 was not as good a predictor of bird species richness ($\underline{r}^2 = 0.44$, $\underline{P} < 0.05$) and total number of territorial pairs ($\underline{r}^2 = 0.47$, $\underline{P} < 0.05$) as site elevation.

The other four components did not vary significantly with elevation ($\underline{P} > 0.1$). PC2 represented a shrub size continuum; PC3 represented a gradient of shrub dispersion and cover; PC4 accounted for change in mid-canopy foliage density; PC5 characterized variation in ground cover and surface moisture (Table 7).

Of the five gradients, PC1 and PC4 were most highly correlated with bird population levels (Table 8). Abundances of ten species were significantly positively correlated with PC1, indicating greater affinity for low-elevation sites with high tree density and canopy height. All of these species are members of cluster Groups 1 and 3 (Table 4). High correlations between habitat gradients and suites of covarying species strongly suggest that positive species associations were formed in response to variation in habitat gradients. Significant negative correlations between population levels of Group 5

Table 7. Principal components analysis of 19 vegetation variables resulting in five significant components describing trends in habitat structure across study plots.

Principal component	Eigenvalue	Percent 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 mid-canopy.
5	1.1	5.9	Higher grass forb foliage density and ground cover, dryer sites.

Table 8. Partial correlations of bird abundance with five habitat gradients.^a

Species mnemonic ^b	Group indentification	Habitat gradient defined by PCA ^c				
		1	2	3	4	5
MODO	1	0.91**	0.23	-0.74*	-0.59*	-0.64*
WWPE	1	0.83*	0.20	-0.71*	-0.55*	-0.62*
HOWR	1	0.98***	0.41	-0.78*	-0.52	-0.71*
TRSW	1	0.61*	0.55*	-0.68*	-0.09	-0.63*
DUFL	2	-0.13	-0.12	-0.30	0.84*	0.85*
BRBL	2	-0.46	0.32	-0.19	0.74*	0.46
COYE	2	-0.56*	0.40	-0.13	0.67*	0.44
WIFL	3	0.74*	0.42	0.03	0.71*	-0.66*
YEW	3	0.98***	0.67*	-0.42	0.92**	-0.16
BHCO	3	0.74*	0.48	-0.41	0.71*	-0.18
AMRO	3	0.92**	0.70*	-0.78*	0.54	-0.49
VEER	3	0.55*	0.27	0.26	0.61*	0.14
GRCA	3	0.32	0.03	-0.04	0.41	-0.33
WAVI	3	0.89**	0.33	0.11	0.79*	0.76*
MGWA	4	-0.54	0.30	-0.37	0.56*	-0.06
SOSP	4	-0.05	0.43	-0.11	0.78*	0.13
BTHU	4	-0.16	0.27	0.03	0.77*	0.21
LISP	5	-0.82*	0.19	0.53	-0.69*	0.46
WCSP	5	-0.55*	-0.33	0.29	-0.56*	-0.14
WIWA	5	-0.46	0.15	0.76*	-0.76*	-0.18

^aSignificance levels based on one-tailed t tests of partial correlations are as follows: * $p < 0.1$, ** $p < 0.01$, *** $p < 0.001$.

^bCommon and scientific names are given in Table 3.

^cDescriptions of gradients are given in Table 7.

species and PC1 demonstrated preference for high-elevation treeless habitats. PC4 was an important gradient, significantly predicting fluctuations in 15 of the 20 species. PC4 was the only habitat gradient to predict variation in numbers of broad-tailed hummingbirds, MacGillivray's warblers, and song sparrows, the three species composing Group 4. Brewer's blackbird, common yellowthroat, and dusky flycatcher, the three members of Group 2, were also significantly positively correlated with this gradient. Positive correlation signifies greater dependence on sites with high foliage density at mid-canopy or shrub height. Thus, species that select shrub-willow habitats may differentiate among sites on the basis of availability of protective foliage cover for resting, nesting, or foraging purposes.

The shrub size gradient (PC2) was important to two species in Group 3, American robins and yellow warblers, which prefer to nest in large willows in shrub-willow habitat (Finch unpubl. data). Group 3 members showed a more uniform affinity for the foliage density gradient (PC4), with only robins and catbirds exhibiting no significant preference. These two species are much larger in body size than other Group 3 members, possibly explaining why foliage density was less important (in fact, it may even impede travel). Gray catbird, which was the only species not significantly correlated with any habitat gradient, loaded highest on PC4. However, specific habitat features related to territory establishment or nest site selection may better explain catbird distribution and abundance patterns.

American robin was the only species in Group 3 to demonstrate a significant negative relationship with PC3, the shrub density and cover gradient. Negative correlation, also shown by all four species in Group 1, indicates affinity for more open understory. In contrast, Wilson's warbler distribution was positively correlated with increasing shrub density and foliage density of low understory.

The moisture-ground cover gradient (PC5) was significantly negatively correlated to population levels of species that typically nest or forage near water. These species included willow flycatcher, western wood pewee, tree swallow and mourning dove. Doves frequently drink and bathe in ponds, flycatchers nest along creeks, and tree swallows forage over water. House wrens were also negatively related to PC5, possibly in response to differences in availability of invertebrate food sources, a factor that is typically dependent on site moisture (Busby and Sealy 1979, Hamas 1982). Species more abundant in dryer sites were dusky flycatcher and warbling vireo.

Controlling for the Effects of Habitat and Elevation.--To determine if similarity in elevational zone preferences or habitat affinities was an important underlying cause of the 48 significant correlations between species pairs, I conducted a second test of species associations, this time controlling for shared habitat gradients and elevation using partial correlation analysis. If the resulting number of significant correlations is no longer greater than that expected by chance, the null hypothesis of no biotic association between pairs of species cannot be rejected. Results showed that when

the influences of habitat and elevation were removed, the number of significant correlations ($P < 0.05$) between species decreased from 48 to 8, a six-fold change. Because the number of correlations was similar to that expected by chance, I could not reject H_0 . The two tests of species associations are compared to Table 9. I concluded that common responses of species to similar habitat features and elevational changes were more successful at predicting species association patterns.

Of the eight remaining correlations, the only negative one was between white-crowned sparrow and yellow warbler. Because these species never co-occurred on the same site, competition between them is doubtful. The remaining positive correlations were between mourning dove vs. all Group 1 species, tree swallow vs. all Group 1 species, common yellowthroat vs. dusky flycatcher, and brown-headed cowbird vs. veery. Although these correlations may have been stochastically produced, possible alternative explanations besides positive interaction or habitat selection include common responses to resources such as nest sites and materials, or food. The influence of other resources was not addressed in this investigation, but because the availability and composition of resources are typically correlated with vegetational physiognomy and diversity, I feel that habitat variation and elevation alone were successful in predicting population dynamics.

Table 9. Comparison between correlational analysis testing the null hypothesis of no association among species and partial correlational analysis testing the null hypothesis of no association with habitat effects removed.

Description	1st Test	2nd Test
Null Hypothesis	No Association	No Association (Habitat Removed)
Statistical Analysis	Pearson Product-moment correlation	Partial Correlation
No. Significant correlations	48	8
VS. Expected ^a	Greater Than Observed	Less Than Observed
Conclusion	H ₀ Rejected	H ₀ Not Rejected

^aComparison of observed number of significant correlations versus expected number.

DISCUSSION

The analyses of associations yielded a fairly organized set of relationships among bird species and vegetation features in riparian habitats. Numerous close correlations were first found in the abundances of pairs of species across an elevational habitat cline. The number of significant correlations was much greater than that expected by chance alone. Thus, the null hypothesis of no association was rejected. In addition, five suites of covarying species were detected. When habitat zones changed, species were added or lost, and population levels predictably increased or decreased. Population levels changed in a positive or negative direction within groups of covarying species. At first glance, such consistent patterns of species coexistence and covariation suggested that these communities were structured and that the distribution and abundance of individual species depended to a large extent on the habitat occupancy patterns of other species. One explanation for positive correlations is that the best adapted sets of species comprise communities (Cody 1966), and that set compositions were shaped by past competition. However, correlational analyses of bird species with riparian habitat zones and gradients revealed that species responded in an individual manner to variation in habitat structure, but that individual responses can be grouped with regard to major habitat trends. Furthermore, once the effects of habitat ecotonal changes were removed, the number of significant correlations between species decreased dramatically, implying

that positively correlated pairs of species occupied similar elevational zones because they independently responded to the same habitat gradients. Likewise, negatively associated species occupied different habitat zones because their habitat preferences were dissimilar. Although negative relationships can also be interpreted as evidence for competitive exclusion or competitive-driven density compensation, such interpretations are tenuous without further substantiation using an independent data set to test specific hypotheses about competition.

Even the correlational analyses presented here do not adequately address the underlying reasons for patterns of association and disassociation. Why do riparian bird species in the central Rockies exhibit so many more significant correlations in abundance than do the Great Basin shrubsteppe birds studied by Wiens and Rotenberry (1981)? The extent of correlation was so minor in the Wiens and Rotenberry investigation that they felt the correlations revealed may well have been spurious, reinforcing the view that biotic interactions probably play a minor role in shaping communities. Although the degree of correlation in my study was extensive before I controlled for the influence of habitat and elevation, once these influences were removed, I agreed with Wiens and Rotenberry on the role of interactions. I differ from Wiens and Rotenberry in suggesting that Rocky Mountain riparian bird communities are structured along elevational gradients because my data showed considerable pattern in response to habitat trends. Nevertheless, correlational analysis, while manifesting

surface trends, may not disclose the real foundation for pattern. Because pattern is especially evident along relatively sharp elevational clines (Noon 1981a; Terborgh 1971, 1985; Knopf 1985), it can be readily discerned in local systems with rapid spatial turnover in species and resources. Wiens and Rotenberry failed to detect pattern on a local level but did find pattern on a broad geographical scale, which suggests that local shrubsteppe habitats were too invariant 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 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.

Despite the failure of PCA to explain 35% of the variation in riparian habitat characteristics, variation that it did account for was important in explaining trends in bird abundance. However, much of the dynamics of species' densities was not related to the habitat gradients defined by PCA. The remainder of the spatial variation in population levels may be explained by several effects. First, habitat features critical to some species may not have been measured. Second, by reducing the number of habitat variables to a set of five using PCA, the variation in avian abundance accounted for by individual habitat features such as preferred plant species may have been obscured. Third, resources unrelated to habitat physiognomy may be

significant in predicting population trends. Fourth, only a segment of each species' distributional range was considered, therefore an incomplete picture was provided. Fifth, some variation may be a result of chance alone.

In conclusion, the analyses presented here were useful in attaining the original goal of finding pattern in riparian bird communities. Patterns of co-occurrence were detected in central Rocky Mountain riparian bird communities that appear to be determined by environmental changes rather than produced solely by chance. By sampling species population dynamics across an altitudinal cline, sufficient habitat variability was encompassed to produce correlational effects on bird populations. The underlying processes that elicit covariation patterns were not readily revealed, but the high number of significant habitat associations strongly suggested that species are arrayed across the riparian continuum according to individual habitat selection. Suites of co-occurring species were formed because habitat affinities coincided, probably in response to sharp, highly visible structural changes that defined the ecotones of three dominant habitat types. The null hypothesis of no potentially interactive association among species could not be rejected because when the habitat influence was controlled, significant correlations between species' abundances were suppressed. However, a future experimental approach designed to falsify the null hypothesis should offer a more rigorous test than correlation analysis.

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CHAPTER 2
SPECIES ABUNDANCES, GUILD DOMINANCE PATTERNS, AND
COMMUNITY STRUCTURE OF BREEDING RIPARIAN BIRDS

Abstract.--Riparian habitats in the central Rocky Mountains vary substantially in their capability to support high numbers of birds. I investigated trends in bird species' populations, guild structure, and bird communities along a riparian altitudinal cline in the Medicine Bow National Forest of southeastern Wyoming. Streamside habitats were divided into three elevational zones: low-elevation (2050-2260 m) cottonwood zone, mid-elevation (2290-2530 m) mixed shrub willow zone, and high-elevation (2590-2990 m) subalpine willow zone. Analyses of habitat characteristics indicated significant trends of decreasing vegetational complexity from low to high zones, with loss in number of vertical habitat layers, and increased shrub foliage density and dominance of dwarf willows. Changes in avian guild structure corresponded to habitat elevational changes. Ground and lower-canopy foragers dominated all three zones, but upper-canopy foragers, aerial foragers, and bark foragers declined in numbers with increased elevation, altogether disappearing in the subalpine zone. Loss of overstory trees, cavity-nest sites, and flycatching perches probably accounted for the loss of these three guilds in the subalpine zone. Highest similarities within foraging guilds were between low- and mid-elevation zones,

whereas fewest guild species were shared between low- and high-elevation zones. By relating guild occupancy patterns to the presence or absence of habitat layers in each elevational zone, trends in avian numbers were explained. Greater habitat stratification in low-elevation cottonwood communities resulted in greater capability to support avian species, via effects on guild members. Evaluations of zone variation in population levels of individual species and whole avian communities were not as valuable in explaining the underlying reasons for variation in bird numbers.

INTRODUCTION

Studies of bird-habitat relationships in streamside plant communities in the western United States have demonstrated that bird species diversity and bird densities are markedly greater in riparian habitats than in surrounding upland vegetation or in most other terrestrial habitats (Carothers et al. 1974, Gaines 1977, Knopf 1985). In the central Rocky Mountains, 177 (81.6%) of 217 bird species breed or winter in various successional stages of cottonwood riparian habitats and 28% of these species use riparian habitats exclusively (computed from Hoover and Wills 1984). Hirsch and Segelquist (1978) indicated that 70-90 percent of riparian habitat in the U.S. has already been extensively altered from disturbances such as livestock grazing, mining, irrigation, and urban development. Because riparian vegetation typically comprises less than 0.5 percent of total land area in the West (Sands and Howe 1977), protection measures for this critical wildlife habitat are essential. Yet, few studies of bird-habitat relationships have compared and rated habitat values among different riparian plant associations. Riparian habitats that vary along environmental gradients may differ substantially in their capability to support high bird numbers (e.g., Best et al. 1978, Stauffer and Best 1980, Bull and Skovlin 1982, Finch 1985, Knopf 1985).

One approach to managing diverse riparian habitats is to use guilds to indicate the capability of habitats to sustain avian populations (Severinghaus 1981, Short and Burnham 1982, Verner 1984, Block et al. 1986). Root (1967) originally defined a guild as a group of species that use the same kinds of resources in a similar manner. Verner (1984) reasoned that responses in guild members to habitat changes are most likely to be similar if guilds are defined in terms of associations with subdivisions of the habitat rather than with diet or foraging methods. To supplement analyses of species populations and communities, I used Verner's guild approach to investigate bird responses to variation in habitat stratification along a riparian elevational cline. Species were grouped into guilds based on the vertical habitat layers in which they foraged. If the stratification of riparian habitats substantially varies along an elevational gradient, dominance and distributional patterns within and among guilds should change as a consequence.

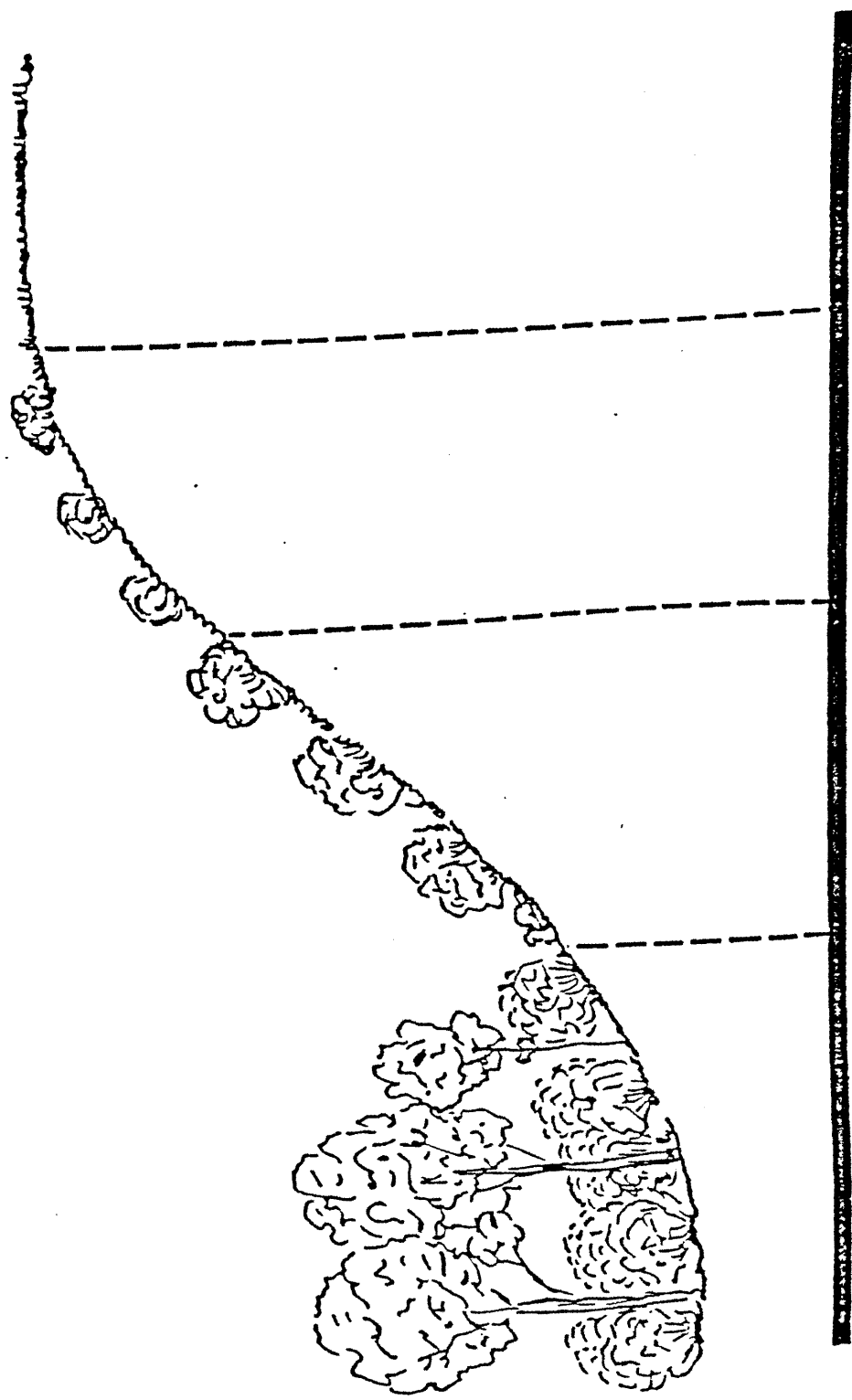
To investigate trends in species' populations, guild structure, and whole bird communities, I asked the following questions: 1) Do population levels of riparian birds remain constant over a three-year period? By accounting for this temporal source of variation, I could better explain patterns of avian distribution and abundance related to spatial changes. 2) How do bird populations adjust to habitat transitions associated with different elevational zones? 3) Do the same guilds occupy each elevational zone? Is guild composition

affected by variation in year or elevational zone? 4) How similar or dissimilar are bird communities among three riparian habitat zones?

