Species Abundances, Guild Dominance Patterns, and Community Structure of Breeding Riparian Birds

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Abstract: 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 to 2260 m) cottonwood zone, mid-elevation (2290 to 2530 m) mixed shrub willow zone, and high-elevation (2590 to 2990 m) subalpine willow zone. Vegetational complexity decreased from low to high zones, with loss of vertical habitat layers and increased foliage density and dominance of dwarf willows. 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. Highest similarities within foraging guilds were between low- and mid-elevation zones, whereas fewest guild species were shared between low- and high-elevation zones. Trends in avian numbers were explained by relating guild occupancy patterns to the presence or absence of habitat layers in each elevational zone. Greater habitat stratification in low-elevation cottonwood communities resulted in greater capability to support avian species.

INTRODUCTION

In the western United States, bird species diversity and bird densities are greater in riparian habitats than in surrounding upland vegetation or in most other north temperate 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

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habitats, and 28% of these species use riparian habitats exclusively (computed from Hoover and Wills, 1984). Hirsch and Segelquist (1978) and Anderson (1985) indicated that 70 to 90% of riparian habitats in the U. S. are improperly managed and have already been extensively altered from disturbances such as livestock grazing, mining, irrigation, and urban development. Because riparian vegetation typically comprises less than 2% of total land area in the West (Sands and Howe, 1977; Pase and Layser, 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 uses the same kinds of resources in a similar manner. Verner (1984) reasoned that responses of 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 bird populations, guild structure, and whole bird communities, I asked the following questions: (1) Do population levels of riparian birds remain constant? By accounting for this temporal source of variation over a 3-year period, 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 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 (Finch, 1987). Each rectangular 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 (3060 ft), encompassing a spectrum of streamside plant species and vegetational communities (Fig. 1).

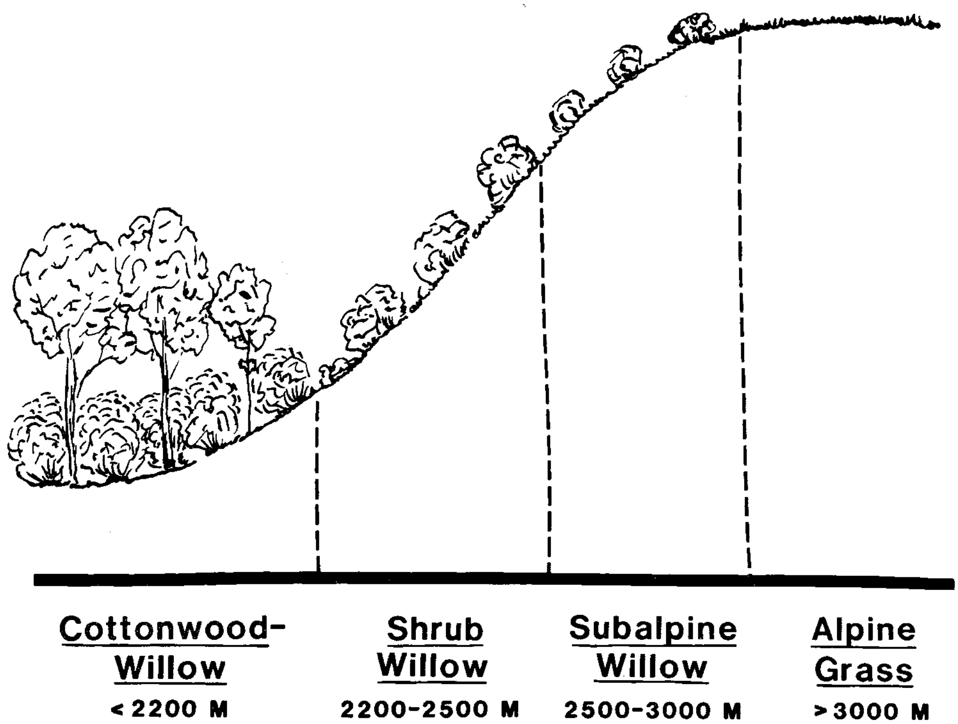

Fig. 1 Distribution of riparian habitat zones along an elevational cline in southeastern Wyoming.

