Bird-habitat Relationships in Subalpine Riparian Shrublands of the Central Rocky Mountains

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Abstract--Breeding birds were counted in 1982, 1983, and 1984 using the spot-map method on seven 8.1-ha plots in the Medicine Bow National Forest, Wyoming. At elevations of 2,280 to 3,000 m, riparian habitats were structurally simple, dominated by one or more bush willow species. Subalpine riparian avifaunas were depauperate with only four abundant species-- song sparrow, white-crowned sparrow, Lincoln's sparrow, and Wilson's warbler. Habitat requirements overlapped among these species but differed significantly from randomly-sampled habitat in the same areas. Results indicated that species preferred densely-foliated ground and shrub layers, and higher effective vegetation height. Factors complicating efforts to characterize bird-habitat relationships are discussed.

Many factors complicate efforts to characterize relationships between wildlife abundance and habitat structure (Best and Stauffer 1986). These factors include population and species variability in time or space, measurement or sampling error, sampling scale, and inappropriate statistical methods. Models of wildlife-habitat relationships that are derived from limited or misrepresentative data sets produce indices that are not predictive or reliable.

Population size can vary from year to year, from season to season, and from site to site (Gaud et al. 1986). Factors that cause temporal and spatial variability in populations of terrestrial bird species include changes in weather and climate (Wiens 1981a, Szaro and Balda 1986, Hejl and Beedy 1986, Diehl 1986), qualitative and quantitative changes in food and habitat resources along environmental gradients (Karr 1980, Noon 1981a, Rice et al. 1983), and interspecific interactions (Terborgh and Weske 1975, Terborgh 1985). Error in estimating population size may result from observer differences, measurement error, inappropriate census methods, or insufficient sample size (Ralph and Scott 1980, Verner 1985, Stauffer and Best 1986). Scale of observation may affect evaluation of animal responses to habitat trends (Wiens 1981b, Wiens 1986, Maurer 1985, Morris 1987, but see Bock 1987). Sampling at a single site, multiple sites in a local area, or many geographical areas may produce different interpretations of species requirements, depending on the level of resolution.

A greater understanding of the factors that complicate interpretations of wildlife-habitat relationships is needed to reduce estimation error. Multiple year studies over a large number of sites, vegetation types, and localities are the best designs for explaining variation in bird abundance, but time and expenses may be prohibitive. In this paper, I examine associations between bird abundance, habitat structure measured at random sites, and habitat measured at bird locations in subalpine riparian shrublands. I considered the confounding effects of 1) year-to-year variation in numbers of four breeding bird species, 2) variation in bird abundance across sampling plots, 3) variation in species responses to habitat structure, and 4) sampling at plot and gradient levels of resolution.

Methods

Study Areas

Seven 8.1-ha study grids were established in the summer of 1981 in shrub willow habitats along drainages in the Medicine Bow National Forest of southeastern Wyoming (table 1). Each grid was posted at 33.5-m intervals with wooden stakes painted fluorescent orange and marked with grid coordinates. Grid dimensions were adapted to the variable widths of the streams

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Table 1.--Three-year (1982, 1983, 1984) means + standard deviations of numbers of spot-map pairs of four subalpine bird species counted on seven 8.1 ha riparian plots in the Medicine Bow National Forest, southeastern Wyoming. Plot drainages are arranged in ascending elevational order. F-ratios and probability levels of two-way ANOVA testing YEAR and PLOT effects on species counts are given.

