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Patterns of Breeding Songbird Diversity and Occurrence in Riparian Habitats of the Eastern Sierra Nevada

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ABSTRACT. We determined several vegetation and environmental features that predicted breeding bird species diversity and focal species occurrence in riparian habitats across three watersheds of the eastern Sierra Nevada bioregion, California. Conducting point counts and associated vegetation assessments at 480 individual riparian points between 1998 and 2000 permitted us to investigate bird and habitat relationships at different spatial scales ranging from the entire study area to specific habitat types within climate zones falling along elevational and latitudinal gradients. In particular, Aspen and Black Willow habitats were positively correlated with breeding species diversity, as were tree species richness, width of the riparian zone and elevation. Habitat models predicting the occurrence of Yellow Warblers (*Dendroica petechia*), Warbling Vireos (*Vireo gilvus*), Song Sparrows (*Melospiza melodia*) and Black-headed Grosbeaks (*Pheucticus melanocephalus*) accurately classified 65-83% of test sites, and highlighted the importance of habitat features including aspen (*Populus tremuloides*) cover, riparian width, grass cover, tree species richness and tree height. This effort is the first of its kind for the region, and results can be applied to local and statewide riparian management and restoration efforts.

INTRODUCTION

California's eastern Sierra Nevada encompasses three distinct biogeographic regions: the Sierra Nevada, the Great Basin Desert, and the Mojave Desert (Smith 2000). Accordingly, riparian habitats in the area vary, representing elevational, climatic, geomorphological and vegetative diversity (Taylor 1982; Kondolf et al. 1987). Eastern Sierra riparian vegetation provides habitat for up to 75% of local wildlife (Kondolf et al. 1987) and, similar to other riparian habitats throughout the west, songbirds especially benefit (Knopf et al. 1988; Ohmart 1994). Historically, eastern Sierra riparian habitats hosted a wide variety of breeding songbirds, including all 14 California Partners In Flight riparian focal species (CalPIF focal species; Fisher 1893; Rowley 1939; Grinnell and Miller 1944; RHJV 2000).

Located mostly in the Mono Lake and Owens River watersheds, riparian habitat within our study area is managed primarily by a host of federal, state and city agencies, including the Bureau of Land Management - Bishop Field Office (BLM), Inyo National Forest (USFS) and the Los Angeles Department of Water and Power (LADWP). Historic and current management of the habitat includes water diversions for hydroelectric projects and the Los Angeles Aqueduct, livestock grazing, recreation, and non-native fish stocking (Brothers 1984; Stine et al. 1984).

Bird habitat relationships derived from analyses of data from the entire study region should allow us to identify riparian habitat features currently of importance to songbirds. Similar broad-scale approaches have determined habitat and landscape characteristics that influence western bird populations at large spatial scales in California's Klamath bioregion (Alexander 1999), the Northern Rocky Mountains (Hutto and Young 1999) and the Columbia Plateau (Holmes and Geupel 2000). Managers can use results derived from these approaches to determine which vegetative features to manage for regionally (Hutto and Young 1999). It is sometimes inappropriate to extrapolate bird habitat relationships derived from a small study area (Wiens 1981; Knopf and Samson 1994), and large-scale conservation efforts are rarely orchestrated from the management unit level where research and monitoring is conducted. Therefore, state and bioregional riparian songbird and habitat conservation efforts (e.g. RHJV 2000) need data derived from larger scale projects to fulfill some of their more general objectives.

There is also justification for taking a finer scale approach. Our study area, and the eastern Sierra in general, is made up of riparian drainages of various geophysical settings and structures, and it is therefore difficult to make generalizations about vegetation across the entire study area (Kondolf et al. 1987; Harris et al. 1987). Also, bird habitat relationships derived from an area covering numerous habitat types and geomorphologic regions may not be meaningful or applicable to local management efforts. By bracketing our study sites within climate zones and habitat types, we take some of this variation into consideration and are able to offer suggestions to managers at more local scales. Previous western studies, two of which occurred near or within our study area, have taken this smaller scale approach, incorporating one river drainage, or a few creeks within a general region (Jones and Stokes 1993; Lynn et al. 1998; Sanders and Edge 1998).