Replicate sites were established in three elevational zones: Zone 1 = three sites ranging from 2050 m (6740 ft) to 2260 m (7400 ft); Zone 2 = three sites ranging from 2290 m (7500 ft) to 2530 m (8300 ft); Zone 3 = four sites ranging from 2590 m (8500 ft) to 2990 m (9800 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 interspersed with 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 was 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 1. 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

TABLE 1

Mean (± S.E.) Values and Significant Differences of Nine Selected Vegetation Features in Three Riparian Elevational Zones*

Habitat variable	Sampling method	Zone 1	Zone 2	Zone 3	*P*†
Tree density	Number of trees >3 cm DBH/ha	144.9 ± 23.2	6.3 ± 1.0	0.0 ± 0.0	‡
Shrub height	Mean height (m) of nearest shrubs in each quadrant	2.0 ± 0.1	2.1 ± 0.1	1.5 ± 0.1	‡
Vertical foliage density in grass-forb layer (VFD1)	Mean number of vegetation contacts falling against vertical rod in <0.3 m interval	2.0 ± 0.1	2.8 ± 0.2	2.9 ± 0.1	n.s.
Vertical foliage density in low shrub layer	Same as VFD1, but in 0.3 to 1 m interval	0.5 ± 0.1	1.3 ± 0.1	1.7 ± 0.1	‡
Vertical foliage density in high shrub layer	Same as VFD1, but in 1 to 2 m interval	0.2 ± 0.0	0.8 ± 0.1	0.3 ± 0.1	‡
Vertical foliage density in lower overstory	Same as VFD1, but in 2 to 9 m interval	1.0 ± 0.1	0.5 ± 0.1	0.0 ± 0.0	‡
Vertical foliage density in upper overstory	Same as VFD1, but in >9 m interval	0.5 ± 0.1	0.01 ± 0.0	0.0 ± 0.0	‡
Percent willow	Proportion of shrub species that is willow	25.8 ± 2.8	78.6 ± 2.5	90.7 ± 4.2	‡
Woody cover	Percent cover of woody plants (<1 m tall), saplings, and downed logs measured with ocular tube	13.5 ± 1.7	24.3 ± 2.5	57.6 ± 4.2	‡

*Zone 1 = low-elevation cottonwood habitat; Zone 2 = mid-elevation shrub willow habitat; Zone 3 = high-elevation subalpine willow habitat.

†Based on one-way ANOVA evaluating differences among habitat zones.

‡$P < .001$; n.s. = not significant ($P > .05$).

(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 an 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 permitting 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 1) 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 2 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

Numbers 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 recorded once or twice were considered visitors and were not included in the analyses. Each study site was visited a minimum of eight times each year, and each visit extended from 2 to 4 hours. Low-elevation sites were visited up to 15 times per year to encompass early (April and May) and late (June and July) breeding periods of different species. To improve the accuracy of spot-map counts, intensive 2-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 × 10.7 m nets, each with a mesh size of 1.3 cm. Nets were monitored on each site from 600 hours to 1900 hours for 5 sequential days. Netting and banding information was used to substantiate the presence of pairs in cases where mapping information was inconclusive (Verner, 1985).

Each bird species was assigned to one of six foraging guilds based on a modification of DeGraaf et al.'s (1985) criteria: ground forager–gleaner, lower-canopy (shrub) forager-gleaner, upper-canopy (tree) forager-gleaner, air sallier-screener, bark driller-gleaner, freshwater forager. The freshwater guild was a catchall 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 the Appendix.

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 3 years and three to four 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 3-year bird count data were averaged for each species in each foraging guild. One-way ANOVAs 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. ANOVAs were computed using the SPSS package (Nie et al., 1975). Jaccard Similarity Indexes (Goodall, 1978) were computed from presence-absence data to estimate percent similarity in guild species composition among elevational zones. Similarities were computed using averaged 3-year counts.