Reference number	Drainage	Elevation (m)	Wilson's Warbler	Song Sparrow	Lincoln's Sparrow	White-crowned Sparrow
1	Wagonhound Creek	2,286	0	8.7 ± 1.8	0	0
2	S. Lodgepole Creek	2,470	0	10.3 ± 2.9	12.0 ± 4.6	0
3	N. Lodgepole Creek	2,530	0	9.0 ± 3.1	13.3 ± 2.2	0.3 ± 0.3
4	Douglas Creek	2,591	19.0 ± 2.7	3.0 ± 0.6	27.3 ± 3.5	8.0 ± 1.5
5	Lake Creek	2,789	5.5 ± 0.5	0	17.0 ± 0.0	4.0 ± 0.6
6	Lower Middle Fork Little Laramie River	2,930	6.0 ± 0.6	0	13.3 ± 1.7	4.0 ± 0.6
7	Upper Middle Fork Little Laramie River	2,987	6.0 ± 0.6	0	9.3 ± 0.3	10.0 ± 1.2
	F-Ratio (P)[a]					
	YEAR effect		3.18 (N.S.)	0.96 (N.S.)	0.15 (N.S.)	3.19 (N.S.)
	PLOT effect		4.99 (*)	6.50 (*)	22.40 (*)	31.65 (*)

[a] $^*P < 0.01$, N.S. = not significant. Numerator and denominator degrees of freedom are 2 and 12 for YEAR effect and 6 and 12 for PLOT effect.

in the following combinations: 3 x 24 squares (plots 4, 5, 9 and 10); 2 x 36 (plot 6); 4 x 18 (plot 7); and 6 x 12 (plot 8).

Study grids were distributed over an elevational continuum ranging from 2,286 m to 2,987 m. Vegetation on plots 1 to 3 was dominated by one or several shrub willow species including *Salix bebbiana, S. exigua, S. geyeriana, S. planifolia, S. boothii,* and *S. lasiandra*. Additional shrubs that were locally common on these mixed willow plots were thinleaf alder *(Alnus tenuifolia)*, western snowberry *(Symphoricarpus occidentalis)*, common chokecherry *(Prunus virginiana)*, serviceberry *(Amelanchier alnifolia)*, and red-osier dogwood *(Cornus stolonifera)* (see Finch 1987 for complete shrub list). Small isolated patches of quaking aspen *(Populus tremuloides)* were also present. Surface understories were dominated by *Calamagrostis canadensis* and *Carex* spp. These drainages were typically bordered by sagebrush *(Artemisia tridentata)*, grassland, and lodgepole pine *(Pinus contorta)* forest.

On higher elevation (> 2,600 m) plots, *S. planifolia* was found in monocultures or mixed with *S. wolfii*. The subalpine parks formed by these willow thickets were associated with wet, boggy meadows of *Deschampsia cespitosa* and *Carex* spp., 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).

Sampling Bird Populations

Birds were counted on the seven study grids using the spot-map method (Robbins 1970) from mid-May through early July of 1982, 1983, and 1984. A minimum of eight visits was made to each study plot each year, and each visit lasted from 2 to 4 hours beginning at daylight. Edge clusters were counted as belonging to the plot if more than half of the observations were recorded within or on the plot boundaries. Netting and banding information were used to substantiate the presence of pairs in cases where mapping information was inconclusive (Verner 1985). See Finch (1986, 1987) for more details on procedures for counting birds, and overall count results.

Sampling Habitat Structure

Four bird species were selected for analyses of bird-habitat relationships based on their high relative abundances in subalpine riparian communities: Wilson's warbler *(Wilsonia pusilla)*, song sparrow *(Melospiza melodia)*, Lincoln's sparrow *(Melospiza lincolnii)*, and white-crowned sparrow *(Zonotrichia leucophrys)*. Habitat structure was sampled in July and August of 1982, 1983, and 1984 within the mapped territories of these four species, either near nest sites or at male singing locations. Bird-centered vegetation sampling was developed by James (1971) and recommended by Larson and Bock (1986) as a powerful tool for evaluating habitat relationships because it is precise and efficient, and because data can be pooled at various spatial scales (e.g., study plots, set of local plots, or geographical region). A total of 134 territories were sampled across the set of study plots. Sample data were pooled for each species to give estimates of associated habitat characteristics at each study plot as well as over all plots. These data were used to assess the effects of habitat variation among plots separately from species responses to habitat, but only values for habitat features averaged over all plots are reported here.