Our efforts fit in the context of ongoing state, regional, and local conservation activities. State riparian habitat and songbird conservation efforts (e.g. RHJV 2000) promote the idea that managing for riparian associated songbirds will benefit other wildlife and the quality of riparian ecosystems in general. Current BLM and USFS landbird monitoring and management plans (BLM 1993; USFS 1996) provide directives to evaluate riparian area suitability for avian species of special concern and to evaluate riparian habitats before implementing management. Primary goals of the LADWP and Inyo County Water Department (ICWD) Lower Owens River Project (LORP) include the establishment of a "healthy, functioning Lower Owens River riverine-riparian ecosystem" while "providing for the continuation of sustainable uses" (LORP 1999).

Intelligent management of bird populations requires information about the habitat relationships of those populations (Wiens and Rotenberry 1981). Yet, we are unaware of any previous investigations into the relationships between riparian habitat features and bird numbers in the eastern Sierra that incorporate the diversity of habitats nor the breadth of scale that we do here. We provide this information by identifying habitat characteristics that relate to overall breeding bird species diversity (BSD), and the occurrence of four CalPIF riparian focal species: Yellow Warbler, Warbling Vireo, Song Sparrow and Black-headed Grosbeak (latin names for all bird species included in the study are presented in Table 2).

METHODS

Study area

The study area consists of riparian habitat along 27 separate creeks and one major river, encompassing a 250 km latitudinal stretch of the eastern Sierra Nevada and Great Basin regions of Inyo and Mono counties, California (38º 16' N, 119º 11' W to 36º 14' N, 118º 4' W, Figure 1). The area falls into two Jepson Climate Zones (JCZ, Hickman 1993) and ranges from 1135m to 2512m in elevation. Riparian widths of study site streams range from zero to greater than 100m, and several riparian habitat types are represented (Taylor 1982; Sawyer and Keeler-Wolf 1995; Table 1).

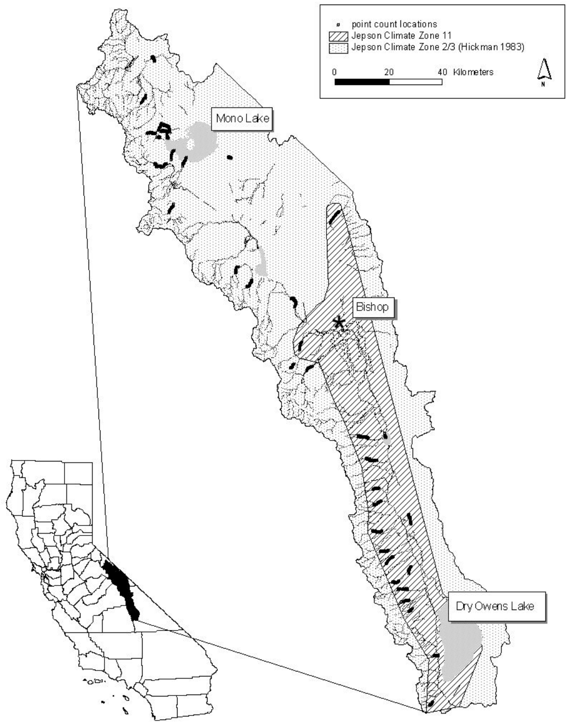
Climate zones roughly coincide with latitudinal and elevational gradients, with 90% of JCZ 11 sites falling between 36º 14' N and 37º 05' N, while 90% of JCZ 2/3 sites fall between 37º33' N and 38º 16' N (Figure 1). Study sites within JCZ 11 that extend north of 37º 05' N latitude have an avifauna more similar to the rest of that climate zone than to that of JCZ 2/3. Similarly, JCZ 2/3 sites that extend south of 37º 33' N have an avifauna more similar to the rest of that climate zone than to that of JCZ 11 (Heath et al. 2001).

Lower elevation sites are in JCZ 11, characterized by high desert climate with hot, windy summers, longer

Table 1. Number of point count stations and streams, range in elevation and riparian width, and percent of point count stations in each Sawyer and Keeler-Wolf habitat type within Jepson Climate Zone 11 and Jepson Climate Zone 2/3, for eastern Sierra Nevada California study sites, 1998-2000.