RESULTS

Variation in Habitat Stratification Among Elevational Zones

Vertical foliage density (VFD) in the herbaceous layer remained relatively constant across elevational zones ($P > .05$), but VFD increased in the low shrub layer ($P < .001$) and peaked in the high shrub layer in Zone 2, then declined ($P < .001$). In contrast, both the lower and upper overstory declined considerably with increase in elevation ($P < .001$) (Table 1). Other habitat characteristics also indicated trends toward reduced vegetational complexity in Zone 3, the subalpine zone. Tree density (primarily cottonwoods) declined from 144.9 trees/ha in Zone 1 to virtually no trees in Zone 3. Shrub height was similar between Zones 1 and 2 but was about 40% lower in Zone 3. On the other hand, woody cover at the <1 m level increased from 13.5% in Zone 1 to 57.6% in Zone 3 ($P < .001$), and the proportion of willow (*Salix* spp.) in the shrub community increased from 26% to 91% ($P < .001$) (Table 1). 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 Zones on Bird Numbers

Zone 1, the cottonwood zone, had highest bird species richness in all 3 study years. Species richness in Zone 1 ranged from 15 to 23 species among sites and years (Table 2). In Zone 2, the mid-elevation shrub willow zone, species richness varied from 12 to 19 species. The range of species richness in Zone 3 was much lower: 3 to 11 species. ANOVA results indicated that mean species richness remained stable within each elevational zone from 1982 to 1984 (F = .01, P = .907 for YEAR effect) but substantially decreased from Zone 1 to Zone 3 (F = 55.3, P < .001 for ZONE effect) (Table 2). The effects of YEAR and ZONE were independent (F = .15, P = .960 for interaction effect).

TABLE 2

Number of Breeding Species and Number of Territorial Pairs of Riparian Birds on Ten 8.1-ha Plots in Three Elevational Zones (Low, Middle, High) in 1982, 1983, and 1984*

Replicate site	Elevation, m	No. of species			No. of pairs		
		1982	1983	1984	1982	1983	1984
		Zone 1: Low elevation					
1	2054	21	22	19	130	115	104
2	2097	23	18	22	107	93	102
3	2256	20	16	15	84	78	76
Mean ± S. D.	2135.7 ± 106.40	21.3 ± 1.53	18.3 ± 2.52	18.7 ± 3.51	107.0 ± 23.0	95.3 ± 18.61	94.0 ± 15.62
		Zone 2: Middle elevation					
1	2286	13	14	12	61	59	63
2	2470	15	14	17	73	72	89
3	2530	19	20	19	79	111	98
Mean ± S. D.	2428.7 ± 127.14	15.7 ± 3.06	15.7 ± 3.79	16.0 ± 3.61	71.0 ± 9.17	80.0 ± 27.40	83.3 ± 18.18
		Zone 3: High elevation					
1	2591	8	11	9	67	78	58
2†	2789	-	4	5	-	28	30
3	2930	3	3	3	24	18	27
4	2987	4	3	3	29	24	26
Mean ± S. D.	2824.3 ± 176.37	5.0 ± 2.65	5.3 ± 3.86	5.0 ± 2.83	40.0 ± 23.52	34.0 ± 27.64	35.3 ± 15.26

*Values for three to four replicate sites in each zone are given.
†Study site 2 in Zone 3 was added in 1983 to complete range of elevational positions.

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 in 1984 to a high of 130 in 1982, whereas Zone 2 ranged from 61 (1982) to 111 pairs (1983), and Zone 3 ranged from 18 (1983) to 78 pairs (1983). YEAR and interaction effects were not significant ($F = .03$ and $.22$, respectively; $P > .05$), but mean number of pairs varied markedly among zones ($F = 23.7$; $P < .001$).