For comparison, 40 random locations in each study grid were sampled in a mode identical to the bird-centered samples. Random sampling sites were located by selecting grid coordinates from a table of random numbers. Random sample data were pooled to give estimates of habitat features for each plot 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 (1981b) for shrub habitats. Habitat features were sampled by dividing each location into four quadrants oriented in the cardinal compass directions. Twenty-one of the original variables were deleted from the final analyses because they were invariant, highly correlated with other variables, or irrelevant with regard to subalpine shrub habitats. Descriptions and sampling techniques for the remaining 13 variables are presented in table 2.

Data Analyses

Two-way ANOVA was performed to detect variation in number of pairs of each species among years and among study plots. Data for three years and seven plots were used to determine main effects of the two factors, YEAR and PLOT. Because no interaction was observed between YEAR and PLOT, the three-year bird count data were averaged for each species in other analyses.

Nested design analysis of variance was used to test for differences in habitat structure between random and bird-centered locations (BIRD effect) among seven plots (PLOT effect). Random and bird-centered sites were compared (nested) within each plot before PLOT effect was computed so that plot-to-plot variation in habitat structure would not interfere with assessment of bird-habitat associations. Each of the thirteen habitat variables was analyzed using a univariate approach. Only the BIRD effect is reported here in order to focus on the factor of main interest. Nested ANOVA's were also used to assess variation in habitat selection among the four bird species (SPECIES effect), and between all birds pooled versus random sites (ALLBIRD effect) across seven plots.

The relationship between trends in each habitat variable and numbers of pairs of each species across the seven plots was examined using Pearson product-moment correlation coefficients. Averaged three-year count data and averaged random habitat data for each study plot were used to produce positive or negative bird-habitat associations. Significant associations were determined using two-tailed t tests.

Analyses were performed using SPSS and SPSS Update 7-9 statistical packages (Nie et al. 1975, Hull and Nie 1981) and SPSS/PC+ programs (Norusis 1986). Analyses of raw and log-transformed variates (Kleinbaum and Kupper 1978) produced biologically and statistically similar results. Results of raw data analyses are reported here for ease of interpretation.

Results

Trends in Bird Numbers

Mean yearly numbers of avian pairs varied substantially among the four bird species over the seven study areas based on the results of a one-way ANOVA (F-test= 3.57, $P < 0.05$).

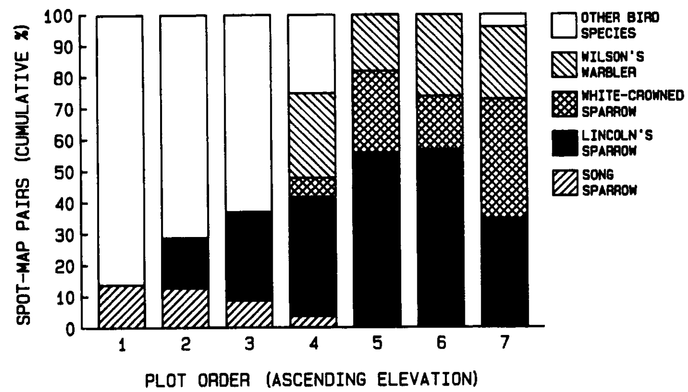

Figure 1.--Population trends of four subalpine bird species counted on seven study areas in 1982, 1983, and 1984. Counts are arranged by plot elevation.

In the three study years, song sparrow numbers declined with increasing plot elevation, disappearing altogether at higher elevations (fig. 1). The distribution of Lincoln's sparrow moderately overlapped with song sparrow, but showed an opposite trend of increasing numbers with ascending elevation (fig. 1). Wilson's warbler and white-crowned sparrow co-occurred on the four highest plots and were absent from lower study areas. Two-way ANOVA indicated that year-to-year variation in population numbers of each species was low compared to variation due to study area differences, and therefore averaged three-year counts were used in analyses of bird-habitat relationships (table 1).