METHODS

Study Areas.--Ten 8.1 ha (20 acre) study grids were established in the summer of 1981 in riparian habitats in (or within 16 km of) the Medicine Bow National Forest of southeastern Wyoming. Each grid was posted at 33.5-m (110 ft) intervals with wooden stakes painted fluorescent orange and marked with grid coordinates. Study sites were distributed over an elevational range of 933 m (3,060 ft), encompassing a spectrum of streamside plant species and habitats (Figure 5). Based on preliminary surveys, replicate sites were established in three elevational zones: Zone 1 = three sites ranging from 2050 m (6,740 ft) to 2260 m (7,400 ft); Zone 2 = three sites ranging from 2290 m (7,500 ft) to 2530 m (8,300 ft); Zone 3 = four sites ranging from 2590 m (8,500 ft) to 2990 m (9,800 ft). The alpine zone (>3000 m, 9840 ft) was not studied because few breeding birds were observed in preliminary surveys. Dominant vegetation in Zone 1 consisted of narrowleaf cottonwood (Populus angustifolia), coyote willow (Salix exigua), and water birch (Betula fontinalis). Zone 2 vegetation was composed of a variety of shrub willow species (S. geyeriana, S. boothii, S. lasiandra) and thin-leaf alder (Alnus tenuifolia) with a ground layer dominated by Calamagrostis canadensis. Zone 3 vegetation was comprised of S. planifolia which formed dense subalpine thickets

Figure 5. Distribution of riparian habitat zones along an elevational cline in southeastern Wyoming.



<u>Cottonwood-</u> <u>Willow</u>	<u>Subalpine</u> <u>Willow</u>	<u>Alpine</u> <u>Grass</u>
< 2200 M	2200-2500 M	> 3000 M

interspersed with wet boggy meadows of Deschampsia caespitosa and Carex spp. The point-centered quarter method (Mueller-Dombois and Ellenberg 1974) was used to estimate dominance of shrubs and trees based on 40 random sampling points established at grid intersections on each plot.

A variety of habitat variables were also measured at these sampling points to assess variation in habitat structure among elevational zones. A list of habitat characteristics that subdivide the vertical habitat into strata is given in Table 10. In particular, vertical foliage density (VFD), or the number of vegetation hits against a vertical rod, gives a good indication of the number and density of habitat layers in each elevational zone. Willow species were identified using the taxonomic keys of Argus (1957) and Nelson (1974) as well as University of Wyoming herbarium facilities. Classification of plant associations into zones was facilitated by reference to Johnston (1984) and Olson and Gerhart (1982).

I used the following criteria to select sites: 1) the stream bottom was large and level enough to establish a 8.1 ha (20-acre) grid (thus habitat types specifically adapted to steep narrow stream courses were excluded); 2) each study area was accessible by road in June so that enough time was permitted for a sufficient number of bird counts; 3) there was little or no evidence of livestock grazing or browsing based on presence of manure, foraging effects, or livestock themselves; 4) little or no human recreational activity was apparent; and 5) each site had similar topography and year-round running

streams. Flooding was an additional disturbance, but because the degree of flooding was unpredictable, it was not used as a criterion in selecting plots. Not all the above criteria were met on each plot, particularly with respect to livestock disturbance. Four of the ten plots were grazed to some extent. Two sites located in plant associations dominated by mixed shrub willows (Table 10), were on a rest rotation grazing system; on one of the cottonwood sites, winter grazing was permitted with cattle removed in May; and on the alder-dominated site, the riparian edge was moderately grazed and browsed. Two cottonwood sites were severely flooded in 1983 so that bird censusing was halted for two weeks. Although a few ground-nesting birds lost their nests in the floods, they retained their territories and built new nests when water levels dropped, and thus no effects on bird numbers were evident.

Bird Populations and Foraging Guilds.--Number of territorial avian pairs were counted from late May to mid-July of 1982, 1983, and 1984 using the spot-map method (Robbins 1970). A minimum of three grouped observations on a map of each study grid constituted a territorial pair. Birds that were recorded only once or twice were considered visitors and were not included in my analyses. Numbers of visits to each plot varied from 8 to 15. Each visit extended from 2-4 hours.

Each bird species was assigned to 1 of 6 foraging guilds based on a modification of DeGraaf et al.'s (1985) criteria: ground-forager-gleaner, lower-canopy (shrub) forager-gleaner, upper-canopy (tree)

Table 10. Mean (+ S.E.) values and significant differences of nine selected vegetation features in three riparian elevational zones (Zone 1 = low-elevation cottonwood habitat; Zone 2 = mid-elevation shrub willow habitat; Zone 3 = high-elevation subalpine willow habitat).

Habitat variable	Sampling Method	Zone 1	Zone 2	Zone 3	P ^a
Tree density	Number of trees > 3 cm DBH in 100 m ² quadrant.	4.67 ± 0.1	0.53 ± 0.1	0.03 ± 0.0	*
Shrub height	Mean height (m) of nearest shrubs in each quadrant.	2.01 ± 0.1	2.08 ± 0.1	1.47 ± 0.1	*
Vertical foliage density in grass-forb layer (VFDI)	Mean number of vegetation contacts falling against vertical rod in < 0.3 m interval.	1.98 ± 0.1	2.81 ± 0.2	2.91 ± 0.1	n.s.
Vertical foliage density in low shrub layer	Same as VFDI, but in 0.3-1 m interval.	0.54 ± 0.1	1.30 ± 0.1	1.72 ± 0.1	*
Vertical foliage density in high shrub layer	Same as VFDI, but in 1-2 m interval.	0.23 ± 0.0	0.84 ± 0.1	0.33 ± 0.1	*
Vertical foliage density in lower overstory	Same as VFDI, but in 2-9 m interval.	1.00 ± 0.1	0.51 ± 0.1	0.02 ± 0.0	*
Vertical foliage density in upper overstory	Same as VFDI, but in > 9 m interval.	0.45 ± 0.1	0.01 ± 0.0	0.00 ± 0.0	*
Percent willow	Proportion of shrub species that are willow.	25.76 ± 2.8	78.60 ± 2.5	90.74 ± 4.2	*
Woody cover	Percent cover of woody plants (< 1 m tall), saplings and downed logs measured with ocular tube.	13.50 ± 1.7	24.33 ± 2.5	57.56 ± 4.2	*

^a Based on oneway ANOVA evaluating differences among habitat zones. * $p < 0.001$; n.s. = not significant ($p > 0.05$).

forager-gleaner, air sallier-screener, bark driller-gleaner, freshwater forager. The freshwater guild was a catch-all term for those species that were attracted to riparian habitats because of the presence of standing or flowing water. Herbivores, carnivores and omnivores were condensed into single foraging substrate categories. Common and scientific names of guild members in each elevational zone are listed in Appendix A.

Analyses of variation and similarity.--Two-way ANOVA was performed to detect variation among years and among elevational zones in number of species, total number of pairs, and number of pairs of each species. Data for three years and 3 to 4 replicate sites within each zone were used to determine main and interaction effects of the two factors, YEAR and ZONE. Twenty bird species with sample sizes sufficient for ANOVA were used in single species analyses.

Because no interaction was observed between YEAR and ZONE, the three-year bird count data were averaged for each species in each foraging guild. One-way ANOVA's with a posteriori pairwise comparisons were then conducted to assess differences among elevational zones in species composition and overall number of pairs within each guild. Pairwise comparisons were computed using Student Newman-Keul's Multiple Range Test with an alpha level of 0.05. ANOVA's were computed using the SPSS package (Nie et al. 1975). Jaccard Similarity Index (Goodall 1978) was performed on presence-absence data to estimate percent similarity in guild species composition among elevational zones. Similarities were computed using averaged three-year counts.

By examining the habitat occupancy patterns of guilds, one can more accurately pinpoint and explain sources of variation in the underlying structure of riparian bird communities.

RESULTS

Variation in Habitat Stratification Among Elevational Zones.--

Vertical foliage density (VFD) in the herbaceous layer remained relatively constant across elevational zones ($\underline{P} > 0.05$), but VFD in the low shrub layer substantially increased ($\underline{P} < 0.001$) at higher zones and VFD in the high shrub layer peaked in Zone 2, then declined ($\underline{P} < 0.001$). In contrast, VFD in the lower overstory and the upper overstory declined considerably with increase in elevation ($\underline{P} < 0.001$) (Table 10). Other habitat characteristics also indicated trends toward reduced vegetational complexity in Zone 3, the subalpine zone. Tree density (primarily cottonwoods) declined from ^{59.74}4.7 trees/100 m² in Zone 1 to virtually no trees in Zone 3 (Table 10). Shrub height was similar between Zones 1 and 2, but was about 40% lower in Zone 3 (Table 10). On the other hand, woody cover at the < 1 m level increased from 13.5% in Zone 1 to 57.6% in Zone 3 ($\underline{P} < 0.001$), and the proportion of willow (Salix spp.) in the shrub community increased from 26% to 91% ($\underline{P} < 0.001$). These marked changes signify a trend toward decreasing vegetational complexity along the elevational cline, with loss in number of vertical vegetation layers, increased foliage density in the low shrub layer, and dominance of dwarf willow (primarily S. planifolia) in the subalpine zone.

Effects of Year and Elevational Zone on Bird Numbers.--Zone 1, the cottonwood zone, had highest bird species richness in all three study years. Site variation in Zone 1 ranged from 20-23 species in 1982, 16-22 species in 1983, and 15-22 species in 1984 (Table 11). In Zone 2, the mid-elevation shrub willow zone, species richness varied among sites from 13-19 species in 1982, 14-20 species in 1983, and 12-19 species in 1984. The range of species richness in Zone 3, did not even overlap with values in Zones 1 and 2; values reached lows of 3-8 species in 1982, 3-11 species in 1983, and 3-9 species in 1984. ANOVA results indicated that mean species richness remained stable within each elevational zone from 1982 to 1984 ($\underline{P} > 0.05$ for YEAR effect) but substantially decreased from Zone 1 to Zone 3 ($\underline{P} < 0.001$ for ZONE effect) (Tables 11 and 12). The effects of YEAR and ZONE were independent ($\underline{P} > 0.05$ for interaction effect) (Table 12).

Similar YEAR and ZONE trends were also evident for numbers of territorial pairs. Number of pairs in Zone 1 ranged from a low of 76 pairs in 1984 to a high of 130 pairs in 1982, whereas Zone 2 ranged from 61 pairs (1982) to 111 pairs (1983), and Zone 3 ranged from 18 pairs (1983) to 78 pairs (1983). YEAR and interaction effects were not significant ($\underline{P} > 0.05$), but mean number of pairs varied markedly among zones ($\underline{P} < 0.001$) (Table 12).

Species diversity was similar between Zone 1 and Zone 2 (3.2-3.7 in Zone 1 vs. 3.1-3.8 in Zone 2) but was about two times higher than Zone 3 (1.4-2.4) (Table 11). Despite highest species richness and pair abundance in Zone 1, the equitability or evenness of species

Table 11. Number of breeding species, number of territorial pairs, breeding species diversity and equitability of riparian birds on ten 8.1 ha plots in three elevational zones (low, middle, high) in 1982, 1983, and 1984. Values for three to four replicate sites in each zone are given.

Site	Elevation (M)	No. of Species			No. of Pairs			Species Diversity ^a			Equitability ^a		
		1982	1983	1984	1982	1983	1984	1982	1983	1984	1982	1983	1984
Zone 1: Low Elevation													
1	2054	21	22	19	130	115	104	3.65	3.56	3.41	0.83	0.81	0.80
2	2097	23	18	22	107	93	102	3.68	3.22	3.50	0.81	0.77	0.79
3	2256	20	16	15	84	78	76	3.38	3.33	2.82	0.78	0.83	0.72
Mean ±	2135.7 ±	21.3 ±	18.3 ±	18.7 ±	107.0 ±	95.3 ±	94.0 ±	3.57 ±	3.37 ±	3.23 ±	0.81 ±	0.81 ±	0.77 ±
S.D.	106.40	1.53	2.52	3.51	23.0	18.61	15.62	0.16	1.84	0.37	0.02	0.03	0.04
Zone 2: Middle Elevation													
1	2286	13	14	12	61	59	63	3.26	3.16	3.12	0.88	0.83	0.87
2	2470	15	14	17	73	72	89	3.50	3.32	3.63	0.90	0.90	0.89
3	2530	19	20	19	79	111	98	3.81	3.55	3.78	0.90	0.82	0.89
Mean ±	2428.7 ±	15.7 ±	15.7 ±	16.0 ±	71.0 ±	80.0 ±	83.3 ±	3.53 ±	3.34 ±	3.51 ±	0.89 ±	0.85 ±	0.88 ±
S.D.	127.14	3.06	3.79	3.61	9.17	27.40	18.18	0.28	0.20	0.35	0.01	0.04	0.01
Zone 3: High Elevation													
1	2591	8	11	9	67	78	58	2.15	2.45	2.40	0.72	0.71	0.76
2 ^b	2789	--	4	5	--	28	30	--	1.53	1.75	--	0.77	0.75
3	2930	3	3	3	24	18	27	1.36	1.42	1.43	0.86	0.90	0.90
4	2987	4	3	3	29	24	26	1.69	1.58	1.50	0.85	0.99	0.95
Mean ±	2824.3 ±	5.0 ±	5.3 ±	5.0 ±	40.0 ±	34.0 ±	35.3 ±	1.74 ±	1.74 ±	1.77 ±	0.81 ±	0.84 ±	0.84 ±
S.D.	176.37	2.65	3.86	2.83	23.52	27.64	15.26	0.40	0.47	0.44	0.08	0.13	0.10

^aSpecies diversity and equitability (uniformity of species abundances) were computed using the Shannon-Weiner Index (Pielou 1966).

^bStudy site 2 in Zone 3 was added in 1983 to complete range of elevational positions.

Table 12. F-values and significance levels of main, joint and two-way interaction effects of year (1982, 1983, 1984) and elevational zone (low, middle, high) on species richness and total number of territorial pairs.

Effect	Species Richness		Number of Pairs	
	<u>F</u> -value	<u>P</u>	<u>F</u> -value	<u>P</u>
YEAR	0.01	0.907	0.03	0.972
ZONE	55.34	0.001	23.71	0.001
Interaction	0.15	0.960	0.22	0.923

abundances was greater in Zone 2 (0.82 to 0.90) than in Zone 1 (0.72-0.83) which resulted in comparable diversity values between the two zones (Table 11). Equitability was highly variable in Zone 3 but reached a maximum of 0.99 on some subalpine sites indicating very uniform abundance distributions in the few codominating bird species.

Population levels of the 20 most common bird species are listed by elevational zone and year in Table 13, along with acronyms. Yellow warbler was the most abundant species in the two lower zones with a range from 1982 to 1984 of 27.0-33.3 pairs or about 30% of all birds in Zone 1, and a range of 12.3-18.0 pairs or 17% of all birds in Zone 2 (Table 13). American robin reached second highest densities in Zone 1 (11.0-17.3 pairs, ~14%) but fourth highest population levels in Zone 2 (6.3-7.3 pairs, ~9%) being replaced in dominance by song sparrow (6.7-11.7 pairs, ~12%) and Lincoln's sparrow (4.0-11.0 pairs, ~11%). House wren had third highest population levels in Zone 1 (11.3-13.0 pairs, ~12.5%), but virtually disappeared in Zones 2 and 3 where trees suitable for wren cavity nests were lacking. A similar trend in zone preference was also evident for less common cavity-nesting species (tree swallow, Table 6, violet-green swallow, yellow-bellied sapsucker, and Northern flicker as well as for open-nest species that built nests (at least in this study) exclusively in upper woodland canopies (mourning dove and Western wood pewee, Table 13).

In Zone 3, three species comprised approximately 92% of the total avifauna. Lincoln's sparrow dominated subalpine willow habitats,

Table 13. Mean number of territorial pairs/8.1 ha ($\pm$ S.E.) of 20 bird species in three riparian elevational zones (low, middle, high) in 1982, 1983 and 1984. Number of pairs are averaged across three to four spot-map plots within each zone.