Population levels of the 20 most common bird species are listed by elevational zone and year in Table 3. Yellow warbler was the most abundant species in the two lower zones: about 30% of all birds in Zone 1 and 17% of all birds in Zone 2 (Table 3). American robin reached second highest densities in Zone 1 (~14%) but fourth highest population levels in Zone 2 (~9%) being replaced in dominance by song sparrow (~12%) and Lincoln's sparrow (~11%). House wren had third highest population levels in Zone 1 (~12.5%) but virtually disappeared in Zones 2 and 3 where trees with cavities suitable for nests were lacking. A similar trend in zone preference was also evident for less common cavity-nesting species (tree swallow, violet-green swallow, yellow-bellied sapsucker, and Northern flicker), as well as for species that built nests (at least in this study) exclusively in upper woodland canopies (mourning dove and Western wood pewee, Table 3).

In Zone 3, three species comprised approximately 92% of the total avifauna. Lincoln's sparrow dominated subalpine willow habitats, reaching yearly abundance levels of 15 to 20 pairs (Table 3) or ~47% of all birds counted. Wilson's warbler comprised about 26% of the subalpine avifauna, followed by white-crowned sparrow with ~19%.

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 ($P << .01$), influencing the population levels of the 20 common species with the exception of gray catbird (Table 4). As in the earlier analyses of species richness and pair abundances, the effect of YEAR on population levels of all 20 species was insignificant ($P > .05$) nor was there any interaction between the effects of ZONE and YEAR ($P > .05$) (Table 4).

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 ($P > .05$), 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 5). Number of ground-foraging pairs did not vary significantly among zones ($P > .05$), but the number of species was significantly higher in Zone 1 than in Zone 3, despite the disproportionately higher percentage of ground foragers in Zone 3 (Table 5).

Lower-canopy foragers showed a similar trend, having slightly fewer species than the ground-foraging guild in all zones but more pairs in Zones 1 and 2 (Table 5). Numbers of lower-canopy species differed significantly only between the two lower zones and the upper zone, but 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

TABLE 3

Mean Number of Territorial Pairs/8.1 ha (± S.E.) of 20 Bird Species in Three Riparian Elevational Zones (Low, Middle, High) in 1982, 1983, and 1984*

Species†	Zone 1: low elevation			Zone 2: middle elevation			Zone 3: high elevation		
	1982	1983	1984	1982	1983	1984	1982	1983	1984
Mourning dove	4.0 ± 0.8	3.0 ± 1.7	3.3 ± 1.3						
Broad-tailed hummingbird	2.0 ± 0.7	1.7 ± 0.7	1.3 ± 0.8	5.0 ± 0.3	4.7 ± 0.4	6.7 ± 0.3		0.5 ± 0.7	
Western wood pewee	2.7 ± 1.4	2.3 ± 0.8	3.3 ± 0.9						
Willow flycatcher	3.0 ± 1.7	3.3 ± 1.3	3.0 ± 1.7	1.7 ± 1.3	1.0 ± 1.0	0.3 ± 0.6			
Dusky flycatcher	2.0 ± 1.1	0.7 ± 0.4	1.3 ± 1.2	3.7 ± 1.0	2.3 ± 1.0	2.0 ± 1.1			
Tree swallow	5.7 ± 1.0	2.3 ± 1.5	2.7 ± 1.1	0.3 ± 0.6	0.7 ± 0.8	1.7 ± 1.3			
House wren	13.0 ± 0.7	11.3 ± 0.8	12.3 ± 0.6	0.7 ± 0.4	1.0 ± 1.0				
Veery	3.3 ± 1.0	3.0 ± 0.9	1.2 ± 0.3	2.0 ± 0.8	3.7 ± 0.8	3.7 ± 0.8			
American robin	17.3 ± 1.3	12.7 ± 0.7	11.0 ± 0.4	7.3 ± 0.1	6.3 ± 0.7	7.3 ± 0.4		0.3 ± 0.5	0.5 ± 0.7
Gray catbird	0.7 ± 0.8	0.7 ± 0.8	1.3 ± 0.8	0.7 ± 0.8	0.7 ± 0.8	1.3 ± 0.8			
Warbling vireo	4.3 ± 0.6	3.3 ± 0.7	3.3 ± 0.7	2.7 ± 0.9	1.0 ± 0.6	1.7 ± 0.7			
Yellow warbler	27.0 ± 0.2	30.3 ± 0.4	33.3 ± 0.3	12.3 ± 0.7	18.0 ± 1.0	15.3 ± 0.5			
MacGillvray's warbler				2.7 ± 0.7	1.3 ± 0.6	2.7 ± 0.8			
Common yellowthroat				1.3 ± 0.6	2.3 ± 1.0	2.3 ± 1.0	0.3 ± 0.6	0.3 ± 0.5	
Wilson's warbler							9.0 ± 1.0	10.5 ± 1.4	8.8 ± 1.1
Song sparrow	4.7 ± 0.6	4.0 ± 0.3	3.0 ± 0.7	9.7 ± 1.0	11.7 ± 0.6	6.7 ± 0.3	1.3 ± 1.2	0.8 ± 0.9	0.5 ± 0.7
Lincoln's sparrow	0.3 ± 0.6	0.3 ± 0.6	0.3 ± 0.6	4.0 ± 1.3	10.3 ± 1.6	11.0 ± 1.7	20.0 ± 1.5	16.0 ± 1.1	15.5 ± 0.6
White-crowned sparrow				0.3 ± 0.6			7.0 ± 0.7	6.3 ± 0.8	7.0 ± 0.6
Brewer's blackbird		1.0 ± 1.0		2.0 ± 1.4	6.3 ± 1.6	6.3 ± 1.6			
Brown-headed cowbird	3.7 ± 0.4	1.3 ± 0.6	1.0 ± 1.0	1.3 ± 0.8	1.7 ± 0.3	1.3 ± 0.6			