On two of the lowest-elevation plots, Lincoln's sparrow and song sparrow shared the habitat with a complex bird species assemblage (Finch 1987), and as a consequence, both species comprised only 14-37% of the avifauna (fig. 2). In contrast, Lincoln's sparrow alone dominated the four higher subalpine plots, composing 35-57% of the avian community, followed by Wilson's warbler with 18-27% and white-crowned sparrow with 6-38% (fig. 2). These three subalpine species constituted 75-100% of the riparian avifauna censused at elevations of 2,600 m and above.

Avian Habitat Selection

Thirteen structural features were useful in describing within-plot habitat selection patterns of subalpine riparian bird species. In the ground layer of vegetation, vertical foliage density was significantly higher at sites occupied by Wilson's warbler and white-crowned sparrow than at randomly-measured sites, and in the low shrub layer, foliage was denser at sites selected by all four species than at random sites (table 2). Selection for dense foliation in the low shrub stratum is reflected in the significant variation in this habitat feature between random sites and all bird species pooled (ALLBIRD effect, table 2). Vertical foliage density in the tall shrub layer did not differ significantly between random and bird-centered sites. All four species also selected sites with greater-than-random effective vegetation height, which is an alternate

Erratum

This table was left out of: Finch, Deborah M. 1987. Bird-habitat relationships in subalpine riparian shrublands of the central Rocky Mountains. p. 167-172. *In:* Troendle, Charles A., Merrill R. Kaufmann, Robert H. Hamre, and Robert P. Winokur, technical coordinators. Management of Subalpine Forests: Building on 50 Years of Research. USDA Forest Service General Technical Report RM-149, 253 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

The first reference to it appears on page 169 of this article.

Table 2. Means ± standard errors of 13 habitat variables for all random sites and 4 subalpine bird species. Significance of nested design ANOVA results that tested for habitat differences between random and species locations (BIRD effect) among 7 plots (PLOT effect) are indicated for BIRD effect in the Mean column: *$\underline{P}$ < 0.05; **$\underline{P}$ < 0.001; *$\underline{P}$ < 0.0001. Correlation coefficients and significance levels for the relationship between spot-map densities (3-year mean) and mean habitat characteristics on 7 plots are given for each bird species. ANOVA significance results examining habitat variation among species (SPECIES effect) and between all birds and random sites (ALLBIRD effect) also are reported.**

	Random (N=280)	Wilson's Warbler (N=28)		Song Sparrow (N=28)		Lincoln's Sparrow (N=59)		White-crowned Sparrow (N=24)		ANOVA	
Habitat variable	**Mean**	**Mean**	$\underline{r}$	**Mean**	$\underline{r}$	**Mean**	$\underline{r}$	**Mean**	$\underline{r}$	**Species effect**	**Allbird effect**
Vertical Foliage Density[1]											
Surface Layer	2.87 ± 0.11	3.29 ± 0.37***	0.58	2.75 ± 0.40	0.15	3.27 ± 0.26	0.81*	3.15 ± 0.39***	0.04	N.S.	N.S.
Low Shrub Layer	1.54 ± 0.09	1.75 ± 0.23***	0.73*	1.82 ± 0.35*	-0.24	1.32 ± 0.15*	0.31	1.72 ± 0.29***	0.34	N.S.	**
Tall Shrub Layer	0.55 ± 0.07	0.30 ± 0.11	-0.46	1.09 ± 0.21	0.87*	0.41 ± 0.11	-0.40	0.19 ± 0.10	-0.51	N.S.	N.S.
Effective Veg. Height (m)[2]	0.57 ± 0.03	0.93 ± 0.08***	0.73*	1.35 ± 0.16***	-0.31	0.92 ± 0.09***	0.28	0.86 ± 0.09**	0.43	*	***
Percent Canopy Cover	9.24 ± 1.33	0.00 ± 0.00	-0.70	20.18 ± 4.16*	0.86**	8.68 ± 2.99	-0.47	1.04 ± 1.04	-0.75*	N.S.	N.S.
Percent Ground Cover[3]											
Shrubs < 1 m	28.17 ± 2.74	44.32 ± 6.51***	0.56	35.61 ± 5.64*	-0.69	31.98 ± 3.77	0.49	45.88 ± 6.73***	0.37	*	*
Grass/Forbs	52.49 ± 3.24	37.00 ± 6.17***	-0.77*	37.81 ± 6.01*	0.76*	45.64 ± 4.12	-0.42	39.04 ± 7.38	-0.64	*	N.S.
Woody Cover	43.32 ± 2.82	58.18 ± 6.40***	0.84*	50.36 ± 5.90*	-0.77*	43.83 ± 4.07	0.59	55.79 ± 6.77***	0.65	N.S.	N.S.
Bare Ground	5.57 ± 0.87.	2.14 ± 0.88*	-0.43	5.79 ± 3.05	0.05	5.42 ± 1.39	-0.72*	0.50 ± 0.50	0.02	*	N.S.
Shrub Characteristics											
Crown Diameter (m)	1.33 ± 0.05	1.23 ± 0.11***	0.04	1.55 ± 0.20*	0.49	1.38 ± 0.08	0.42	1.45 ± 0.16	-0.40	***	N.S.
Dispersion (m)[4]	4.57 ± 0.35	2.01 ± 0.33	-0.26	2.69 ± 0.84	0.24	2.63 ± 0.30*	0.05	3.02 ± 0.42*	-0.09	***	*
Height (m)	1.73 ± 0.05	1.64 ± 0.33***	-0.18	2.00 ± 0.16	0.85*	1.59 ± 0.07	-0.11	1.40 ± 0.06	-0.58	***	N.S.
% Fruiting Shrubs[5]	11.25 ± 1.35	1.79 ± 1.79	-0.45	12.50 ± 3.96	0.12	3.39 ± 1.12*	-0.75*	4.17 ± 4.17***	0.10	N.S.	*