Species (Mnemonic) ^a	Zone 1: Low Elevation		Zone 2: Middle Elevation		Zone 3: High Elevation	
	1982	1983	1982	1983	1982	1983
Mourning Dove (MODO)	4.0 $\pm$ 0.8	3.0 $\pm$ 1.7	3.3 $\pm$ 1.3			
Broad-tailed Hummingbird (BTHU)	2.0 $\pm$ 0.7	1.7 $\pm$ 0.7	1.3 $\pm$ 0.8	5.0 $\pm$ 0.3	4.7 $\pm$ 0.4	6.7 $\pm$ 0.3
Western Hood Pewee (WMPE)	2.7 $\pm$ 1.4	2.3 $\pm$ 0.8	3.3 $\pm$ 0.9			0.5 $\pm$ 0.7
Willow Flycatcher (WIFL)	3.0 $\pm$ 1.7	3.3 $\pm$ 1.3	3.0 $\pm$ 1.7	1.7 $\pm$ 1.3	1.0 $\pm$ 1.0	0.3 $\pm$ 0.6
Dusky Flycatcher (DUFL)	2.0 $\pm$ 1.1	0.7 $\pm$ 0.4	1.3 $\pm$ 1.2	3.7 $\pm$ 1.0	2.3 $\pm$ 1.0	2.0 $\pm$ 1.1
Tree Swallow (TRSW)	5.7 $\pm$ 1.0	2.3 $\pm$ 1.5	2.7 $\pm$ 1.1	0.3 $\pm$ 0.6	0.7 $\pm$ 0.8	1.7 $\pm$ 1.3
House Wren (HOWR)	13.0 $\pm$ 0.7	11.3 $\pm$ 0.8	12.3 $\pm$ 0.6	0.7 $\pm$ 0.4	1.0 $\pm$ 1.0	
Veery (VEER)	3.3 $\pm$ 1.0	3.0 $\pm$ 0.9	1.2 $\pm$ 0.3	2.0 $\pm$ 0.8	3.7 $\pm$ 0.8	3.7 $\pm$ 0.8
American Robin (AMRO)	17.3 $\pm$ 1.3	12.7 $\pm$ 0.7	11.0 $\pm$ 0.4	7.3 $\pm$ 0.1	6.3 $\pm$ 0.7	7.3 $\pm$ 0.4
Gray Catbird (GRCA)	0.7 $\pm$ 0.8	0.7 $\pm$ 0.8	1.3 $\pm$ 0.8	0.7 $\pm$ 0.8	0.7 $\pm$ 0.8	1.3 $\pm$ 0.8
Warbling Vireo (WAVI)	4.3 $\pm$ 0.6	3.3 $\pm$ 0.7	3.3 $\pm$ 0.7	2.7 $\pm$ 0.9	1.0 $\pm$ 0.6	1.7 $\pm$ 0.7
Yellow Warbler (YEWA)	27.0 $\pm$ 0.2	30.3 $\pm$ 0.4	33.3 $\pm$ 0.3	12.3 $\pm$ 0.7	18.0 $\pm$ 1.0	15.3 $\pm$ 0.5
MacGillivray's Warbler (MGWA)				2.7 $\pm$ 0.7	1.3 $\pm$ 0.6	2.7 $\pm$ 0.8
Common Yellowthroat (COYE)				1.3 $\pm$ 0.6	2.3 $\pm$ 1.0	2.3 $\pm$ 1.0
Wilson's Warbler (WIMA)						0.3 $\pm$ 0.6
Song Sparrow (SOSP)	4.7 $\pm$ 0.6	4.0 $\pm$ 0.3	3.0 $\pm$ 0.7	9.7 $\pm$ 1.0	11.7 $\pm$ 0.6	6.7 $\pm$ 0.3
Lincoln's Sparrow (LISP)	0.3 $\pm$ 0.6	0.3 $\pm$ 0.6	0.3 $\pm$ 0.6	4.0 $\pm$ 1.3	10.3 $\pm$ 1.6	11.0 $\pm$ 1.7
White-crowned Sparrow (WCSP)				0.3 $\pm$ 0.6		20.0 $\pm$ 1.5
Brewer's Blackbird (BRBL)		1.0 $\pm$ 1.0				16.0 $\pm$ 1.1
Brown-headed Cowbird (BHCO)	3.7 $\pm$ 0.4	1.3 $\pm$ 0.6	1.0 $\pm$ 1.0	1.3 $\pm$ 0.8	1.7 $\pm$ 0.3	1.3 $\pm$ 0.6
						7.0 $\pm$ 0.7
						6.3 $\pm$ 0.8
						7.0 $\pm$ 0.6

^aScientific names of bird species are given in Appendix A.

reaching yearly abundance levels of 15.5-20.0 pairs (Table 13) or ~47% of all birds counted. With a range of 8.8-10.5 pairs, Wilson's warbler comprised about 26% of the subalpine avifauna, followed by white-crowned sparrow with summer population levels of 6.3-7.0 pairs (~19% of all birds).

The simple and even structure of high-altitude riparian bird communities sharply contrasts with the complexity of communities in lower elevation habitats. Such a pronounced ZONE effect was highly significant ($P \ll 0.01$), influencing the population levels of 19 of the 20 common species (Table 14). Gray catbird was the only species that apparently did not respond to zone transitions ($P > 0.05$). As in the earlier analyses of species richness and pair abundances, the effect of YEAR on population levels of all 20 species was insignificant ($P > 0.05$), nor was there any interaction between the effects of ZONE and YEAR ($P > 0.05$) (Table 14).

Variation in Foraging Guild Structure Among Elevational Zones.--

Six foraging guilds occupied riparian habitats, but guild structure varied among elevational zones. Because guild structure did not significantly vary among years ($P > 0.05$), averaged numbers of species and pairs were used in the following analyses. Ground and lower-canopy foragers dominated all three zones. For example, ground foragers composed 34% of all species and 28% of all pairs in Zone 1; 39% of all species and 34% of all pairs in Zone 2; and 58% of all species and 69% of all pairs in Zone 3 (Table 15). Number of ground-foraging pairs did not vary significantly among zones ($P > 0.05$), but

Table 14. Two-way analysis of variance testing for the main and interaction effects of year (1982, 1983, 1984) and elevational zone (low, middle, high elevations) on population levels of 20 common riparian bird species.

Species ^a Acronym	Significance Level		
	YEAR Effect	ZONE Effect	YEAR-ZONE Interaction
MODO	.878	.001	.965
BTHU	.980	.001	.532
WWPE	.935	.001	.988
WIFL	.952	.006	.995
DUFL	.262	.005	.285
TRSW	.653	.005	.478
HOWR	.813	.001	.818
VEER	.714	.001	.900
AMRO	.597	.001	.493
GRCA	.739	.090	.962
WAVI	.528	.001	.915
Yewa	.125	.001	.399
MGWA	.670	.001	.765
COYE	.933	.016	.416
WIWA	.938	.001	.995
SOSP	.923	.001	.723
LISP	.250	.001	.754
WCSP	.832	.001	.986
BRBL	.916	.001	.992
BHCO	.245	.001	.126

^a Common and scientific species names are given in Table 13 and Appendix A.

Table 15. Oneway analysis of variance contrasting number of species and number of territorial pairs within foraging guilds among three elevational zones (1 = low, 2 = middle, 3 = high). The years 1982, 1983, and 1984 were used for ANOVA replicates. Numbers in parentheses are proportions of each zone avifauna that each guild composes.

Foraging Guild ^a	Number of Species			Number of Pairs			Comparisons ^c
	Zone 1	Zone 2	Zone 3	Zone 1	Zone 2	Zone 3	
Ground	12 (34%)	11 (39%)	7 (58%)	27.6 (28%)	26.6 (34%)	25.2 (69%)	n.s. n.s.
Lower Canopy	7 (20%)	8 (29%)	3 (25%)	48.4 (49%)	41.5 (54%)	10.2 (28%)	*** abc
Upper Canopy	5 (14%)	2 (7%)	0	4.9 (5%)	2.4 (3%)	0	* c
Aerial	7 (20%)	3 (11%)	0	11.8 (12%)	3.9 (5%)	0	* ac
Bark	1 (3%)	0	0	2.0 (2%)	0	0	** ac
Freshwater	3 (9%)	4 (14%)	2 (17%)	4.0 (4%)	3.1 (4%)	1.1 (3%)	n.s. n.s.

^aSpecies were classified into guilds using standards established by DeGraaf et al. (1985).

^b* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. = not significant.

^cPairwise comparisons among elevational zones were computed using Student Newman Keul's Range Test.

Significant differences ($p < 0.05$) between zones are symbolized by: a = Zone 1 (low elevation) vs. Zone 2 (middle elevation), b' = Zone 2 vs. Zone 3 (high elevation), c = Zone 1 vs. Zone 3. The abbreviation n.s. = not significant.

the number of species was significantly higher in Zone 1 than in Zone 3, despite disproportionate percentage of ground-foragers in Zone 3 (Table 15).

Lower-canopy foragers showed a similar trend, having slightly fewer species than the ground-foraging guild in all zones, but more counted pairs in Zones 1 and 2 (Table 15). Numbers of lower-canopy species differed significantly among Zones 1 and 3, and Zones 2 and 3, but not between Zones 1 and 2. Numbers of lower-canopy pairs differed significantly in all pairwise zone comparisons. American robin was the most abundant ground-forager in Zone 1, but was outnumbered by Lincoln's sparrow and song sparrow in Zone 2. Lincoln's sparrow achieved greatest dominance as a ground-forager in Zone 3. Yellow warbler outnumbered all other lower-canopy foragers in Zones 1 and 2, replaced by Wilson's warbler in Zone 3.

Upper-canopy foragers were surprisingly scarce (5% of all counted pairs) in the cottonwood-willow zone (Table 15), despite the presence of an overstory layer of vegetation (Table 10). Warbling vireo was the most common species in this guild. Numbers of species and pairs in the upper-canopy guild were equivalent in Zones 1 and 2 ($P > 0.05$). Zone 3 had no upper-canopy guild because the habitat lacked a tree overstory. The treeless nature of subalpine willow habitat also resulted in the loss of aerial and bark-foraging guilds from Zone 3. Thus, numbers of species and pairs in these two guilds differed significantly in all pairwise comparisons with Zone 3 (Table 15). Aerial foragers were twice as numerous in species richness and

abundance in Zone 1 than in Zone 2 ($P < 0.05$) (Table 15) indicating that this guild selected habitats with tree overstories. A good example of tree preference is the cavity-nesting tree swallow which was the dominant species in the aerial foraging guild. Only one bark forager, the yellow-bellied sapsucker, was recorded as a breeding species, occupying Zone 1 only. Few sapsucker pairs were counted because territory size can be as large as one study site. Freshwater foragers did not vary in species richness or pair abundance among zones ($P > 0.05$), composing only a small proportion of total bird numbers across the elevational cline. Spotted Sandpiper was consistently the most abundant freshwater guild species, regardless of elevation.

To summarize, number of species within guilds varied to the greatest extent between Zones 1 and 3. Species densities in 5 of 6 guilds differed significantly between Zones 1 and 3, whereas three guilds differed significantly between Zones 2 and 3, and only the aerial foraging guild differed substantially between Zones 1 and 2.

Similarity in Species Composition Among Guilds.--Based on the presence or absence of species in each elevational zone, greatest overall similarity was between Zone 1 cottonwood habitats and Zone 2 shrub willow habitats which shared 43% of all species (Table 16). Zone 2 and Zone 3 had 30% similarity in species and Zone 1 and Zone 3 had a minimum of 13% similarity.

In guild comparisons between Zones 1 and 2, similarities were highest in the bark-foragers (1.0), lower-canopy foragers (0.7) and

Table 16. Jaccard Similarity Index based on presence/absence data measuring similarities in species composition in foraging guilds and overall bird assemblages between pairs of elevational zones.^a

Foraging Guild	Zone 1 vs. Zone 2	Zone 2 vs. Zone 3	Zone 1 vs. Zone 3
Ground	0.33	0.50	0.13
Lower Canopy	0.70	0.30	0.20
Upper Canopy	0.17	0.00	0.00
Aerial	0.33	0.00	0.00
Bark	1.00	0.00	0.00
Freshwater	0.50	0.25	0.50
Overall ^b	0.43	0.30	0.13

^aElevational zones are Zone 1 = low-elevation cottonwood habitat, Zone 2 = mid-elevation shrub willow habitat, and Zone 3 = high-elevation subalpine willow habitat.

^bOverall = all guilds combined.

freshwater foragers (0.5), while upper-canopy foragers were least similar (0.17) (Table 16). Zone 2 and Zone 3 shared fewer species, with the ground-foraging guild being most similar (0.5), followed by lower-canopy foragers (0.3) and freshwater foragers (0.25). No species were shared in common between Zone 3 vs. other zones in upper-canopy, aerial or bark foraging guilds because these guilds did not occur in Zone 3. In guild comparisons between Zones 1 and 3, freshwater foragers attained highest similarity (0.5), followed by low similarities in lower canopy foragers (0.2) and ground foragers (0.13). To summarize, highest guild similarities were between Zones 1 and 2, whereas fewest guild species were shared between Zones 1 and 3.

DISCUSSION

Examination of substructural changes in bird assemblages was helpful in explaining large-scale zonal variation in whole communities. Species richness and bird abundance were community attributes that could be evaluated at resolution levels below that of the whole community. By subdividing the avian assemblage into six foraging guilds, each assigned to a habitat stratum, intra-guild trends in numbers of birds and species were revealed. These trends were related to structural changes within habitat layers as well as to changes in number of layers among zones. Thus, by using a subcommunity, or guild approach, specific sources of variation were discovered that could explain spatial fluctuations in whole avian communities.

Bird numbers remained remarkably constant within each vegetational zone over the three-year period of this study, but varied substantially among elevational zones. Decreases in species richness, overall bird abundance, and number of foraging guilds were inversely related to elevation (Finch 1986), but elevation was probably not the only causal factor influencing bird numbers. Habitat structures varied significantly with elevation: tree density, shrub height, number of vegetation layers, and foliage density within vegetation layers all decreased as elevation increased (Table 10). At high altitudes, severe climate and weather and short growing seasons create a difficult environment for plant and animal survival. Riparian plant communities that are adapted to these subalpine conditions are structurally less variable, composed of essentially two vertical habitat layers: herbaceous and low shrub. The decline in plant community complexity was likely the main cause of the significant decline in bird species diversity and the loss of three foraging guilds.

Guilds that depended on tree trunks or tree canopies for their food supply automatically dropped out of riparian avifaunas when cottonwoods disappeared at higher elevations. Loss of bark foraging substrate explains the disappearance of yellow-bellied sapsuckers, and loss of overstory foliage explains the decline in upper-canopy foragers. Loss of tall perches for sit-and-wait predators (e.g., flycatchers), and in the case of cavity-nesting swallows, loss of nest sites, generally accounts for the disappearance of aerial foragers in subalpine zones. Thus, loss of upper habitat layers in subalpine

plant communities prevented habitat occupancy of certain foraging guilds, consequently resulting in declines in total bird abundance and species richness.

Subalpine riparian habitats supplied habitat strata suitable for guilds that foraged in water, on the ground or in low shrubs. However, even these suitably-adapted guilds had extremely low species numbers. Species composition in these guilds differed considerably from the same guilds at lower elevations. Despite the same lack of a tree overstory in both mid- and high-elevation zones, guild species composition and density were less similar between these two zones than between mid- and low-elevation zones, suggesting environmental conditions and habitat quality in subalpine communities were suboptimal for most riparian bird species, regardless of guild membership. Lincoln's sparrow, the only subalpine species that occurred in other riparian zones, placed all nests found in lower elevation zones in dwarf shrubby thickets, analagous to these found in subalpine habitat. Because its populations peaked in subalpine habitats, selection for habitats with monotonous shrubby thickets seems obvious. Exclusive selection of these simple habitats by Wilson's warblers and white-crowned sparrow suggests that these two species are specifically adapted to subalpine conditions within the range of riparian habitats studied.

With respect to guild distributional patterns among zones, the most striking aspect was the homogeneity of pair abundances in the ground-foraging guild despite significant variation in number of

species. Even though abundance remained constant, the ground-foraging guild achieved dominance in Zone 3 because canopy species were absent in response to overstory loss. However, foliage density in the herbaceous layer did not change across zones. Lack of zonal variation in the ground layer of vegetation may result in similar carrying capacities across zones which in turn may explain constancy in abundance in the ground-foraging guild.

In conclusion, using a whole guild approach to assess avian responses to a riparian environmental gradient proved successful. Although Szaro (1986) criticized the use of avian guilds as a means of predicting bird responses to habitat structure, I found that by relating the occupancy patterns of guilds to the presence or absence of habitat layers in each elevational zone, trends in avian numbers could be tracked in relation to zonal variation in habitats. Greater habitat layering in low-elevation cottonwood associations resulted in greater capability to support avian species. Examination of the zone associations of individual species and communities supported guild-based explanations, but were not as useful in explaining the underlying causes of large-scale variation in bird numbers. Because of the short-term nature of this study, annual fluctuations in species' populations were not detected. However, I believe that long-term bird responses to climatic variation will not overshadow or substantially alter my contention that elevation, and its consequent effect on habitat dimensionality, significantly affected riparian bird community structure via effects on guild members.

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CHAPTER 3
HABITAT SIZE AND HABITAT OVERLAP OF
RIPARIAN BIRDS IN THE CENTRAL ROCKY MOUNTAINS

INTRODUCTION

Numerous studies have demonstrated that complex habitats support richer species assemblages than structurally simple habitats because more resource dimensions are available that can be exploited in more ways (MacArthur and MacArthur 1961, Pianka 1967, Recher 1969, Karr and Roth 1971, Rosenzweig 1973, Røv 1975, Cody 1974, Dueser and Shugart 1978, Cody 1981). A popular tool used to explore strong correlations between vegetation structure, species diversity, and species coexistence patterns has been Hutchinson's (1958) spatial model of the niche (e.g., James 1971, Inger and Colwell 1977, Anderson and Shugart 1974, Findley 1976, Smith 1977, Whitmore 1975, 1977, Holmes et al. 1979, Sabo 1980, Sabo and Holmes 1983). Factors that are typically proposed to influence species diversity and community development include the breadth and diversity of the resource base; the extent that an average species can use these resources or mean niche breadth; and the degree that these resources can be shared or the amount of niche overlap (MacArthur 1972). Given the conditions of resource limitation and competition, community species diversity is predicted to increase with increased diversity of available resources, increased niche overlap, and/or reduced average niche size (Pianka 1979). Because resource

limitation and competition are seldom demonstrated in natural communities (Wiens 1984), these forces do not adequately explain evident trends in niche size and overlap.

A complicating factor in the study of community structure and complexity is scale of observation. Allen and Starr (1982) proposed that community boundaries be defined at different levels of resolution because as levels are changed, the behavior of the system changes, and structures of complex communities can be understood by observing these behavioral changes. Hierarchical structures are inherent in complex systems, and different levels within hierarchies must be viewed at different scales using methods appropriate for each scale (Allen and Starr 1982, Allen et al. 1984). Spatial and temporal variation in the environment are commonly considered in ecological scaling studies (Wiens 1973, Johnson 1980, Wiens 1981), although other hierarchies such as those defined by taxonomic, phenotypic, or age boundaries may exist within a spatial or temporal hierarchical level (Maurer 1985).