*Numbers of pairs are averaged across three to four spot-map plots within each zone.
†Scientific names of bird species are given in the Appendix.

TABLE 4

Two-Way Analysis of Variance Testing for the Main and Interaction Effects of Year (1982, 1983, 1984) and Elevational Zone (Low, Middle, High) on Population Levels of 20 Common Riparian Bird Species

	Significance level		
Species*	YEAR effect	ZONE effect	YEAR–ZONE interaction
Mourning dove	.878	.001	.965
Broad-tailed hummingbird	.980	.001	.532
Western wood pewee	.935	.001	.988
Willow flycatcher	.952	.006	.995
Dusky flycatcher	.262	.005	.285
Tree swallow	.653	.005	.478
House wren	.813	.001	.818
Veery	.714	.001	.900
American robin	.597	.001	.493
Gray catbird	.739	.090	.962
Warbling vireo	.528	.001	.915
Yellow warbler	.125	.001	.399
MacGillvray's warbler	.670	.001	.765
Common yellowthroat	.933	.016	.416
Wilson's warbler	.938	.001	.995
Song sparrow	.923	.001	.723
Lincoln's sparrow	.250	.001	.754
White-crowned sparrow	.832	.001	.986
Brewer's blackbird	.916	.001	.992
Brown-headed cowbird	.245	.001	.126

*Scientific species names are given in the Appendix.

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 5), despite the presence of an overstory layer of vegetation. Warbling vireo was the most common species in this guild. Numbers of pairs in the upper-canopy guild were equivalent in Zones 1 and 2 ($P > .05$), but numbers of species were lower ($P < .01$) in Zone 2. Zone 3 had no upper-canopy, aerial, or bark-foraging guilds because the habitat lacked a tree overstory.

Aerial foragers were twice as numerous in species richness and abundance in Zone 1 as in Zone 2 ($P < .05$) (Table 5), indicating that this guild strongly 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.