[1] *Vertical foliage density is the mean number of vegetation contacts falling against a vertical rod marked in intervals: < 0.3 m (surface), 0.3-1 m (low shrub), and 1-2 m (tall shrub).*

[2] *Effective vegetation height is the height at which a 20-cm wide board is > 90% obscured by vegetation at a distance of 5 m (Wiens 1969).*

[3] *Ground cover variables do not sum to 100% because the variable "Woody Cover" is a conglomerate that includes shrubs < 1 m, as well as larger shrubs, saplings, trees, and downed wood. Also, percentage water cover was not included because it was not significant in any tested relationship.*

[4] *Shrub dispersion is the mean distance (m) to nearest shrub (≥ 1 m tall) in each quadrant.*

[5] *Other than fruiting shrubs, woody vegetation was composed primarily of willow species.*

measure of vegetation volume. This habitat feature also varied among bird species (SPECIES effect) as well as between random sites and all birds pooled (table 2).

Song sparrow chose territorial sites within plots that had greater-than-random canopy cover, but the other three bird species showed no trend (table 2). Wilson's warbler and white-crowned sparrow strongly ($\underline{P} < 0.0001$) selected sites that were thickly covered by shrubs < 1 m (mean cover > 44%) and other woody material (mean cover > 56%). In contrast, at random sites, small shrub coverage was only 28%, and coverage by woody matter was only 43%. To a lesser extent ($\underline{P} < 0.05$), song sparrow also chose sites with greater shrub and woody cover, but Lincoln's sparrow was distributed in a close-to-random manner with respect to all ground cover features. Sites with grass/forb coverage as high as the random value of 52.5% were not used by Wilson's warblers and song sparrows, and Wilson's warbler also avoided sites with bare ground (table 2). Percent cover by small shrubs, grass/forbs, and bare ground varied substantially among the four species, but only small shrub cover varied between random sites and the entire group of species.