In this paper, habitat niche relationships in communities of birds breeding in riparian habitats of southeastern Wyoming are viewed at two spatial scales of observation. The first spatial scale was the entire elevational continuum. Because habitat structure and complexity varies along the altitudinal cline, I also studied avian communities at the resolution level of the elevational zone. Changes in the spatial distribution of trees, shrubs, and ground cover produce overall differences in habitat structure that can be classed using

elevational limits (Chapters 1 and 2). Variation in habitat niche relationships at the zonal level is examined because zonal variation in habitat structure and complexity may constrain development of avian community structure through effects on niche size and overlap.

Previously, I showed that negative associations among bird species in this system were uncommon and could be explained by dissimilarities in habitat affinities, and that habitat variation alone sufficed to explain spatial fluctuations in bird numbers (Chapter 1). Increased species richness in lowland cottonwood habitats was partially explained by increased number of guilds and within-guild numbers produced by increased habitat layering (Chapter 2). Given this base, further insight into mechanisms that regulate bird numbers and distribution may be provided by this examination of niche metrics at different spatial scales. I asked the following questions: (1) Are the habitat niches of lowland riparian birds smaller (i.e., more specialized) than subalpine species, allowing greater species packing and consequently higher species diversity? This question can be partially answered by testing the null hypothesis that there is no difference in mean species habitat niche size among zones. If mean sizes do not vary, then is substantial overlap of habitat use an alternative process permitting high species richness? (2) What is the relationship between average species niche size in different riparian zones and the size or variability of the underlying habitat resource spectrums? The null hypothesis is that species niche size is equal to the size of the habitat resource base in each zone.

- (3) Is there a relationship between habitat niche size and habitat restriction? For example, does a species that occupies multiple riparian zones have a larger habitat size than a zone-restricted species? The null hypothesis is that there is no difference in mean habitat niche size in zone-dependent and zone-independent species.
- (4) If habitat niches are examined at different spatial scales, what is the effect of such alteration of perspective on niche interpretations? The null hypothesis is no effect of spatial scale.
- (5) What processes best explain patterns of habitat niche size and overlap, and species diversity among riparian bird species?

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 potentially important in a thorough analysis of niche patterns. Although my analyses and discussion do not address these more refined methods of resource partitioning, their probable existence is acknowledged, especially among species with high habitat overlap.

METHODS

Study Area.--The investigation was performed on or within 16 km of the Medicine Bow National Forest in Albany and Carbon Counties, southeastern Wyoming. Ten 8.1-ha study areas were established in streamside habitats over an elevational cline ranging from 2054 m to

2987 m. Each site was gridded at 33.5 m intervals with wooden stakes painted fluorescent orange and labelled with grid coordinates. At lower elevations (2050 to 2250 m), sites were dominated by narrowleaf cottonwood (Populus angustifolia) and tree and shrub willow (Salix sp.), but at elevations above 2285 m, shrub willow species covered the land surface area. In subalpine forests, riparian habitats were composed of shrubby thickets of S. planifolia interspersed with boggy meadows. Site selection criteria and vegetation composition of the study areas are described in greater detail in Finch (Chapters 1 and 2).

Sampling Random Habitat and Bird Territories.--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 male singing locations. Bird-centered vegetation sampling was developed by James (1971) and has commonly been used to assort and partition sets of habitat features selected by different bird species and individuals (e.g., Whitmore 1975, Roth 1979, Karr and Freemark 1983, Larson and Bock 1986). Larson and Bock (1986) recommended bird-centered sampling as a more powerful tool for evaluating habitat relationships 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).

Territory locations were determined by spot-mapping avian pairs on each site from mid-May through early July of the three study years. Chapter 1 fully describes this counting procedure. Samples were

located in proportion to the abundance of each species on each study area. A total of 461 territories were sampled over the elevational continuum. For a species to be retained in the final analysis, a minimum sample size of seven territories was prescribed, which resulted in the examination of 20 bird species and overall 444 territories. Refer to Table 3 (Chapter 1) for descriptions of species mnemonic acronyms used in this chapter. Sample data were pooled in each species to give estimates of habitat characteristics over all plots as well as within each of three elevational zones (See Chapter 2 for zone descriptions).

For comparison, 40 random locations on each study grid were sampled in a mode identical to the territory-centered samples. Random sampling sites were located by selecting grid coordinates from a table of random numbers (Rohlf and Sokal 1969). Random sample data were pooled to give estimates of habitat features of each plot, groups of plots within elevational zones, and all plots combined.

At each sampling location, a set of 34 structural habitat variables was measured following a point-centered quarter sampling procedure recommended by Noon (1981). Habitat features were sampled by dividing each location into four quadrants oriented in the cardinal compass directions. Sixteen of the original variables were deleted from the final analyses because they were invariant or highly correlated with other variables. Within a group of highly correlated variables, the variable retained was that which had a sampling distribution most closely approaching normality. Descriptions and

sampling techniques for the remaining 19 variables are presented in Table 2 (Chapter 1).

Data Analysis.--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 bird-centered samples were entered into the PCA. Scores in each resultant habitat factor were summed and averaged for each species and for the random group at three spatial scales: study area, elevational zone, and all plots combined. Because of sample size limitations, only the latter two scales were used in the bird-centered data.

The position of species centroids in n-dimensional space to a centroid representing randomly available habitat resources was considered a measure of habitat niche position (Dueser and Shugart 1979, Reinert 1984, James and Lockerd 1986). Habitat position was calculated as the Euclidian distance of each species centroid in principal components space to the random habitat centroid (Carnes and Slade 1982). Multidimensional measures of species habitat breadth or habitat size were computed as the mean squared distances of individual species scores from the centroid of that species (Carnes and Slade 1982). Mean squared distance reflects the sum of variation within species and is relatively unaffected by sample size or position of the origin of PCA axes (Carnes and Slade 1982). These variances indicate the degree of specialization in habitat use by each species. Statistical comparisons of habitat size were accomplished using

F ratios (Carnes and Slade 1982). At a narrower spatial scale, changes in habitat size within a species were examined in those species occupying more than one elevational zone to determine if habitat size shifts with elevation. Habitat sizes of each species within each zone and across all plots were statistically compared to that of randomly available resources at the same spatial scale to determine if species habitat size differed significantly from random habitat size. Habitat sizes of the ten random plots were also computed to detect trends in habitat variability with increase in elevation and distance from the master centroid of pooled random plots.

Species habitat overlap on each principal component axis was calculated using Maurer's (1982) formula, modified from Harner and Whitmore (1977):

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

where d is the distance between species centroids, and s₁ and s₂ 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 on Cyber 730 and 760 computers using SPSS and SPSSX programs (Nie et al. 1975, Hull and Nie 1981, SPSS Inc. 1986). Analysis of three data sets comprised 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 log-transformed data analyses 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, $P < 0.001$). An overall PCA of 20 species and random habitat produced five factors with eigenvalues exceeding 1.0 (Table 17). These factors accounted for 66.8% of the total variance, each factor explaining a successively smaller proportion. Means and standard deviations of factor scores for each group on the five principal component axes are presented in Table 18. Interpretation of the principal component axes and the positions of species and random habitat centroids are illustrated for the first three axes in Figure 6 and for the last two axes in Figure 7.

Oneway ANOVA's indicated that species habitat centroids differed significantly on all five factors (Table 17). Biological interpretations of each factor are based upon the habitat variables that are

Table 17. Summary statistics of a principal components analysis of random and bird-centered habitat data, and varimax-rotated factor matrix. 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 ^a	14.89***	4.18***	1.54*	3.89***	1.67*
Factor Matrix					
CANHT	<u>0.858</u>	-0.187	0.213	0.104	0.008
TDEN	<u>0.883</u>	-0.230	-0.161	0.020	-0.074
SHBA	-0.272	-0.034	<u>0.761</u>	-0.044	0.019
SHCD	-0.073	-0.137	<u>0.894</u>	0.063	0.037
SHHT	0.099	0.020	<u>0.675</u>	0.320	0.076
SHDIS	0.064	-0.684	<u>0.202</u>	-0.186	0.002
VFD1	-0.138	<u>0.219</u>	0.164	-0.138	<u>0.409</u>
VFD2	-0.221	<u>0.632</u>	-0.042	-0.034	<u>0.092</u>
VFD3	-0.087	<u>0.396</u>	0.120	<u>0.605</u>	-0.004
VFD4	<u>0.498</u>	-0.100	0.101	<u>0.628</u>	-0.103
VFD5	<u>0.623</u>	-0.016	-0.085	<u>0.041</u>	0.014
CANCOV	<u>0.610</u>	-0.052	0.119	-0.609	0.005
COVER	-0.114	<u>0.596</u>	-0.038	-0.011	-0.167
WILL	-0.686	<u>0.123</u>	0.375	0.005	0.067
EVH	-0.136	<u>0.743</u>	0.081	0.015	0.084
FRUIT	-0.593	-0.268	-0.171	0.137	-0.113
BARE	<u>0.491</u>	-0.326	-0.067	0.109	-0.323
GRASS	-0.032	-0.118	-0.022	0.036	<u>0.678</u>
WATER	-0.166	0.045	0.158	-0.061	-0.139

^aResults of ANOVA for 19 variables and 21 groups (20 species plus random group) testing for habitat differences among species on each principal components axis (* $P < 0.01$, *** $P < 0.0001$).

Table 18. Means + standard errors of principal components (PC) scores for 20 species.

Group	N	PC1	PC2	PC3	PC4	PC5
Random	400	-0.15 + 0.05	-0.13 + 0.05	-0.11 + 0.05	-0.06 + 0.04	0.01 + 0.04
MODO	11	1.04 + 0.18	-0.55 + 0.30	-0.08 + 0.28	-0.01 + 0.29	-0.14 + 0.30
BTHU	16	0.09 + 0.18	0.01 + 0.18	0.32 + 0.18	0.05 + 0.29	0.07 + 0.16
WWPE	15	1.14 + 0.12	-0.58 + 0.20	-0.12 + 0.24	-0.25 + 0.22	-0.23 + 0.24
WIFL	11	1.12 + 0.34	0.09 + 0.20	-0.21 + 0.29	0.34 + 0.20	0.02 + 0.24
DUFL	7	-0.50 + 0.10	0.36 + 0.30	0.53 + 0.34	0.79 + 0.32	0.47 + 0.09
TRSW	8	0.80 + 0.29	-1.23 + 0.45	-0.20 + 0.34	0.37 + 0.19	-0.80 + 0.44
HOWR	30	1.16 + 0.15	-0.25 + 0.14	-0.14 + 0.17	0.07 + 0.18	-0.16 + 0.17
VEER	21	0.31 + 0.21	0.10 + 0.15	0.26 + 0.20	0.25 + 0.20	-0.06 + 0.18
AMRO	41	0.66 + 0.13	0.02 + 0.13	0.13 + 0.16	0.29 + 0.13	0.08 + 0.13
GRCA	9	0.29 + 0.32	0.03 + 0.30	-0.25 + 0.29	-0.05 + 0.26	0.38 + 0.13
WAVI	16	1.07 + 0.25	0.05 + 0.16	-0.02 + 0.25	0.17 + 0.22	0.11 + 0.19
YEWB	60	0.29 + 0.12	0.17 + 0.11	0.20 + 0.11	0.28 + 0.11	0.07 + 0.09
NGWA	10	-0.39 + 0.10	0.44 + 0.15	0.67 + 0.24	0.17 + 0.26	0.43 + 0.11
COYE	12	-0.40 + 0.12	0.54 + 0.16	0.38 + 0.20	-0.12 + 0.24	0.52 + 0.16
WIWA	28	-0.69 + 0.03	0.54 + 0.11	-0.04 + 0.15	-0.56 + 0.06	-0.12 + 0.13
SOSP	40	-0.17 + 0.11	0.33 + 0.15	0.21 + 0.15	0.48 + 0.13	-0.16 + 0.16
LISP	60	-0.65 + 0.03	0.31 + 0.08	0.06 + 0.10	-0.31 + 0.10	-0.06 + 0.09
WCSP	24	-0.71 + 0.03	0.37 + 0.10	0.01 + 0.18	-0.60 + 0.11	-0.07 + 0.13
BRBL	17	-0.30 + 0.18	0.20 + 0.18	0.36 + 0.21	0.19 + 0.22	0.48 + 0.09
BHCO	8	0.38 + 0.28	-0.27 + 0.27	0.29 + 0.46	0.37 + 0.32	-0.24 + 0.39

^aSpecies acronyms are described in Table 3.

Figure 6. Positions of species and random centroids of the first three principal axes with pictorial interpretation of associated habitat gradients. Names associated with species acronyms are given in Table 3.

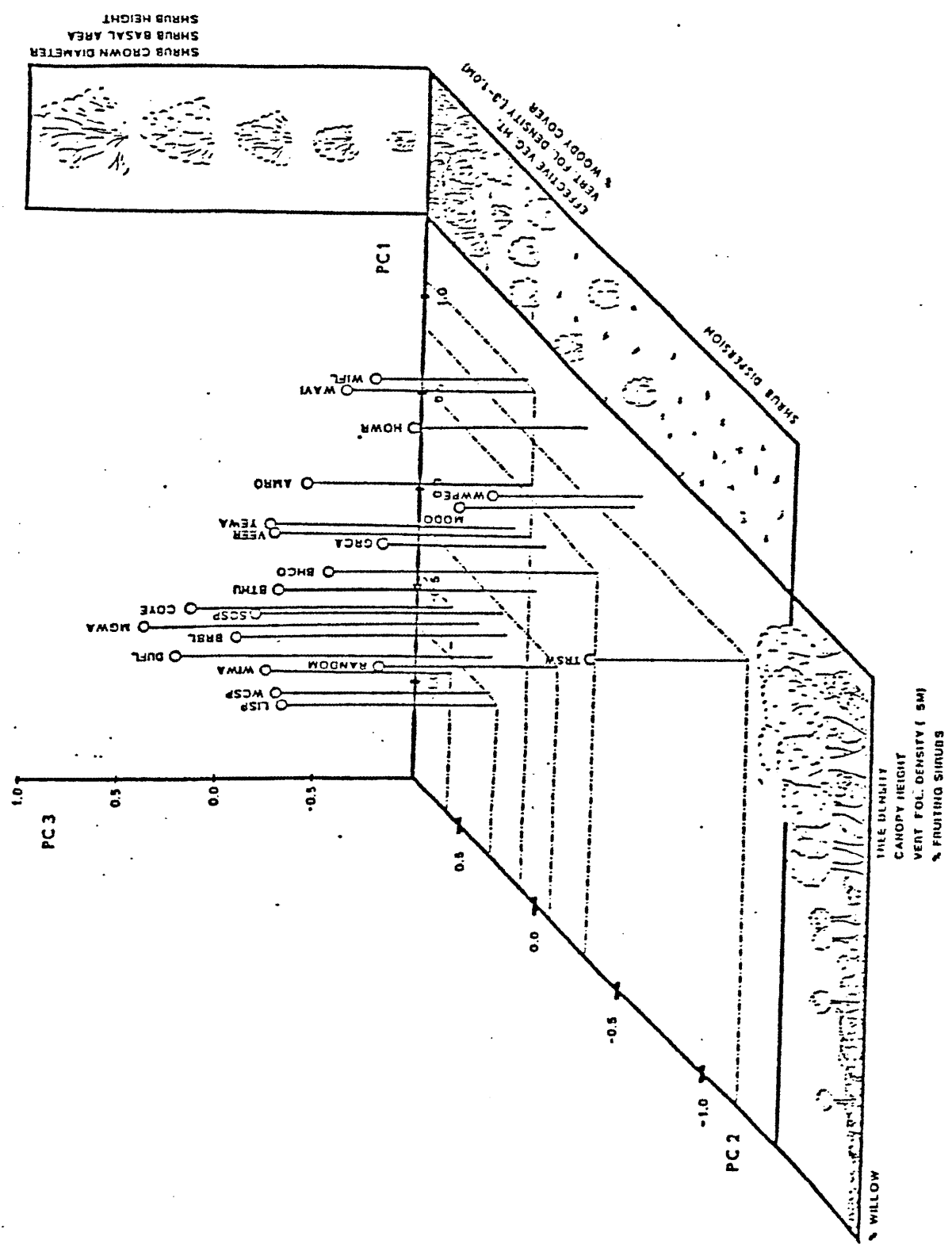
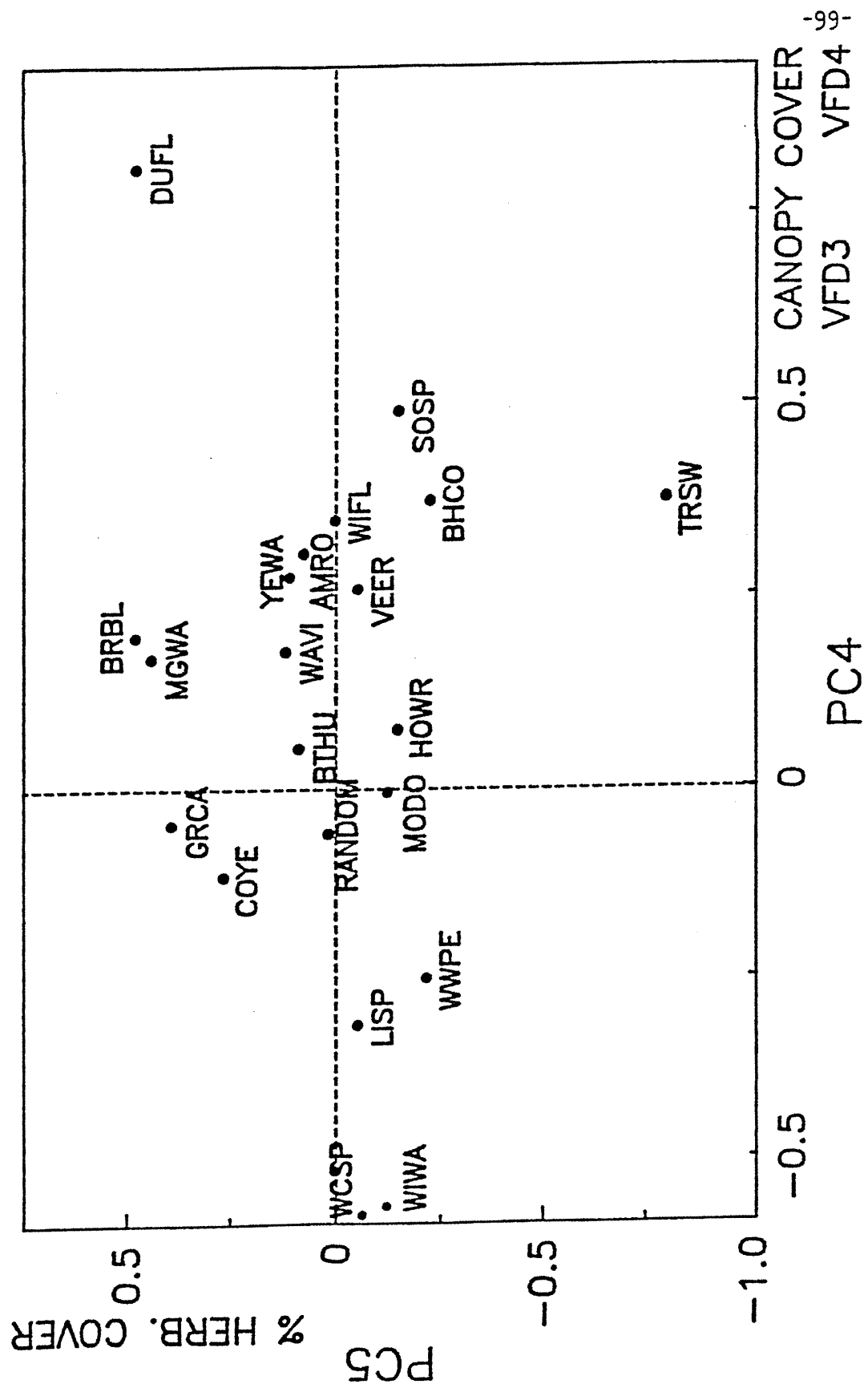