TABLE 5

One-Way Analysis of Variance Contrasting Number of Species and Number of Territorial Pairs Within Foraging Guilds Among Three Elevational Zones*†

	Number of species‡					Number of pairs‡				
Foraging guild§	**Zone 1**	**Zone 2**	**Zone 3**	***P***	**Comparisons¶**	**Zone 1**	**Zone 2**	**Zone 3**	***P***	**Comparisons¶**
Ground	12 (34%)	11 (39%)	7 (58%)	<.05	c	27.6 (28%)	26.6 (34%)	25.2 (69%)	n.s.**	n.s.
Lower canopy	7 (20%)	8 (29%)	3 (25%)	<.001	bc	48.4 (49%)	41.5 (53%)	10.2 (28%)	<.001	abc
Upper canopy	5 (12.9%)	2 (16.1%)	0	<.01	abc	4.9 (5%)	2.4 (3%)	0	<.05	c
Aerial	7 (20%)	3 (11%)	0	.001	abc	11.8 (12%)	3.9 (5%)	0	<.05	ac
Bark	1 (3%)	0	0	<0.01	ac	2.0 (2%)	0	0	<.01	ac
Freshwater	3 (9%)	4 (14%)	2 (17%)	n.s.	n.s.	4.0 (4%)	3.1 (4%)	1.1 (3%)	n.s.	n.s.

*The years 1982, 1983, and 1984 were used for ANOVA replicates.

†Zone 1 = low, Zone 2 = middle, Zone 3 = high.

‡Numbers in parentheses are proportions of each zone avifauna that each guild composes.

§Species were classified into guilds using standards modified from DeGraaf et al. (1985).

¶Pairwise comparisons among elevational zones were computed using Student Newman-Keul's Range Test. Significant differences ($P < .05$) 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." means not significant.

Freshwater foragers did not vary in species richness or pair abundance among zones ($P > .05$), 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, numbers of species within guilds varied to the greatest extent between Zones 1 and 3. Species densities in five of six 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

Zone 1 cottonwood habitats and Zone 2 shrub willow habitats shared 43% of all species (Table 6). Zone 2 and Zone 3 subalpine willow habitat had 30% similarity in species, while Zone 1 and Zone 3 had only 13% similarity.

TABLE 6

Jaccard Similarity Indexes Based on Presence/Absence Data Measuring Similarities in Species Composition in Foraging Guilds and Overall Bird Assemblages Between Pairs of Elevational Zones*

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	0.00	0.00	0.00
Freshwater	0.50	0.25	0.50
Overall†	0.43	0.30	0.13

*Elevational zones are Zone 1 = low-elevation cottonwood habitat, Zone 2 = mid-elevation shrub willow habitat, and Zone 3 = high-elevation subalpine willow habitat.
†Overall = all guilds combined.

In guild comparisons between Zones 1 and 2, similarities were highest in lower-canopy foragers (0.7) and freshwater foragers (0.5), while bark-foragers and upper-canopy foragers were least similar (0.0 and 0.17, respectively) (Table 6). Zone 2 and Zone 3 shared fewer species, with the ground-foraging guild being most similar, followed by lower-canopy foragers and freshwater foragers. In guild comparisons between Zones 1 and 3, freshwater foragers attained highest similarity followed by low similarities in lower canopy foragers and ground foragers. To summarize, highest guild similarities were between Zones 1 and 2, whereas fewest guild species were shared between Zones 1 and 3.

DISCUSSION

Subdividing the bird community into six foraging guilds, each assigned to a habitat stratum, revealed intraguild trends in numbers of birds and species. 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 3-year period of this study but varied substantially among elevational zones. Decreases in species richness, overall bird abundance, and number of foraging guilds are inversely related to elevation (Finch, 1986, 1987), but elevation is 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 1). At high elevations, severe climate and weather and short growing seasons create a difficult environment for plant and animal survival. Riparian plant communities adapted to these subalpine conditions are structurally simple, composed of essentially two vertical habitat layers: herbaceous and low shrub. The decline in plant community complexity is likely the main cause of the significant decline in bird species richness and the loss of three foraging guilds.