	Number Points	Number Streams	Elevation Range (m)	Rip. Width Range (m)	Sawyer and Keeler-Wolf Habitat Type	% Points
Jepson Climate Zone 11	256	16	1135-2022	1 - > 100	Water Birch	50
					Mixed Willow	31
					Black Cottonwood	5
					Oak Riparian	5
					Black Willow	4
					Cattail/Bullrush	3
					Wild Rose	1
					Russian Olive	1
Jepson Climate Zone 2/3	224	12	1940-2515	0 - > 100	Montane Wetland Shrub	44
					Aspen	25
					Water Birch	12
					Black Cottonwood	8
					Jeffrey/Lodgepole Pine	7
					Wild Rose	3

Figure 1. Study area in the eastern Sierra Nevada, California, 1998-2000.



growing seasons, and extreme temperature variations. These sites are mostly situated along the alluvial fan and floor of the Owens River Valley in Inyo County, with the exception of one site flowing west out of the White Mountains in Mono County. Alluvial fan streams generally run west to east and are narrow, quick-flowing watercourses comprised of water birch (*Betula occidentalis*) and a mixture of shrub willow species (mostly *Salix exigua* and *S. lasiolepis*) with patches of black cottonwood (*Populus trichocarpa*) and rarely oak (*Quercus kelloggii* or *Quercus wislizenii*). Valley floor sites are located along undiverted and diverted sections of the north to south flowing Owens River, and are characterized by mature black willow trees (*Salix gooddingii*), mixed shrub willow, and patches of wetland species (*Scirpus* spp. and *Typha* spp.) or invasive species such as Russian olive (*Elaeagnus angustifolia*) and salt cedar (*Tamarix* spp.). Upland habitats are dominated by a mixture of sagebrush associated species (*Artemisia tridentada*, *Purshia tridentada* and *Chrysothamnus* spp.) or saltbush *(Atriplex* spp.).

Higher elevation sites are within JCZ 2/3, characterized by shorter (150 to 160 d) growing seasons and regular frost. These sites are located along west to east flowing tributary streams of Mono Lake and the headwater reaches of the Owens River and East Walker River watersheds, mostly in Mono County. Headwater streams and higher reaches of Mono Basin streams are predominantly in glacially carved valleys, comprised of aspen (*Populus tremuloides*), a mixture of willow species (mostly *Salix lucida*, *S. lutea*, and *S. exigua*), water birch and black cottonwood. The lower reaches of Mono Basin streams are undergoing restoration (LADWP 1996), or are partially diverted, resulting in large patches of early successional mixed willow or wild rose (*Rosa woodsii*), young black cottonwood saplings, or large but decadent black cottonwood trees. Adjacent habitats are comprised of Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), sagebrush associated species, or grass, sedge (*Carex* spp.) or rush (*Juncus* spp.) meadows.

Point Counts

We conducted 5-minute 50m fixed-radius point counts at 480 independent stations, following standards recommended by Ralph et al. (1993, 1995). We conducted all counts during the peak songbird breeding season, May 15 to July 10, 1998-2000 (Heath et al. 2001). We installed 36 transects of these stations, totaling approximately 120 stream-km and 180 ha of riparian habitat within 50m of point count stations. We situated stations within riparian vegetation following most stream courses in the area and placed them every 250m regardless of habitat type.

Biologists familiar with the songs and calls of the species in the area and trained in distance estimation visited all stations three times each season, spacing visits at least 7 days apart. We rotated observers for each of the three yearly visits when possible. We conducted censuses from within 30 minutes after local sunrise until approximately 4 hours later, and did not conduct them in excessively windy or rainy conditions. We separated birds detected within 50 m of the station from those detected at greater distances. We evaluated breeding status for each species detected using nest-searching and mist-netting data collected on the same streams (Heath et al. 2001), as well as from incidental behavioral observations recorded by field biologists conducting the counts.

Habitat Assessments

We collected vegetation and environmental data at all point count stations to determine major structural and compositional characteristics and some biophysical features. Following a slightly modified version of the relevé method described by Ralph et. al (1993), we estimated percentage cover by height category for every species of plant located within 50 m (7854 m^2) of the count stations. Height categories were “herb" (0 - 0.5 m), “shrub” (0.5 - 5 m) and “tree” (> 5 m, > 8 cm diameter at breast height (DBH)). We determined the percentage of the plot that consisted of riparian vegetation as opposed to upland vegetation (percent riparian) and the width of the riparian zone at each point.

Finally, we determined elevations using 7.5' USGS topographical maps. We conducted four hundred and five assessments in 1998, 9 in 1999, and 66 in 2000. These efforts yielded 170 vegetation and environmental variables for consideration.