Figure 7. Positions of species and random centroids on the fourth and fifth principal components axes. Species acronyms are described in Table 3.



most highly correlated ($r > 0.4$) with each factor (Table 17). The first factor was most highly correlated with the following habitat variables (listed in descending order of importance): TDEN, CANHT, VFD5, WILLOW, CANCOV, FRUIT, VFD4, and ROCK. Opposite habitat trends were indicated by the negative or positive signs associated with each correlation. For example, the first factor signified a condition where tree density and canopy height increased (TDEN, $r = 0.883$; CANHT, $r = 0.858$) as percent shrub willow decreased (WILLOW, $r = -0.686$). Taking other variables into account in this way, the first factor 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, which accounted for the greatest amount (27.4%) of variation in the data, distinguished species that strongly preferred habitats dominated by cottonwoods from species choosing shrub willow areas (Figure 6).

Important variables in the second factor were EVH, SHDIS, VFD3, and 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 explained 14.3% of the total variance and clearly separated species preferring open, shrubless sites (e.g., tree swallow, western wood pewee and mourning dove) from species selecting dense shrub cover (e.g., Wilson's warbler, common yellowthroat) (Figure 6).

Factor three accounted for 12.6% of the total variance and was highly correlated with SHCD, SHBA, and SHHT. This factor which represented a shrub size gradient from tall, large-diametered shrubs to small shrubs, separated species found at sites with tall shrub layers (e.g., dusky flycatcher, MacGillivray's warbler) from species selecting the opposite extreme (e.g., western wood pewee, house wren) (Figure 6).

The fourth factor had highest correlations with VFD4, CANCOV, and VFD5, and accounted for 7.3% of the total variance. This factor described a foliage density gradient from a dense, closed canopy to a sparsely foliated overstory (Figure 7). This axis distinguished white-crowned sparrow, Wilson's warbler, Lincoln's sparrow and western wood pewee from a variety of species selecting dense canopies (e.g., dusky flycatcher, song sparrow, tree swallow, brown-headed cowbird).

Factor five accounted for 5.3% of the total variance and had high positive correlations with GRASS and VFD1. This factor described ground surface features varying from sites covered with a dense, herbaceous ground layer to sites with few grasses and forbs (Figure 7). Species most strongly associated with the positive extreme were Brewer's blackbird, MacGillivray's warbler, gray catbird and dusky flycatcher whereas tree swallow had a strong negative relationship.

The habitats chosen by each species are represented by a combination of all five habitat dimensions derived from PCA. Multifactor habitat centroids and mean habitat vectors for each group were used to describe general patterns of habitat selection among the

20 species (Tables 18 and 19). 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 practical reference point for evaluating positions of species centroids in multidimensional space. Species using habitats with denser and taller canopies and more trees than the average random habitat site ($CANHT = 4.0$ m, $CANCOV = 22.9\%$, $TDEN = 1.5/100 \text{ m}^2$) were mourning dove, western wood pewee, willow flycatcher, tree swallow, house wren, veery, American robin, and warbling vireo (Table 19). In these habitats, bare ground (BARE) comprised up to 50% of the surface area at any species-selected site in contrast to 14.3% at the average random site, and shrub-cover was always less than the random average ($COVER = 34.4\%$) (Table 19). 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 ($TDEN < 0.6/100 \text{ m}^2$), dense shrub cover ($SHDIS < 2.0$ m), high percentage of willow species ($WILLOW > 70\%$), and high shrub foliage density ($VFD2 > 1.0$ hits) 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,

Table 19. Means $\pm$ standard errors of original variables for 20 species. Refer to Table 18 for sample sizes; Table 2, Chapter 1 for definitions of habitat variables and Table 3, Chapter 1 for species names.

Variable	RANDOM	MODD	BTNU	WVFE	VIPL	DUFL	TSW
CANHT (m)	4.00 $\pm$ 0.19	8.31 $\pm$ 0.92	4.58 $\pm$ 0.79	7.87 $\pm$ 0.60	7.94 $\pm$ 1.44	2.94 $\pm$ 0.98	7.43 $\pm$ 1.24
TDCN (100 m ²)	1.50 $\pm$ 0.20	3.90 $\pm$ 1.90	1.00 $\pm$ 0.40	3.30 $\pm$ 0.80	13.70 $\pm$ 8.90	0.10 $\pm$ 0.00	4.20 $\pm$ 1.20
CANCOV (%)	22.90 $\pm$ 1.70	51.27 $\pm$ 11.39	21.25 $\pm$ 7.03	41.87 $\pm$ 8.79	62.73 $\pm$ 11.32	23.00 $\pm$ 13.64	33.23 $\pm$ 12.18
SHCA (m ²)	0.28 $\pm$ 0.03	0.12 $\pm$ 0.05	0.27 $\pm$ 0.04	0.13 $\pm$ 0.05	0.33 $\pm$ 0.18	0.46 $\pm$ 0.17	0.33 $\pm$ 0.13
SHCD (cm)	132.32 $\pm$ 4.19	132.05 $\pm$ 30.60	132.35 $\pm$ 15.62	123.50 $\pm$ 19.80	127.85 $\pm$ 21.67	176.36 $\pm$ 36.17	153.31 $\pm$ 39.46
SHHT (m)	1.81 $\pm$ 0.05	1.84 $\pm$ 0.22	2.04 $\pm$ 0.14	2.23 $\pm$ 0.56	1.79 $\pm$ 0.21	2.94 $\pm$ 0.98	1.98 $\pm$ 0.25
SHDIS (m)	4.91 $\pm$ 0.31	4.84 $\pm$ 3.53	3.34 $\pm$ 0.51	6.31 $\pm$ 1.78	2.42 $\pm$ 0.63	2.40 $\pm$ 0.82	13.00 $\pm$ 5.15
VFO1 (Phlita)	2.60 $\pm$ 0.09	1.88 $\pm$ 0.29	1.91 $\pm$ 0.32	1.44 $\pm$ 0.19	1.79 $\pm$ 0.29	2.91 $\pm$ 0.55	1.30 $\pm$ 0.32
VFO2 (Phlita)	1.24 $\pm$ 0.07	0.50 $\pm$ 0.19	0.82 $\pm$ 0.28	0.33 $\pm$ 0.12	0.49 $\pm$ 0.26	0.77 $\pm$ 0.31	0.08 $\pm$ 0.05
VFO3 (Phlita)	0.45 $\pm$ 0.05	0.26 $\pm$ 0.26	0.87 $\pm$ 0.34	0.11 $\pm$ 0.07	0.40 $\pm$ 0.14	1.31 $\pm$ 0.49	0.16 $\pm$ 0.08
VFO4 (Phlita)	0.44 $\pm$ 0.05	1.40 $\pm$ 0.53	0.58 $\pm$ 0.28	0.67 $\pm$ 0.25	1.76 $\pm$ 0.61	0.73 $\pm$ 0.38	0.44 $\pm$ 0.26
VFO5 (Phlita)	0.14 $\pm$ 0.03	0.21 $\pm$ 0.18	0.07 $\pm$ 0.05	0.27 $\pm$ 0.10	0.67 $\pm$ 0.29	0.00 $\pm$ 0.00	0.10 $\pm$ 0.10
COVER (%)	34.38 $\pm$ 2.14	10.18 $\pm$ 2.83	36.69 $\pm$ 7.83	8.33 $\pm$ 2.93	26.09 $\pm$ 9.61	21.29 $\pm$ 9.75	10.88 $\pm$ 9.28
VILL (%)	67.60 $\pm$ 1.93	27.27 $\pm$ 12.92	62.50 $\pm$ 8.23	20.00 $\pm$ 7.40	18.18 $\pm$ 9.59	89.29 $\pm$ 5.05	34.38 $\pm$ 14.89
EVM (m)	0.49 $\pm$ 0.02	0.54 $\pm$ 0.24	0.58 $\pm$ 0.12	0.23 $\pm$ 0.04	0.37 $\pm$ 0.15	1.35 $\pm$ 0.31	0.10 $\pm$ 0.04
FRUIT (%)	24.21 $\pm$ 1.68	50.00 $\pm$ 12.15	28.13 $\pm$ 7.17	56.67 $\pm$ 7.89	65.91 $\pm$ 11.81	3.57 $\pm$ 3.57	65.63 $\pm$ 14.89
BAKE (%)	11.30 $\pm$ 1.27	41.00 $\pm$ 9.89	11.00 $\pm$ 5.95	47.53 $\pm$ 8.86	18.18 $\pm$ 8.00	0.00 $\pm$ 0.00	59.38 $\pm$ 16.32
GRASS (%)	52.08 $\pm$ 2.45	48.82 $\pm$ 9.61	51.56 $\pm$ 8.59	44.13 $\pm$ 10.09	53.35 $\pm$ 11.24	75.14 $\pm$ 9.08	29.75 $\pm$ 15.33
WATER (%)	3.37 $\pm$ 0.63	0.00 $\pm$ 0.00	0.75 $\pm$ 0.75	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	3.57 $\pm$ 3.57	0.00 $\pm$ 0.00

Variable	BOVE	VEER	AMRD	CECA	SAVZ	TEWA	NEVA
CANHT (m)	9.43 $\pm$ 0.83	6.08 $\pm$ 1.16	7.89 $\pm$ 0.64	5.90 $\pm$ 1.52	9.09 $\pm$ 1.43	5.80 $\pm$ 0.57	2.57 $\pm$ 0.42
TDCN (100 m ²)	6.60 $\pm$ 2.40	2.30 $\pm$ 1.00	3.40 $\pm$ 1.70	2.00 $\pm$ 1.20	4.90 $\pm$ 1.90	1.80 $\pm$ 0.50	0.10 $\pm$ 0.10
CANCOV (%)	53.13 $\pm$ 7.02	38.86 $\pm$ 7.73	44.71 $\pm$ 5.74	29.33 $\pm$ 13.35	63.44 $\pm$ 9.51	36.02 $\pm$ 4.43	12.60 $\pm$ 4.99
SHCA (m ²)	0.13 $\pm$ 0.04	0.24 $\pm$ 0.06	0.24 $\pm$ 0.05	0.17 $\pm$ 0.05	0.12 $\pm$ 0.05	0.29 $\pm$ 0.05	0.79 $\pm$ 0.24
SHCD (cm)	122.43 $\pm$ 13.81	147.87 $\pm$ 16.69	139.18 $\pm$ 14.40	101.84 $\pm$ 14.34	142.19 $\pm$ 23.99	143.81 $\pm$ 10.05	191.63 $\pm$ 22.98
SHHT (m)	2.12 $\pm$ 0.26	2.18 $\pm$ 0.16	2.11 $\pm$ 0.15	1.59 $\pm$ 0.16	1.94 $\pm$ 0.20	1.97 $\pm$ 0.09	2.35 $\pm$ 0.37
SHDIS (m)	4.40 $\pm$ 0.88	2.76 $\pm$ 0.49	3.88 $\pm$ 0.81	3.08 $\pm$ 1.31	2.73 $\pm$ 0.35	3.01 $\pm$ 0.54	2.20 $\pm$ 0.26
VFO1 (Phlita)	1.51 $\pm$ 0.19	1.84 $\pm$ 0.23	2.39 $\pm$ 0.24	2.33 $\pm$ 0.43	2.27 $\pm$ 0.62	2.54 $\pm$ 0.27	4.19 $\pm$ 0.62
VFO2 (Phlita)	0.37 $\pm$ 0.12	1.23 $\pm$ 0.36	0.82 $\pm$ 0.16	0.97 $\pm$ 0.37	0.59 $\pm$ 0.20	1.19 $\pm$ 0.19	1.44 $\pm$ 0.53
VFO3 (Phlita)	0.31 $\pm$ 0.11	0.44 $\pm$ 0.17	0.50 $\pm$ 0.13	0.29 $\pm$ 0.20	1.14 $\pm$ 0.32	0.67 $\pm$ 0.13	0.15 $\pm$ 0.11
VFO4 (Phlita)	0.97 $\pm$ 0.21	0.51 $\pm$ 0.17	1.09 $\pm$ 0.21	0.29 $\pm$ 0.20	0.53 $\pm$ 0.16	0.14 $\pm$ 0.06	0.00 $\pm$ 0.00
VFO5 (Phlita)	0.56 $\pm$ 0.16	0.14 $\pm$ 0.09	0.27 $\pm$ 0.10	0.09 $\pm$ 0.09	0.53 $\pm$ 0.16	31.35 $\pm$ 3.85	25.10 $\pm$ 8.76
COVER (%)	18.60 $\pm$ 3.69	19.48 $\pm$ 3.92	22.88 $\pm$ 3.50	17.89 $\pm$ 6.99	17.88 $\pm$ 4.42	35.97 $\pm$ 5.01	75.00 $\pm$ 9.86
VILL (%)	17.77 $\pm$ 4.03	52.76 $\pm$ 7.44	46.54 $\pm$ 6.44	50.00 $\pm$ 13.82	31.75 $\pm$ 8.68	35.97 $\pm$ 5.01	1.36 $\pm$ 0.22
EVM (m)	0.33 $\pm$ 0.06	0.85 $\pm$ 0.15	0.76 $\pm$ 0.12	0.75 $\pm$ 0.23	0.64 $\pm$ 0.23	0.96 $\pm$ 0.11	5.00 $\pm$ 3.00
FRUIT (%)	59.17 $\pm$ 6.51	26.62 $\pm$ 6.57	42.68 $\pm$ 7.16	41.67 $\pm$ 11.02	46.88 $\pm$ 10.43	35.98 $\pm$ 5.09	2.40 $\pm$ 1.80
BAKE (%)	34.67 $\pm$ 5.60	22.00 $\pm$ 7.04	21.85 $\pm$ 4.42	9.47 $\pm$ 5.36	22.63 $\pm$ 6.89	18.30 $\pm$ 3.44	66.30 $\pm$ 8.98
GRASS (%)	43.90 $\pm$ 5.78	53.14 $\pm$ 7.63	54.39 $\pm$ 4.46	69.67 $\pm$ 8.42	59.56 $\pm$ 8.32	49.08 $\pm$ 4.01	6.20 $\pm$ 3.35
WATER (%)	0.43 $\pm$ 0.83	5.38 $\pm$ 2.54	0.88 $\pm$ 0.49	2.78 $\pm$ 2.78	0.00 $\pm$ 0.00	2.90 $\pm$ 1.05	