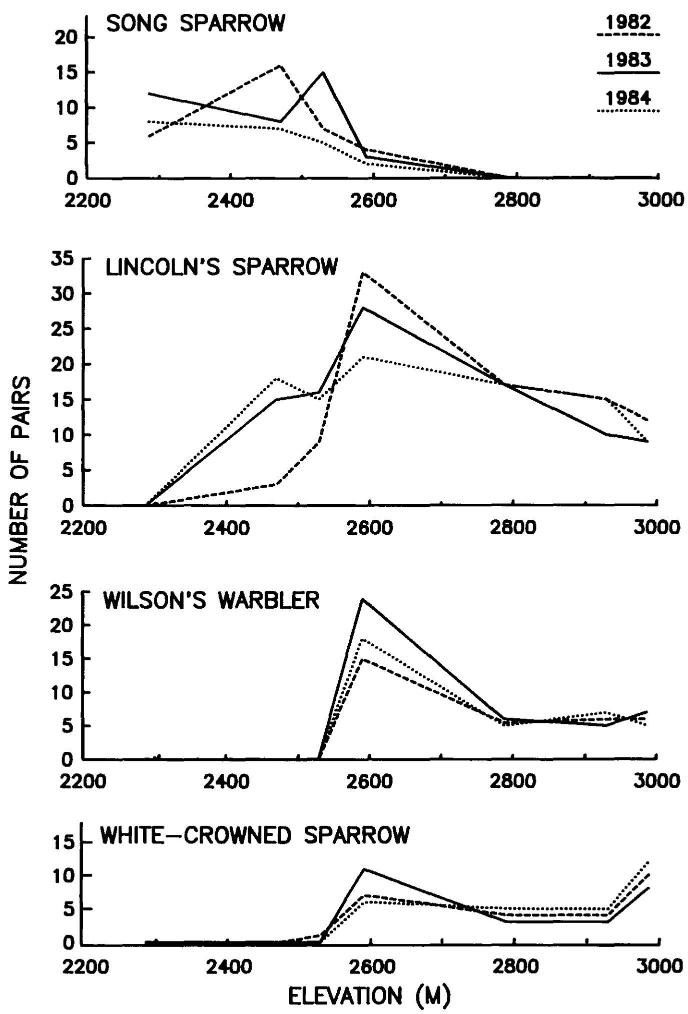

Figure 2.--Dominance patterns of four subalpine bird species based on number of territorial pairs counted on seven study plots listed by ascending elevation.

Wilson's warbler chose subalpine sites with lower shrub crown diameters and shrub height than random sites whereas song sparrow chose sites with larger-than-random shrubs. These two shrub size characteristics were also important in distinguishing among species locations within study areas (SPECIES effect, table 2). In contrast, shrub dispersion and percentage fruiting shrubs were shrub features that differed from random values at sites occupied by Lincoln's sparrow and white-crowned sparrow, as well as at locations selected by all birds (table 2).

Bird Densities and Habitat Trends

I used correlational analyses to identify relationships between mean 3-year counts of each species and mean habitat features over all study areas. This evaluation of abundance patterns substantiated patterns of habitat selection evident in the analyses of random versus bird-centered data, but detected other habitat selection trends as well.

Wilson's warbler plot densities were significantly and positively correlated to foliage density in the low shrub layer, effective vegetation height, and woody cover, and negatively associated with grass/forb cover (table 2). These relationships are similar to those found in the bird-centered habitat data. Numbers of song sparrows were also associated with several features relevant in the bird-centered habitat analysis; additionally, song sparrows increased in numbers on plots with greater foliage density in the tall shrub layer and higher mean shrub height. Higher numbers of Lincoln's sparrow were associated with plots that had high vegetation surface foliage density, and low percentages of bare ground cover and fruiting shrubs. Reduced canopy cover was the only habitat variable significantly associated with increased white-crowned sparrow densities.

Discussion

Temporal Effects

Abundances of four migratory nesting bird species remained relatively stable over the three-year study period, and therefore year-to-year variability did not confound attempts to interpret bird-habitat relationships. Although longer-term studies are needed to verify temporal stability in these subalpine riparian bird populations, other studies have indicated that only numbers of permanent residents varied significantly among years, probably because of severe over-wintering mortality (Beedy 1982, Raphael and White 1984, Hejl and Beedy 1986). Lack of year-to-year differences in migrant abundances in this study suggests that winter conditions were not harsh enough to depress numbers on the wintering grounds, and therefore no changes were observed on the breeding grounds.