We used our vegetation measurements and guidance provided by Sawyer and Keeler-Wolf (1995) to assign dominant series (habitat types) to each point. The most common riparian habitat types on our study sites in JCZ 11 were Water Birch, Mixed Willow, Black Cottonwood, Black Willow and Oak Riparian. The primary riparian habitat types on our study sites in JCZ 2/3 were Montane Wetland Shrub, Aspen, Black Cottonwood and Water Birch (Table 1).

Data Analyses

We calculated bird species diversity (BSD) for each station using a transformation of Shannon's diversity index (or H', Krebs 1989) denoted N_1 (MacArthur 1965). High index scores indicate both high species richness and more equal distribution of individuals among species. The transformation expresses the data in terms of number of species and thus is more easily interpreted. Expressed mathematically:

$$N_1 = e^{H'} \text{ and } H' = \sum_{i=1}^{i=s} (p_i)(\ln p_i)(-1)$$

Where S = total species richness and p_i is the proportion of the total numbers of individuals that were each species (Nur et al. 1999).

We further limited the species included in calculation of the diversity index to those that we determined to be most reliably recorded with the point count protocol (Table 2). Thus we removed non-territorial species and species whose territories are typically so large that we could not assure independence of individual observations among points (swallows [*Hirundinidae*], swifts [*Apodidae*], waterfowl [*Anatidae*], shorebirds [*Scolopacidae* and *Charadriidae*], hawks [*Accipitridae*], falcons [*Falconidae*], and ravens [*Corvus corax*]). Nocturnal species were also excluded (owls [*Strigidae* and *Tytonidae*] and nightjars [*Caprimulgidae*]).

We used a three-year average of BSD in the analysis after finding no significant difference in species diversity between years (Kruskall- Wallis equality of populations rank test, $\chi^2 = 2.46$, $P = 0.3$). We used mean BSD as the dependent variable in a series of pairwise correlations with vegetation and environmental measurements. We limited the number of variables in the analyses to 21 (from 170 possible) that we thought were most likely to contribute to models predicting species diversity, abundance or occurrence (Table 3). This selection process benefited from our field experience on the study area and from work using similar methods in other California riparian study areas. We then built the most parsimonious model predicting BSD across the entire study area by entering the 18 significant correlates from the pairwise tests into a stepwise, backwards elimination multiple linear regression.

Because combining sites from a large area including a 1377 m elevation gradient and three watersheds may have little biological meaning or application to local land managers (Meents et. al 1983), we bracketed our data set by JCZ and habitat type. Using the same procedure outlined above, we looked for vegetative correlates and predictors of BSD at stations within JCZ 11, JCZ 2/3 and habitat types with large enough sample sizes. We also compared BSD among habitat types using a one-way ANOVA for each JCZ. When results from ANOVA indicated significant differences among habitat types, we used Kruskall-Wallace tests to evaluate the differences in BSD between specific habitat types in question.

Finally, we selected 4 of the CalPIF focal species that breed in the region which are considered to be good indicators of various kinds of riparian habitat (RHJV 2000): Song Sparrow, Yellow Warbler, Black-headed Grosbeak, and Warbling Vireo. For each of these species, we performed pairwise correlations between the number of individuals detected and the same 21 vegetation and environmental variables (Table 5). We only included points on transects on which these species occurred at least once during the study. Using the significantly correlated variables identified by the pairwise tests, we then attempted to predict these species' abundance using linear models. However the data did not comply with the requirements of this technique: residuals from models were not normally distributed and statistical transformations did not remedy the situation. We therefore chose a non-parametric approach, modeling these species' presence or absence (rather than abundance) within 50m of point count stations using stepwise backwards elimination multiple logistic regression. We built models using half of the point count stations (odd numbered ones) and assessed their predictive power by testing them on the other half (even numbered).

All statistical calculations were performed using Stata (Stata Corp. 1999). Significance was assumed at $P < 0.05$, after Bonferroni adjustment for multiple comparisons, when necessary (Zar 1999). We square root transformed the diversity index in all cases to normalize the distribution of residuals of linear regression models and ANOVA's, and log transformed single species detections for the pairwise correlations (Zar 1999). Residuals from linear regression models

Table 2. The 60 breeding bird species included in species diversity calculations and percent of total point count stations with each species present within 50m (frequency of occurrence) within Jepson Climate Zones (JCZ) and for entire study area 1998-2000.