Guilds that depended on tree trunks or tree canopies for their food supply necessarily 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 account for the disappearance of breeding aerial foragers in subalpine willow 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, similar to those found in subalpine habitats. 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 warbler 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 species composition and number of species. Even though abundance remained constant, the ground-foraging guild achieved dominance in Zone 3 because canopy bird 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 in this habitat stratum 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 associations between habitat trends and 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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APPENDIX

Presence (P) or Absence (Blank) of Breeding Bird Species Classified into Six Foraging Guilds in Three Elevational Zones*

Guild and species	Scientific name	Zone 1	Zone 2	Zone 3
	Ground			
Common snipe	*(Gallinago gallinago)*		P	P
Mourning dove	*(Zenaida macroura)*	P		
Northern flicker	*(Colaptes auratus)*	P		
Mountain bluebird	*(Sialia currucoides)*	P	P	
American robin	*(Turdus migratorius)*	P	P	P
European starling	*(Sturnus vulgaris)*	P		
Green-tailed towhee	*(Pipilo chlorurus)*		P	
Fox sparrow	*(Passerella iliaca)*	P		
Song sparrow	*(Melospiza melodia)*	P	P	P
Lincoln's sparrow	*(Melospiza lincolnii)*	P	P	P
White-crowned sparrow	*(Zonotrichia leucophrys)*		P	P
Dark-eyed junco	*(Junco hyemalis)*		P	P
Red-winged blackbird	*(Agelaius phoeniceus)*		P	P
Brewer's blackbird	*(Euphagus cyanocephalus)*	P	P	
Common grackle	*(Quiscalus quiscula)*	P		
Brown-headed cowbird	*(Molothrus ater)*	P	P	
House finch	*(Carpodacus mexicanus)*	P		
	Lower Canopy			
Broad-tailed hummingbird	*(Selasphorus platycercus)*	P	P	P
Black-capped chickadee	*(Parus atricapillus)*	P		
House wren	*(Troglodytes aedon)*	P	P	
Veery	*(Catharus fuscescens)*	P	P	
Gray catbird	*(Dumetella carolinensis)*	P	P	
Yellow warbler	*(Dendroica petechia)*	P	P	
MacGillvray's warbler	*(Oporornis tolmiei)*		P	
Common yellowthroat	*(Geothlypis trichas)*		P	P
Wilson's warbler	*(Wilsonia pusilla)*			P
American goldfinch	*(Carduelis tristis)*	P	P	
	Upper Canopy			
Ruby-crowned kinglet	*(Regulus calendula)*	P		
Solitary vireo	*(Vireo solitarius)*	P		
Warbling vireo	*(Vireo gilvus)*	P	P	
Black-headed grosbeak	*(Pheucticus melanocephalus)*	P		
Northern oriole	*(Icterus galbula)*	P		
Pine siskin	*(Carduelis pinus)*		P	

(Appendix table continued on next page.)

APPENDIX (Cont'd)

Presence (P) or Absence (Blank) of Breeding Bird Species Classified into Six Foraging Guilds in Three Elevational Zones*

Guild and species	Scientific name	Zone 1	Zone 2	Zone 3
	Aerial			
Red-tailed hawk	*(Buteo jamaicensis)*	P		
Western wood pewee	*(Contopus sordidulus)*	P		
Willow flycatcher	*(Empidonax traillii)*	P	P	
Dusky flycatcher	*(Empidonax oberholseri)*	P	P	
Tree swallow	*(Tachycineta bicolor)*	P	P	
Violet-green swallow	*(Tachycineta thalassina)*	P		
American redstart	*(Setophaga ruticilla)*	P		
	Bark			
Yellow-bellied sapsucker	*(Sphyrapicus varius)*	P		
	Freshwater			
Green-winged teal	*(Anas crecca)*	P	P	
Mallard	*(Anas platyrhynchos)*	P	P	P
Sora	*(Porzana carolina)*		P	
Spotted sandpiper	*(Actitis macularia)*	P	P	P

*Zone 1 = low elevation; Zone 2= middle; Zone 3 = high.