Variable	COTE	MIVA	SOSP	LISP	UCSP	BSRL	SHCO
CANHT (m)	2.61 $\pm$ 0.43	1.64 $\pm$ 0.15	4.00 $\pm$ 0.54	1.69 $\pm$ 0.12	1.40 $\pm$ 0.06	3.81 $\pm$ 1.08	5.91 $\pm$ 1.09
TDCN (100 m ²)	0.20 $\pm$ 0.10	0.10 $\pm$ 0.00	0.60 $\pm$ 0.20	0.10 $\pm$ 0.00	0.10 $\pm$ 0.00	1.10 $\pm$ 1.00	1.90 $\pm$ 0.90
CANCOV (%)	9.42 $\pm$ 4.39	0.00 $\pm$ 0.00	27.63 $\pm$ 4.77	9.58 $\pm$ 3.07	1.04 $\pm$ 1.04	18.53 $\pm$ 5.88	34.63 $\pm$ 11.58
SHCA (m ²)	0.58 $\pm$ 0.19	0.45 $\pm$ 0.11	0.36 $\pm$ 0.08	0.29 $\pm$ 0.03	0.45 $\pm$ 0.12	0.40 $\pm$ 0.09	0.39 $\pm$ 0.17
SHCD (cm)	146.62 $\pm$ 20.12	123.22 $\pm$ 11.36	149.37 $\pm$ 16.37	140.76 $\pm$ 8.49	144.75 $\pm$ 16.04	168.21 $\pm$ 22.41	169.23 $\pm$ 38.63
SHHT (m)	2.23 $\pm$ 0.34	1.44 $\pm$ 0.15	2.13 $\pm$ 0.16	1.63 $\pm$ 0.08	1.40 $\pm$ 0.06	1.99 $\pm$ 0.16	2.76 $\pm$ 0.91
SHDIS (m)	1.78 $\pm$ 0.30	2.01 $\pm$ 0.33	2.96 $\pm$ 0.67	2.61 $\pm$ 0.30	3.02 $\pm$ 0.42	2.24 $\pm$ 0.57	3.94 $\pm$ 1.28
VFO1 (Phlita)	2.48 $\pm$ 0.49	3.29 $\pm$ 0.37	2.37 $\pm$ 0.31	3.25 $\pm$ 0.76	3.15 $\pm$ 0.39	3.08 $\pm$ 0.36	2.04 $\pm$ 0.61
VFO2 (Phlita)	1.44 $\pm$ 0.33	1.75 $\pm$ 0.23	1.43 $\pm$ 0.27	1.30 $\pm$ 0.15	1.72 $\pm$ 0.29	1.12 $\pm$ 0.31	0.50 $\pm$ 0.27
VFO3 (Phlita)	0.19 $\pm$ 0.32	0.30 $\pm$ 0.11	0.83 $\pm$ 0.16	0.41 $\pm$ 0.11	0.19 $\pm$ 0.10	0.69 $\pm$ 0.24	0.48 $\pm$ 0.27
VFO4 (Phlita)	0.70 $\pm$ 0.19	0.00 $\pm$ 0.00	0.59 $\pm$ 0.16	0.19 $\pm$ 0.09	0.02 $\pm$ 0.02	0.33 $\pm$ 0.16	0.94 $\pm$ 0.27
VFO5 (Phlita)	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.03 $\pm$ 0.02	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.04 $\pm$ 0.04
COVER (%)	34.33 $\pm$ 7.90	58.18 $\pm$ 6.40	40.53 $\pm$ 4.98	43.52 $\pm$ 4.02	55.79 $\pm$ 6.77	17.41 $\pm$ 3.54	11.00 $\pm$ 6.00
VILL (%)	91.67 $\pm$ 4.70	98.21 $\pm$ 1.79	70.00 $\pm$ 5.16	92.08 $\pm$ 2.41	95.83 $\pm$ 4.17	79.88 $\pm$ 7.61	50.00 $\pm$ 14.94
EVM (m)	1.29 $\pm$ 0.25	0.93 $\pm$ 0.08	1.06 $\pm$ 0.13	0.96 $\pm$ 0.10	0.84 $\pm$ 0.09	0.87 $\pm$ 0.21	0.79 $\pm$ 0.31
FRUIT (%)	2.08 $\pm$ 2.08	1.79 $\pm$ 1.79	20.63 $\pm$ 4.38	3.33 $\pm$ 1.11	4.17 $\pm$ 4.17	12.29 $\pm$ 6.20	40.63 $\pm$ 15.63
BAKE (%)	1.08 $\pm$ 1.08	2.14 $\pm$ 0.88	11.20 $\pm$ 3.44	6.17 $\pm$ 1.55	0.50 $\pm$ 0.50	1.47 $\pm$ 1.47	31.38 $\pm$ 13.42
GRASS (%)	56.25 $\pm$ 8.66	37.00 $\pm$ 6.17	41.40 $\pm$ 5.13	45.30 $\pm$ 4.07	39.04 $\pm$ 7.38	75.24 $\pm$ 4.90	45.13 $\pm$ 10.83
WATER (%)	8.33 $\pm$ 5.44	2.64 $\pm$ 1.49	6.88 $\pm$ 3.01	5.02 $\pm$ 1.50	4.67 $\pm$ 2.33	5.88 $\pm$ 2.88	12.50 $\pm$ 5.33

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 (total elevational continuum) was computed as the distance to the random habitat centroid (all plots pooled) in principal components space (Carnes and Slade 1982) (Table 20). Species located near the random centroid were considered to be using widespread, readily available habitat resources whereas species positioned far from the random centroid used habitat resources that were scarce. Species closest to the random centroid (habitat position < 0.75) were broad-tailed hummingbird, gray catbird, veery, song sparrow, yellow warbler and Lincoln's sparrow (Table 20). These widespread species were distributed over multiple elevational zones, and with respect to yellow warblers, Lincoln's sparrows and song sparrows, were dominant species (Chapter 1). Species positioned farthest from the random centroid (habitat position > 1.30) were tree swallow, western wood pewee, willow flycatcher, house wren, and dusky flycatcher. Of these species, swallows, pewees, and wrens, selected cottonwood woodlands exclusively; willow flycatchers selected dense shrub sites in cottonwood or mixed willow habitats bordered by mixed grass prairie; and dusky flycatchers were found only on shrub plots bordered by coniferous forest. Swallows and wrens, which required cavity nest sites, were abundant in habitats where these requirements were met. The other species were uncommon or rare.

Table 20. Habitat position (distance from a random sample representing mean available habitat to species centroids), and habitat size (mean squared distances of observations from species centroid). Habitat size of the random sample was 3.97. Species with habitat sizes that are significantly smaller than the random sample are marked with *(two-tailed F test, P < 0.05).^a

Species	Habitat position	Habitat size	Homogeneous ^b subsets of habitat size	Zone Dependency
WIWA	1.02	1.47*	a	yes
MGWA	1.10	1.53*	a	yes
WCSP	0.94	1.65*	a	yes
COYE	0.91	1.77*	ab	yes
DUFL	1.31	1.95*	abc	yes
LISP	0.74	2.04*	abc	no
BRBL	0.81	2.55	abcd	no
GRCA	0.62	2.87*	abcde	no
WWPE	1.37	3.04	abcde	yes
BTHU	0.53	3.12	abcde	no
WIFL	1.35	3.34	bcde	no
YEWA	0.71	3.37*	bcde	no
WAVI	1.26	3.48*	cde	yes
VEER	0.70	3.56*	cde	no
AMRO	0.93	3.81	de	no
MODO	1.22	3.89	de	yes
SOSP	0.70	3.91	de	no
HOWR	1.32	3.93	de	yes
BHCO	0.83	4.33	e	no
TRSW	1.71	4.70	e	yes

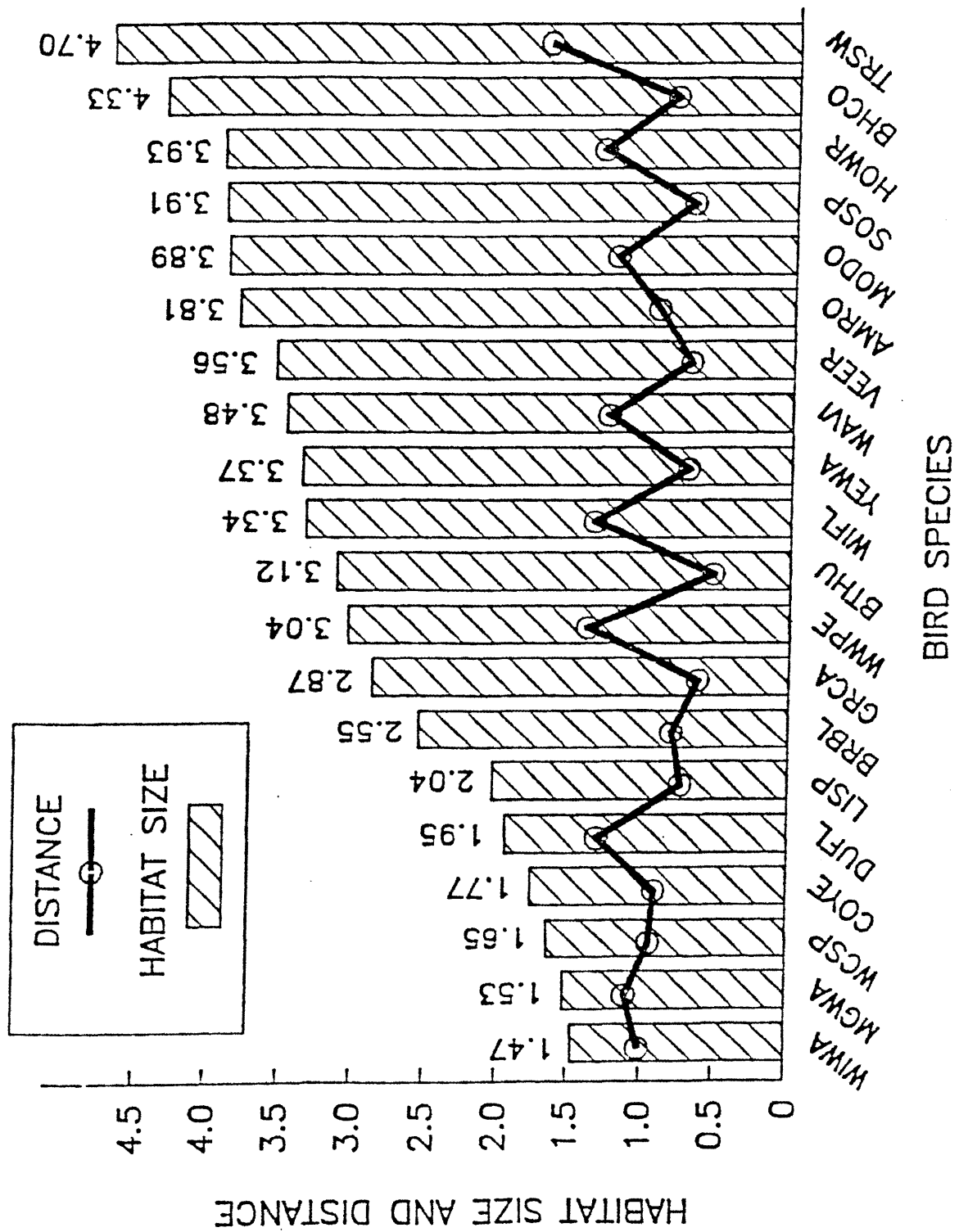
^aSpecies acronyms are described in Table 3.

^bSpecies with the same letter in the homogeneous subset column have habitat sizes that are not significantly different (two-tailed F tests) at P < 0.05.

The degree of specialization in habitat use by each species, referred to as habitat size, is represented by the variance of observations around the species centroid (Carnes and Slade 1982). Two-tailed F-tests were used to statistically compare species habitat sizes to the variance of the random habitat sample. Eleven bird species had significantly smaller habitat sizes than the random habitat variance, suggesting more specialized habitat use than the remaining nine species (Table 20). Wilson's warbler exhibited the narrowest range of habitat selection, followed closely by MacGillivray's warbler, white-crowned sparrow, common yellowthroat, dusky flycatcher and Lincoln's sparrow, all with habitat sizes of 2.0 or smaller. Species using an intermediate range of habitats included gray catbird, yellow warbler, warbling vireo, veery and American robin. High variability in habitat use indicated by species habitat sizes that did not differ significantly from the random sample were exhibited by tree swallow, brown-headed cowbird, house wren song sparrow, mourning dove, willow flycatcher, broad-tailed hummingbird, western wood pewee, and Brewer's blackbird (Table 20).

There was no consistent relationship between habitat position and habitat size of species at this wide scale of all pooled plots ($\underline{r} = 0.14$, $\underline{t} = .60$, $\underline{P} > 0.05$) (Figure 8). For example, Lincoln's sparrow demonstrated narrow use of common habitat (small size, close position) whereas tree swallow, house wren, and mourning dove demonstrated wide use of atypical habitat (large size, far position). I considered species that chose narrow ranges of scarce habitat (small size, far

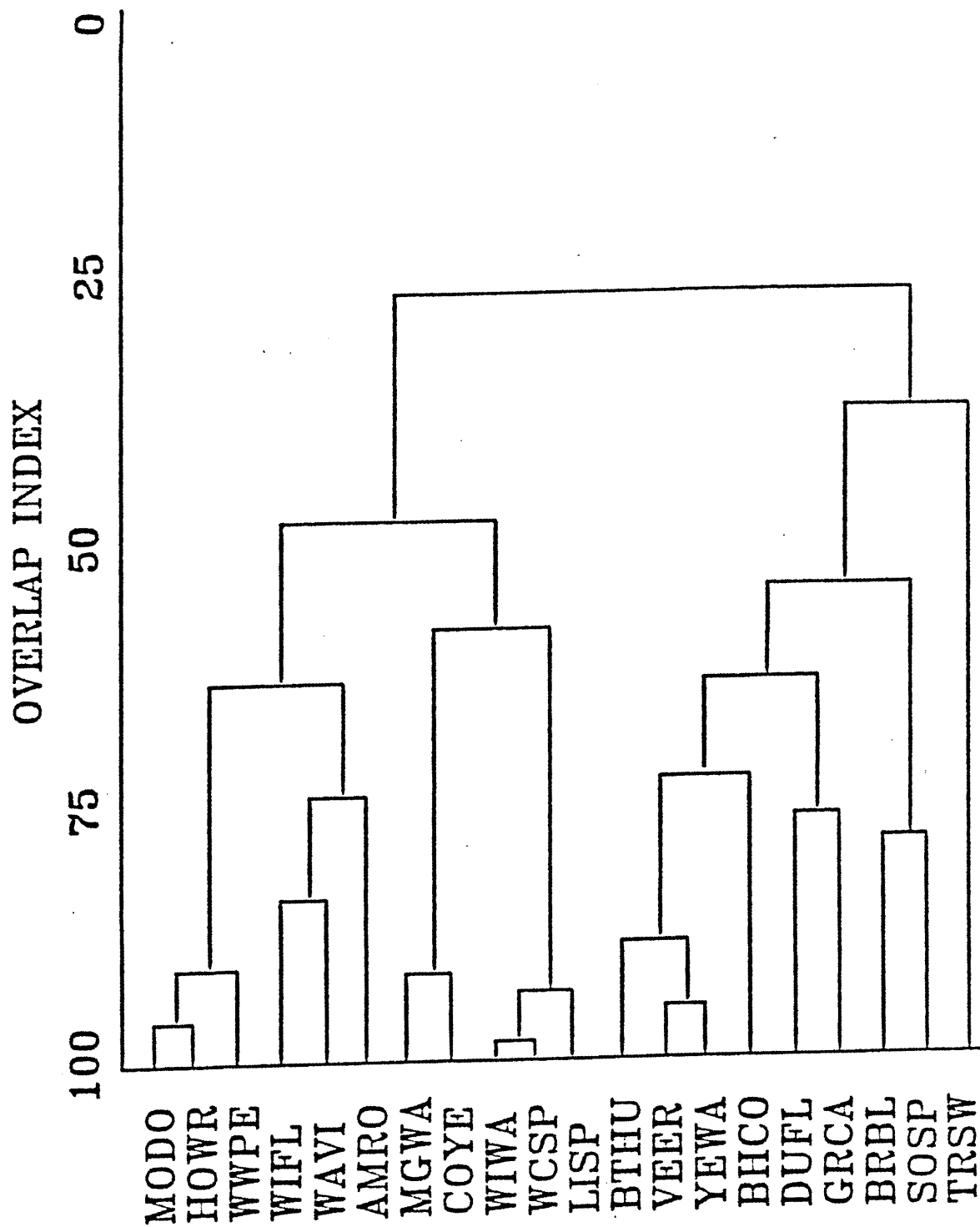
Figure 8. Relationship between habitat size and habitat position (distance) of 20 bird species. Numbers above columns are habitat sizes of each species. Species acronyms are described in Table 3.



position) to be the most specialized user of the overall riparian spectrum. The species, Wilson's warbler, MacGillvray's warbler, and dusky flycatcher belonged to this class. Song sparrow, brown-headed cowbird, and American robin demonstrated widest use of commonly available habitat (large size, close position) and I thus considered these to be the top three generalists of the riparian habitat gradient.

Cluster analysis of the matrix of total overlap values computed at the spatial scale of the entire riparian continuum produced a hierarchical arrangement of species overlaps (Figure 9). The greatest amount of overlap occurred in Wilson's warbler and white-crowned sparrow, species found exclusively in subalpine habitats. Lincoln's sparrow also overlapped heavily with this group. Mourning dove, house wren and western wood pewee, species found exclusively in woodland areas showed heavy overlap. This group was linked to a lesser degree to another heavily overlapped group comprised of willow flycatcher, warbling vireo, and American robin. MacGillvray's warbler and common yellowthroat showed similar habitat alliances, overlapping less extensively with the subalpine group mentioned earlier. Yellow warbler, veery and broad-tailed hummingbird also formed a tight cluster which was linked to brown-headed cowbird at a greater distance. Cowbirds lay their eggs in the nests of yellow warblers and veerys so high habitat overlap is not surprising. Dusky flycatcher and gray catbird also overlapped extensively as did Brewer's blackbird and song sparrow. Tree swallow showed lowest overlap with any group of species, probably because of its unique combination of aerial-foraging

Figure 9. Dendrogram of habitat niche overlaps in 20 bird species. (full names described in Table 3). Overlaps are based on data gathered across the entire elevational cline. 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.