Effects of Plot Variation

Population size of all four bird species varied substantially across sampling plots. The seven study plots represented a vegetational and altitudinal gradient from mixed-shrub willow habitats to subalpine willow parks composed primarily of *Salix planifolia*. Changes in bird abundance were related to two major trends in habitat structure. Structural complexity was reduced at higher elevations as shrub species diversity, shrub size, canopy cover, and foliage density in the tall shrub layer declined (Finch 1987). Concomitantly, woody cover and foliage density in the surface and low shrub layers increased. Probably in response to these habitat changes, Wilson's warbler, white-crowned sparrow and Lincoln's sparrow, species that occupy sites with low, densely-foliated shrubs, reached peak abundance on the higher plots. Lincoln's sparrow was distributed over a greater range of plots usually at higher densities than other species, demonstrating greater flexibility in habitat use. Lincoln's sparrow was absent, however, from the lowest plot, possibly in response to reduction of preferred habitat due to elevational changes. Song sparrow, a species that selects tall shrub sites, had greatest densities on lower plots.

Characterizations of song sparrow-habitat relationships based on these results are only applicable for subalpine riparian habitats. Song sparrows are present at reduced densities in lowland cottonwood-willow habitat in the Rocky Mountains (Finch 1987). By excluding the cottonwood vegetational type from this analysis, data for describing the association between song sparrow abundance and habitat changes are incomplete. Gradient sampling in the other three bird species was probably adequate based on the lack of pronounced truncation in abundance trends (fig. 1).

Variability in Species Responses

In this study, each bird species responded differently to habitat variation. Strategies for managing single bird species in subalpine riparian habitats will therefore differ from those developed for groups of species. Effective management designs should rely on principles derived from bird-centered habitat features that significantly differ from random sites, either for each bird species or for the bird assemblage as a whole.

To produce an increase in Wilson's warbler and white-crowned sparrow numbers, habitats can be enriched if foliage density, cover, and abundance of subalpine willows are increased and coverage by open meadow and bare ground is reduced. Lincoln's sparrow is unrelated to most of the measured habitat features, achieving dominance on most shrub willow sites. Management schemes that emphasize subalpine avian specialists like Wilson's warbler (see Finch 1987) should enhance areas for Lincoln's sparrow as well. Lower-elevation riparian areas with larger shrubs are selected more heavily by song sparrows. Habitats within this range can be enhanced by managing for greater canopy cover, shrub size, and shrub cover than that which is randomly available. To improve habitat for all four species, efforts should concentrate on increasing shrub density and cover while emphasizing diversity in shrub height, crown diameter and dispersion, and surface cover of small shrubs and ground vegetation. Some of the damaging effects of livestock grazing on bird habitat can be mitigated if these recommendations are followed.

Sampling Scale

At the resolution level of the entire spectrum of plots, species densities were related to one or more vegetational features that changed over the elevational cline. Bird-habitat relationships models developed from these kind of data merely require population-monitoring along gradients of randomly-measured habitat. Within a local area, however, birds occupied habitat patches that differed from randomly-available habitat. In this study, each species selected sites within plots that differed from random sites for a variety of habitat features. Thus, sampling random habitat and bird abundance across many plots produced correlational information at a large scale, but the results do not apply for a specific locality.

Choice of sampling scale (e.g., single vs. multiple plots) and sampling intensity (e.g., random sampling only vs. bird-centered sampling) depends on study objectives and time and budget constraints. Site-specific studies using bird-centered data yield more detailed information on bird-habitat associations, but bird-centered data take much greater time and labor to collect, and results may only apply for a local area. I recommend sampling habitat at both bird-centered and random sites over a variety of vegetational types if managing a single species or guild in a specific locality is the goal. Such a sampling regime will provide more complete coverage of an animal's distribution and habitat requirements. Random sampling alone may be necessary if time and cost demands are prohibitive, or if the goal is to characterize habitat associations of large assemblages of birds in multiple habitats.

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