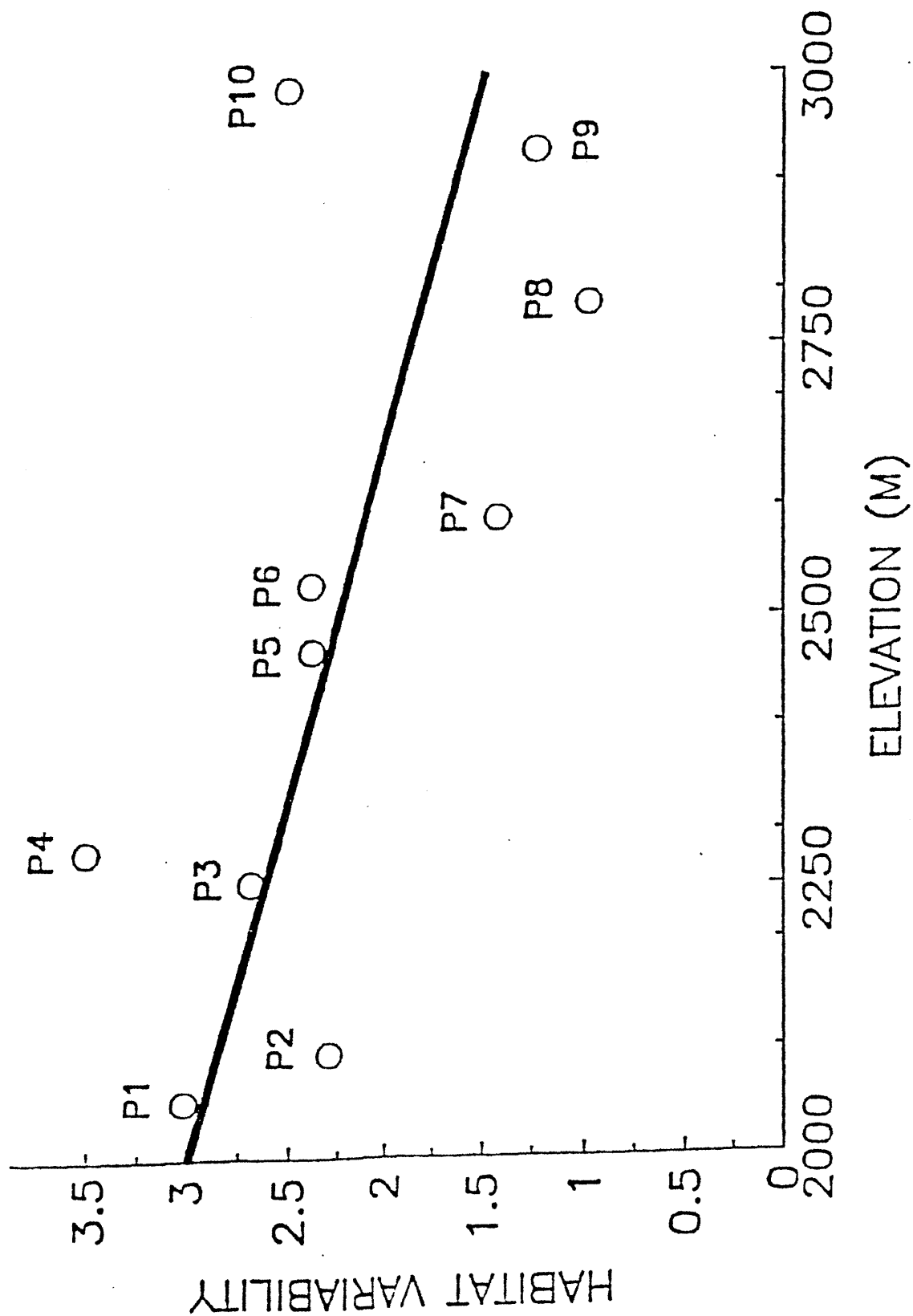
and cavity-nesting habitat precluded substantial similarity in habitat use.

This cluster analysis of overall habitat overlap values produced groups that were similar in species content to those derived from the cluster analysis of bird abundances at the same spatial scale (Chapter 1). These seemingly robust aggregations of species disintegrate, however, at the spatial scale of the elevational zone, as I will show in the section on zonal variation in habitat size.

Zonal Variation in Habitat Size.--Habitat size of individual species can partially be explained by a trend in study plot variability. Applying Carnes and Slade's (1982) estimator of habitat size to random habitat sampled at each of ten study areas revealed a gradient of increasing habitat variability with decrease in elevation ($r = 0.62$, $t = 2.24$, $p < 0.05$) (Figure 10). Therefore, the habitat size of a species that resides in subalpine riparian habitats is limited by the reduced habitat variability present at high elevations. Likewise, generalists occupying high elevation habitats will automatically have smaller habitat sizes than generalists using complex lowland woodlands, even though the habitat sizes of each species may not significantly differ from a random sample at each locality.

To adjust for unequal random habitat variances among elevational zones, I calculated habitat sizes of species within three elevational zones 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 partitioned among zones. Because fewer species

Figure 10. Negative relationship between ascending elevation (m) and habitat variability of ten study plots (P1-P10) sampled at random. Plot numbers were assigned in ascending order of elevation. Habitat variability was computed using the method described in Carnes and Slade (1982) for habitat size.



occupied each zone, fewer species were sampled at this narrower spatial scale. Five species had samples sufficient for intraspecific habitat size comparisons among zones.

In the low-elevation cottonwood zone, 3 of 11 species (warbling vireo, yellow warbler, and veery) exhibited narrower ranges of habitat use than what was randomly present (Table 21). In the mixed shrub willow zone, 5 of 10 ten species (Lincoln's sparrow, broad-tailed hummingbird, MacGillvray's warbler, yellow warbler, veery) used significantly smaller habitat ranges, and in the subalpine willow zone, all three species had habitat sizes that significantly differed from random. Random habitat size differed significantly among the three zones Oneway ANOVA, (F -ratio = 3.82, $p < 0.05$), and in all pairwise comparisons of zones (Duncans Multiple Range Test, $p < 0.05$). Intraspecific comparisons of those species with sufficient samples revealed statistically similar ranges of habitat selection ($p > 0.05$) among Zones 1 and 2 except in broad-tailed hummingbird (Figure 11) which had a narrower range in mixed shrub willow than in lowland woodlands ($p = 0.002$). In comparisons between Zones 2 and 3, habitat size in Lincoln Sparrow, the only species abundant enough to sample, also remained constant ($p > 0.05$). Thus, although variability in random sites significantly differed among zones, variability in sites occupied by species remained the same regardless of zone.

Zonal Variation in Habitat Overlap.--When sample sizes of some groups are small, Raphael (1981) recommended the use of euclidian distance between species centroids as a measure of similarity because

Table 21. Habitat sizes of bird species among three elevational zones: cottonwood-willow (Zone 1), mixed shrub willow (Zone 2) and subalpine willow (Zone 3). Habitat sizes of random samples were: Zone 1 = 3.31 (N = 120); Zone 2 = 3.10 (N = 120); Zone 3 = 2.58 (N = 160). Two-tailed F-tests ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$) were used to compare species habitat sizes to random habitat sizes within each zone.^a

Species	Zone 1		Zone 2		Zone 3	
	N	Size	N	Size	N	Size
MODO	11	3.89				
BTHU	6	2.30	10	2.14**		
WWPE	15	3.04				
WIFL	8	1.98				
DUFL			7	1.95		
TRSW	7	4.39				
HOWR	27	3.54				
VEER	10	2.83**	11	2.49*		
AMRO	29	3.39	12	2.44		
WAVI	13	2.79**				
YEWA	30	2.77*	30	2.30*		
MGWA			10	1.53*		
COYE			12	1.77		
WIWA					28	1.47***
SOSP	12	4.20	28	4.06		
LISP			20	1.71***	39	1.59***
WCSP					24	1.65*
BRBL			14	2.22		

^aSpecies acronyms are described in Table 3.

Figure 11. Intraspecific comparisons of habitat sizes of five species that occupy both cottonwood lowlands (Zone 1) and mixed shrub willow (Zone 2). Habitat variances (size) of random sites in Zones 1 and 2 are also presented for comparison. Species acronyms are described in Table 3.

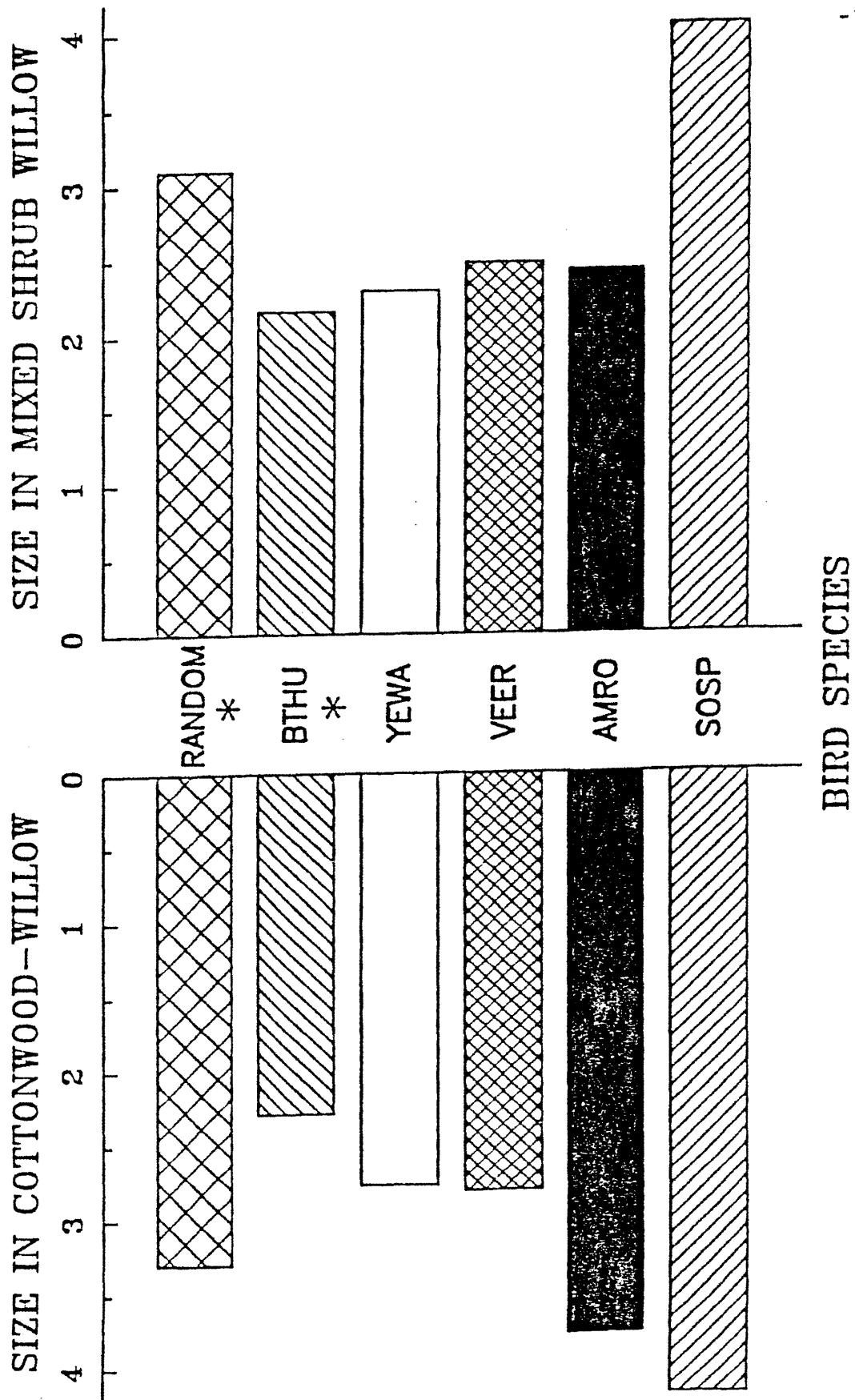


Table 22. Matrix of habitat niche overlaps and euclidian distances between pairs of species in the cottonwood/willow zone. Numbers above the diagonal are overlap values, and numbers below the diagonal are distances.^a

Species Acronym ^b	RANDOM	WWPE	HOWR	AMRO	YENA	SOSP	WIFL	WAVI	MODO	VEER	TRSW
RANDOM											
WWPE	0.433										
HOWR	0.365	0.914									
AMRO	0.283	0.357	0.931								
YENA	0.252	0.619	0.490	0.971							
SOSP	0.724	0.626	0.502	0.863	0.937						
WIFL	0.887	0.997	0.916	0.888	0.824	0.661					
WAVI	0.645	1.085	0.876	0.521	0.589	0.493	0.641				
MODO	0.439	0.936	0.670	1.031	0.993	1.439	0.569	0.732			
VEER	0.692	0.152	0.391	0.608	0.589	0.971	0.713	0.569	0.961		
TRSW	1.601	0.810	0.651	0.501	0.631	0.768	0.569	0.749	0.892	0.809	
		1.412	1.512	1.752	1.811	1.844	0.567	0.738	0.847	0.750	
							0.268	0.403	0.829	0.822	
							0.268	0.542	0.693	0.884	
							0.684	0.571	0.480	0.794	
							1.143	0.955	0.630	0.630	
							1.235	0.690	0.571	0.389	
							1.790	2.011	0.834	0.801	
									1.519	0.721	
										1.856	

^a An overlap value of 0.0 implies maximum dissimilarity between species in use of habitat resources, and an overlap value of 1.0 means that habitat use is identical.

^b Species acronyms are described in Table 3.

Table 23. Matrix of habitat niche overlaps and euclidian distances between pairs of species in the mixed shrub willow zone. All values are computed using five principal components. Numbers above the diagonal are overlap values, and numbers below the diagonal are distances.^a

Species Acronym ^b	RANDOM	COYE	MGWA	AMRO	Yewa	SOSP	DUFL	BTHU	LISP	VEER	BRBL
RANDOM											
COYE	1.010	0.523	0.430	0.451	0.637	0.691	0.523	0.535	0.658	0.852	0.660
MGWA	0.981	0.447	0.823	0.725	0.771	0.643	0.531	0.786	0.785	0.608	0.645
AMRO	0.995	0.804	0.768	0.754	0.638	0.492	0.748	0.667	0.743	0.694	0.757
Yewa	0.894	0.609	0.619	0.454	0.678	0.641	0.650	0.620	0.634	0.454	0.644
SOSP	0.943	0.801	0.901	0.624	0.302	0.908	0.596	0.742	0.810	0.862	0.521
DUFL	0.905	0.963	0.655	0.583	0.625	0.853	0.495	0.710	0.647	0.808	0.505
BTHU	0.656	0.657	0.588	0.596	0.399	0.555	0.596	0.521	0.706	0.713	0.833
LISP	0.670	0.492	0.417	0.569	0.338	0.567	0.553	0.293	0.759	0.801	0.569
VEER	0.491	0.681	0.622	0.533	0.467	0.623	0.548	0.312	0.266	0.856	0.658
BRBL	0.592	0.536	0.481	0.710	0.637	0.841	0.684	0.531	0.332	0.338	0.761

^a An overlap value of 0.0 implies maximum dissimilarity between species in use of habitat resources, and an overlap value of 1.0 means that habitat use is identical.

^b Species acronyms are described in Table 3.

Table 24. Matrix of habitat niche overlaps and euclidian distances between pairs of species in the subalpine willow zone. All values are computed using five principal components. Numbers above the diagonal are overlap values, and numbers below the diagonal are distances.^a

Species Acronym ^b	Random	WIWA	WCSP	LISP
RANDOM		0.710	0.778	0.709
WIWA	0.424		0.895	0.879
WCSP	0.493	0.196		0.766
LISP	0.297	0.238	0.315	

^aAn overlap value of 0.0 implies maximum dissimilarity between species in use of habitat resources, and an overlap value of 1.0 means that habitat use is identical.

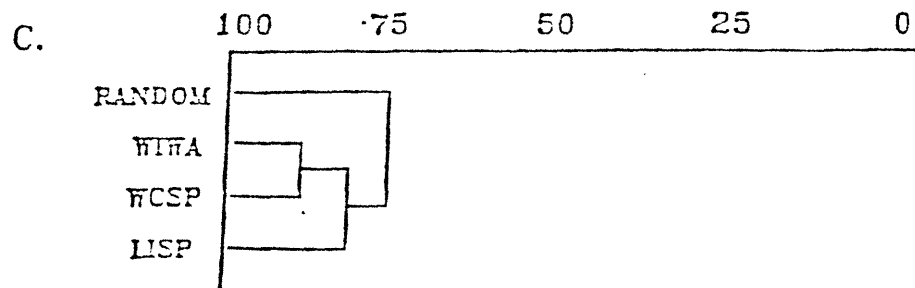
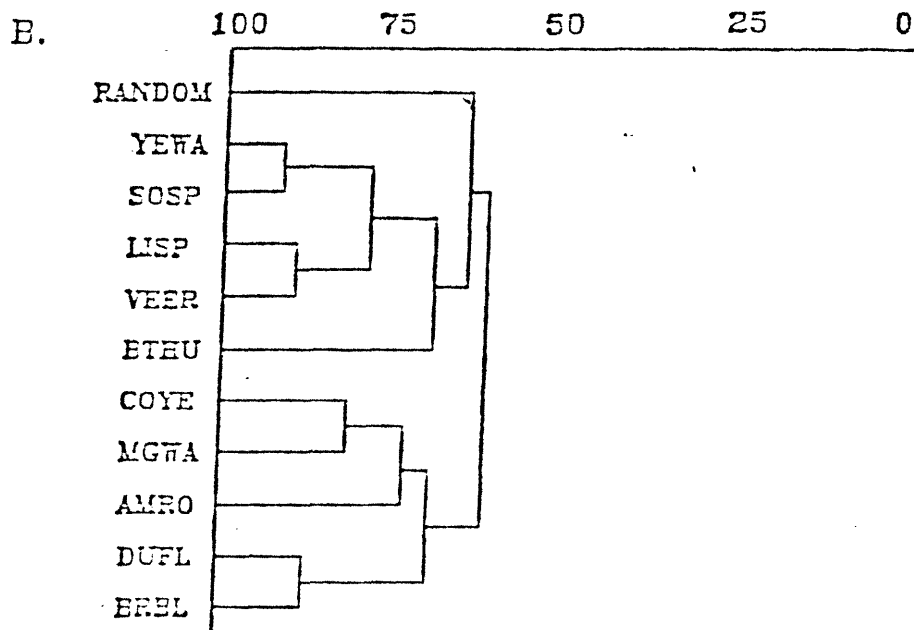
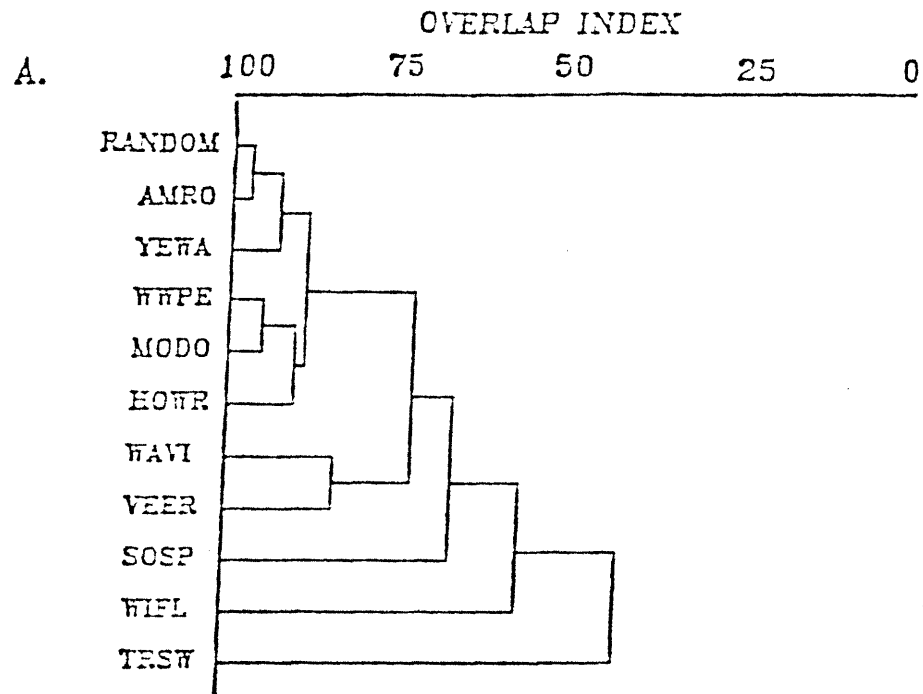
^bSpecies acronyms are described in Table 3.

it was a good predictor of niche overlap in his study. I explored this relationship by comparing distance and overlap matrices in each zone (Tables 22, 23, 24) using correlational analysis. In this study, distance was a poor predictor of niche overlap (Zone 1: $\underline{r}^2 = 0.01$; Zone 2: $\underline{r}^2 = 0.02$, Zone 3: $\underline{r}^2 = 0.40$; all zones $\underline{p} > 0.05$) because variances of habitat centroids were high for some species and low for others (reflected in habitat sizes). Because overlap values convey information about the dispersion of each species about its centroid, they are preferable over distances in cases where sample sizes and dispersion values are highly variable.

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 robins, pewees, doves, wrens and yellow warblers showed heavy habitat overlap ($\hat{a} > .80$) (Figure 12A). This cluster was closely allied to the random sample, with American robin showing highest similarity in habitat distribution to the random sample. Similarity in habitat choice was also high in veery and warbling vireo, but song sparrow, willow flycatcher, and tree swallow showed no strong overlap with any one species or subset of species, instead forming linkages only after all lower order amalgamations were made.

Habitat resources were shared in a different manner in the mixed shrub willow zone where two major clusters of species were formed, each comprised of five species (Figure 12B). Neither group showed the close association with random habitat that was evident in some of the

Figure 12. Dendrograms of species habitat overlaps in three riparian zones. See Figure 8 for interpretation of index values and Table 3 for a description of species acronyms. Figure 12A refers to species common in cottonwood lowlands (Zone 1); 12B refers to mixed shrub willow (Zone 2) species; and 12C specifies subalpine willow (Zone 3) species.



species occupying the cottonwood zone. Likewise, the subalpine willow species overlapped more heavily among themselves than with the random sample (Figure 12C). Mean overlap values for random-to-species centroids were 0.81 ± 0.15 for Zone 1, 0.60 ± 0.13 for Zone 2, and 0.73 ± 0.04 for Zone 3. Mean random: species overlap differed significantly among zones (F -ratio = 6.78, $P < 0.01$). In contrast, mean species: species overlap did not vary among zones (F -ratio = 2.54, $P > 0.05$). Mean species: species overlaps 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 showed high affinity for randomly available habitat resources, but shared less habitat space among each other, whereas species in Zone 2 and 3 showed closer habitat alliances among species and greater use of specialized (non-random) habitat.

COMPARATIVE RESULTS AND DISCUSSION

In this study, I used breeding season data on habitat use, pooled at the spatial scales of the altitudinal cline and the elevational zone, to examine patterns of niche structure among riparian bird species. A summary of community characteristics based on my findings are provided in Table 25. I used data on habitat niche size to test two hypotheses: that mean species habitat size does not differ among elevational zones; and that species niche size is equal to the size of the habitat resource base in the occupied zone. Based only on the results that mean species habitat size was significantly smaller in

Table 25. Summary of community attributes of riparian breeding birds in southeastern Wyoming based on findings from Chapters 1 and 2, and this study. Results are reported at two spatial scales: overall cline and elevational zone.

	Overall Cline	Cottonwood/ Willow	Mixed Shrub Willow	Subalpine Willow
Species Richness/zone ^a	45	35	28	12
Bird Abundance/8.1 ha ^b	N/A ^c	98.8 ± 19.08	78.1 ± 18.25	36.4 ± 22.14
Number of Guilds	6	6	5	3
Mean Random: Species Overlap	N/A ^c	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) ^d	3.97 ± 2.48	3.31 ± 2.35	3.10 ± 2.30	2.58 ± 2.31
Mean Species Habitat Size (B) ^d	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%

^aTotal number of breeding species counted in each zone and across the entire cline.

^bBird abundance was first averaged across plots within each year and zone, then averaged across the three years.

^cN/A = not applicable.

^dRandom habitat size is the variance of random site scores from the random centroid, whereas mean species habitat size is the average of the variances of species scores from each species centroid.

subalpine birds than in lowland birds, I rejected the first hypothesis. Considering, however, that random habitat size was also significantly smaller in subalpine habitat than in cottonwood habitats, I reasoned that species habitat size may simply have been a reflection of the size of the zone resource base (Hypothesis 2). If Hypothesis 2 is accepted for all species then rejection of Hypothesis 1 is no longer legitimate (in fact Hypothesis 1 cannot be tested as stated given those circumstances). My results showed that some species in each zone had significantly smaller habitat sizes than the random habitat size, so Hypothesis 2 was rejected for those species. Rejection of Hypothesis 2 validated rejection of Hypothesis 1.

Species Diversity, Habitat Size, and Resource Base.--Using data derived from my test results, I then asked questions about the relationship between species diversity and habitat niche size. For review, small habitat niche size meant that the range of habitats a species used was narrower than the range of habitat resources available, suggesting nonrandom habitat selection. When the underlying resource base is broad, species diversity should be high compared to narrower-based communities (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 more complex than riparian shrub communities which was reflected by the larger values for mean random habitat size (Table 25). Species richness, overall bird abundance, and number of habitat foraging guilds were substantially higher

(Chapters 1, 2 and Table 25) in lowland 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 1974a,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 random: species overlap values were higher in Zone 1 than in Zones 2 and 3, one must 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 no higher or lower than those in the two shrub willow zones. Thus "species packing" in the most complex habitat was not accomplished by either compression in species habitat size (Schoener 1974b) or by increased species habitat overlap.

Given these Zone 1 conditions, 1) that most species make wide use of the structural resource base, 2) that mean species habitat size is greater than in treeless shrub habitats, and that 3) species habitat overlaps are no higher (or lower), it seems likely that species diversity in narrowleaf cottonwood habitat is greater merely because the structural resource base is broader. Habitat resources are not clearly partitioned in this situation, and therefore competition for habitat space was probably not an internal interactional force driving

avian community development. This conclusion leads to the speculation that narrowleaf cottonwood communities in southeastern Wyoming are not saturated, being composed of an impoverished avifauna that lacks the specialist component 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 must be remembered, however, 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. Nevertheless, it is doubtful that rare species have numbers high enough to substantially alter community structure through interactive pressures.

These results concurred with Knopf's (1986) contention that riparian avifaunas in woodland communities of the central Rocky Mountains were comprised primarily of ecological generalists with continental distributions, or species that occurred primarily in the east or west with the Rocky Mountain region being peripheral to the range. 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, examination of geographic ranges using Knopf's approach revealed that 5 (14.3%) of the 35 woodland species counted on my study had western affinities, 3 (8.5%) had eastern, 1 (2.9%) had central, and the remaining 26 (74.3%) were continental generalists (Appendix A). Continental species have demonstrated their abilities to adapt to a wide variety of environmental

conditions and vegetational types, and it comes as no surprise that the large proportion of cosmopolitan species in my woodland areas produced eurytypism in mean species habitat size. Establishment of riparian forest since the turn of the century apparently permitted recent colonization of woodland birds that were historically prevented from dispersal by the ecological barrier of the Great Plains Grasslands (Knopf 1986). Early photographs and paintings, as well as records and journals of explorers and frontiersmen indicate that cottonwoods traditionally occurred only in local patches in the Great Plains (Williams 1978, Skinner 1986). Planting of shelterbelt woodlands, and damming and irrigation practices allowed cottonwoods to flourish in areas that were too dry and unsuitable before settlement by white man (Williams 1978, Skinner 1986). Establishment of riparian forests provided flight corridors for avian colonization of the central Rockies. The first invasion of colonists were 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 adds new species to communities, building up local diversity (Ricklefs 1987). As diversity increases, the ecological niche is 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 earlier contention that riparian bird communities in cottonwood lowlands of southeastern Wyoming are non-saturated because niche sizes were not compressed, is supported by Knopf's idea that the Great Plains served as a historical geographical limit to dispersal of riparian birds. Local diversity in riparian woodland communities in the central Rockies may therefore increase in time through processes of speciation, immigration, specialization and consequent compression in niche size.

Effects of Zone Restriction at Two Spatial Scales.--Based on whether a species habitat size differed significantly from random size in the specified zone, only 27% (3 of 10) of the examined woodland species chose restricted ranges of structural features, 50% (5 of 10) of mixed shrub willow species selected nonrandom habitat characteristic, and 100% (all three) of subalpine species were stenotypic in habitat choice. Mean species habitat size in mixed shrub willow and subalpine willow differed by 27% and 39% respectively, from random habitat. If habitats in the two shrub willow zones contain more

zone-restricted species than lowland cottonwood communities, a higher proportion of habitat specialists might be predicted. Zone dependency applies to those species requiring resources restricted to that zone. If the required features are not randomly available within a zone, then restricted species may display stenotypic habitat use. Although 29% of the examined woodland species were zone-restricted (mourning dove, Western wood pewee, tree swallow, house wren), none of these restricted species had significant habitat sizes. Habitat data revealed that these four species heavily used densely wooded sites with high canopy cover and high canopy height (Table 19) suggesting that the tree resource itself was the basis of habitat choice. In addition tree swallow, and house wrens are cavity-nesters. Within the woodland zone, narrowleaf cottonwoods were readily available, being the dominant tree. Thus, it is unlikely that trees could have been a limiting resource to zone-restricted woodland species. In contrast, two of the three subalpine species (Wilson's warbler and white-crowned sparrow) were zone-restricted, and both had significant habitat sizes. These species were associated with sites densely covered by heavily foliated willow (Table 19), typically using shrubs that were larger than those randomly available in the subalpine zone ($p < 0.05$ for SHBA and SHCD) (Table 5, Chapter 1). Wilson's warbler and white-crowned sparrow may be restricted to the subalpine zone because they require greater visibility, lower shrubs, and/or greater moisture. Within that zone they select shrubs in a nonrandom manner resulting in stenotypic habitat sizes.

At the spatial scale of the entire elevational continuum, the effects of zone restriction on niche patterns were more pronounced. When habitat niche characteristics are compared between ten zone-dependent species and ten zone-independent species using data pooled over all plots (Table 20), significant differences in mean habitat position ($\underline{t} = 92.34$, $\underline{p} < 0.001$) and habitat size ($\underline{t} = 24.1$, $\underline{p} < 0.001$) were revealed. Species that occupied more than one zone had mean habitat positions (0.79 ± 0.23) that were closer to the random centroid than zone-restricted species (1.22 ± 0.24) and larger mean habitat sizes (3.29 ± 0.68) than zone-dependent species (2.74 ± 1.20). At the resolution level of the overall cline, the null hypothesis of no difference in mean habitat niche size in zone-independent and zone-dependent species can be rejected. Because zone-independent species often had smaller habitat sizes within a particular zone (e.g., yellow warbler, veery, willow flycatcher; Zone 1) than zone-restricted species (e.g., wren, swallow, pewee, dove; Zone 1) (Table 21), zone-restriction differences in habitat size were not as evident at the zone level of resolution. Some zone-dependent species may be classified as stenotypic at the level of the entire cline but eurytypic at the level of the zone. Changing the scale of observation resulted in behavioral changes in the system. Thus, my introductory hypothesis of no effect of spatial scale can also be rejected. 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 in the behavioral changes produced by

altering the scale at which the system is viewed (Allen and Starr 1982).

Other Effects of Spatial Scale.--Habitat use was less similar among all 20 species when viewed at the spatial scale of the entire elevational cline (mean species: species overlap = 0.40) rather than at the zone level (Table 25). Variability in random samples and in bird-centered samples was also generally greater at the scale of the cline than at the zone level (Table 25: Mean habitat size), as to be expected given the wider range of habitat structures. More species and more guilds were also encompassed using the wider scale (Table 25).

CONCLUSION

Constraints placed on species habitat selection and community structure by spatial variation in the environment operated at different spatial scales. Spatial variation in vegetation at the level of resolution of the overall altitudinal cline 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, it

was apparent that individual species preferred specific segments of the habitat gradient as exhibited by abundance patterns. These segments corresponded to habitat zones limited by elevation. Species occupying more than one zone were considered eurytypic at this overview level of resolution whereas zone-dependent species were identified as stenotypic. These definitions were supported by comparisons of average habitat size and overlap in zone-dependent and zone-independent species.

At the smaller observational scale of the elevational zone, these overall community patterns disintegrated, and new patterns of niche size and overlap emerged. Constraints placed on zone species assemblages included within-zone spatial variation in habitat structure and possibly physical proximity of other individuals and species within the zone. As a result, habitat selection patterns were more finely-tuned in species. 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 stenotypic at the wide observational scale, were eurytypic within a zone, and vice versa. A few species remained habitat specialists regardless of scale (Wilson's warbler, white-crowned sparrow, MacGillivray's warbler).

In conclusion, viewing communities at different levels of resolution identified patterns in habitat-species relationships that were obscure or incomplete at a single scale. As Maurer (1982) argued, emphasis on a single observational scale may reduce the

ability of the observer to detect patterns or components of community response that are only clearly visible at other scales. An understanding of complex ecological systems should be considerably enhanced with the use of observational scale.

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Appendix A. Presence (P) or absence (blank) of breeding bird species classified into six foraging guilds in three elevational zones (Zone 1 = low; Zone 2 = middle; Zone 3 = high).

Guild and Species	Scientific Name	Geographic Range ^a	Zone 1	Zone 2	Zone 3
<u>Ground</u>					
Common snipe	(<u>Gallinago gallinago</u>)	C		P	P
Mourning dove	(<u>Zenaida macroura</u>)	C	P		
Northern flicker	(<u>Colaptes auratus</u>)	C	P		
Mountain bluebird	(<u>Sialia currucoides</u>)	C	P	P	
American robin	(<u>Turdus migratorius</u>)	C	P	P	P
European starling	(<u>Sturnus vulgaris</u>)	C	P		
Green-tailed towhee	(<u>Pipilo chlorurus</u>)	W		P	
Fox sparrow	(<u>Passerella iliaca</u>)	C	P		
Song sparrow	(<u>Melospiza melodia</u>)	C	P	P	P
Lincoln's sparrow	(<u>Melospiza lincolni</u>)	C	P	P	P
White-crowned sparrow	(<u>Zonotrichia leucophrys</u>)	C		P	P
Dark-eyed junco	(<u>Junco hyemalis</u>)	C		P	P
Red-winged blackbird	(<u>Agelaius phoeniceus</u>)	C		P	P
Brewer's blackbird	(<u>Euphagus cyanocephalus</u>)	W	P	P	
Common grackle	(<u>Quiscalus quiscula</u>)	E	P		
Brown-headed cowbird	(<u>Molothrus ater</u>)	C	P	P	
House finch	(<u>Carpodacus mexicanus</u>)	C	P		
<u>Lower Canopy</u>					
Broad-tailed hummingbird	(<u>Selasphorus platycercus</u>)	Cen.	P	P	P
Black-capped chickadee	(<u>Parus atricapillus</u>)	C	P		
House wren	(<u>Troglodytes aedon</u>)	C	P	P	

Appendix (continued)

Guild and Species	Scientific Name	Geographic Range ^a	Zone 1	Zone 2	Zone 3
Veery	(<u>Catharus fuscescens</u>)	E	P	P	
Gray catbird	(<u>Dumetella carolinensis</u>)	C	P	P	
Yellow warbler	(<u>Dendroica petechia</u>)	C	P	P	
MacGillivray's warbler	(<u>Oporornis tolmiei</u>)	W		P	
Common yellowthroat	(<u>Geothlypis trichas</u>)	C		P	P
Wilson's warbler	(<u>Wilsonia pusilla</u>)	C			P
American goldfinch	(<u>Carduelis tristis</u>)	C	P	P	
<u>Upper Canopy</u>					
Ruby-crowned kinglet	(<u>Regulus calendula</u>)	C	P		
Solitary vireo	(<u>Vireo solitarius</u>)	C	P		
Warbling vireo	(<u>Vireo gilvus</u>)	C	P	P	
Black-headed grosbeak	(<u>Pheucticus melanocephalus</u>)	W	P		
Northern oriole	(<u>Icterus galbula</u>)	C	P		
Pine siskin	(<u>Carduelis pinus</u>)	C		P	
<u>Aerial</u>					
Red-tailed hawk	(<u>Buteo jamaicensis</u>)	C	P		
Western wood pewee	(<u>Contopus sordidulus</u>)	W	P		
Willow flycatcher	(<u>Empidonax traillii</u>)	W	P	P	
Dusky flycatcher	(<u>Empidonax oberholseri</u>)	W	P	P	
Tree swallow	(<u>Tachycineta bicolor</u>)	C	P	P	
Violet-green swallow	(<u>Tachycineta thalassina</u>)	C	P		

Appendix (continued)

Guild and Species	Scientific Name	Geographic Range ^a	Zone 1	Zone 2	Zone 3
American redstart	(<u>Setophaga ruticilla</u>)	E	P		
<u>Bark</u>					
Yellow-bellied sapsucker	(<u>Sphyrapicus varius</u>)	C	P		
<u>Freshwater</u>					
Green-winged teal	(<u>Anas crecca</u>)	C	P	P	
Mallard	(<u>Anas platyrhynchos</u>)	C	P	P	
Sora	(<u>Porzana carolina</u>)	C		P	
Spotted sandpiper	(<u>Actitis macularia</u>)	C	P	P	P

^aThe distributions of species are categorized into: C = continental, E = eastern, W = western, and Cen = central.