Common Name	Latin Name	Frequency of Occurrence (%)		
		JCZ 11	JCZ 2/3	Entire Study Area
California Quail	*Callipepla californica*	6	3	5
Mourning Dove	*Zenaida macroura*	10	7	9
Black-chinned Hummingbird	*Archilochus alexandri*	8	0	4
Costa's Hummingbird	*Calypte costae*	9	0	5
Calliope Hummingbird	*Stellula calliope*	2	3	3
Lewis's Woodpecker	*Melanerpes lewis*	0	1	0
Red-breasted Sapsucker	*Sphyrapicus ruber*	0	12	6
Nuttall's Woodpecker	*Picoides nuttallii*	1	0	1
Downy Woodpecker	*Picoides pubescens*	0	2	1
Hairy Woodpecker	*Picoides villosus*	1	5	2
Red-shafted Flicker	*Colaptes auratus collaris*	5	19	11
Western Wood-pewee	*Contopus sordidulus*	6	40	22
Dusky Flycatcher	*Empidonax oberholseri*	0	7	3
Black Phoebe	*Sayornis nigricans*	1	0	1
Ash-throated Flycatcher	*Myiarchus cinerascens*	5	0	2
Cassin's Vireo	*Vireo cassinii*	<1	0	<1
Warbling Vireo	*Vireo gilvus*	8	33	20
Steller's Jay	*Cyanocitta stelleri*	7	17	11
Western Scrub-jay	*Aphelocoma californica*	9	0	5
American Magpie	*Pica hudsonia*	1	8	4
Mountain Chickadee	*Poecile gambeli*	0	17	8
Juniper Titmouse	*Baeolophus ridgwayi*	<1	0	<1
Bushtit	*Psaltriparus minimus*	15	9	12
Brown Creeper	*Certhia americana*	0	8	4
Bewick's Wren	*Thryomanes bewickii*	39	11	26
House Wren	*Troglodytes aedon*	5	33	18
Marsh Wren	*Cistothorus palustris*	2	0	1
Blue-gray Gnatcatcher	*Polioptila caerulea*	6	1	4
Townsend's Solitaire	*Myadestes townsendi*	0	1	0
American Robin	*Turdus migratorius*	5	47	25
European Starling	*Sturnus vulgaris*	1	4	2
Phainopepla	*Phainopepla nitens*	2	0	1
Orange-crowned Warbler	*Vermivora celata*	5	5	5
Yellow Warbler	*Dendroica petechia*	6	54	29

table continued on next page

and ANOVA's passed Skewness/Kurtosis tests for normality (*P*>0.05) and Cook-Weisenberg tests for heteroscedasticity (*P*>0.05). Logistic regression models passed goodness of fit χ^2 tests ($P > 0.2$).

RESULTS

Breeding Bird Species Diversity

Entire study area. BSD ranged from 0.7 to 13.3 per station for the entire study area. Of the 21 habitat variables we tested, 18 were correlated with BSD (15 positively and 3 negatively, $P < 0.05$, Table 3). The stepwise regression analysis indicated that BSD was positively correlated with 6 of these variables when the effects of all variables were simultaneously controlled for: riparian width, tree DBH, elevation, ground cover provided by forbs, and tree cover provided by aspen and black willow. Shrub species richness and Jeffrey pine cover were negatively correlated with BSD (Table 4A).

Jepson Climate Zones and Sawyer Keeler-Wolf habitat types. BSD ranged from 0.7 – 8.2 in JCZ 11; it was negatively correlated with 3 habitat features and

Table 2. Continued

Common Name	Latin Name	Frequency of Occurrence (%) JCZ 11	JCZ 2/3	Entire Study Area
Audubon's Warbler	*Dendroica coronata auduboni*	0	11	5
MacGillivray's Warbler	*Oporornis tolmiei*	2	6	4
Common Yellowthroat	*Geothlypis trichas*	3	0	2
Yellow-breasted Chat	*Icteria virens*	2	0	1
Western Tanager	*Piranga ludoviciana*	5	12	8
Green-tailed Towhee	*Pipilo chlorurus*	1	33	16
Spotted Towhee	*Pipilo maculatus*	75	42	59
Brewer's Sparrow	*Spizella breweri*	2	9	5
Vesper Sparrow	*Pooecetes gramineus*	0	1	0
Black-throated Sparrow	*Amphispiza bilineata*	11	0	6
Sage Sparrow	*Amphispiza belli*	19	1	11
Fox Sparrow	*Passerella iliaca*	0	8	4
Song Sparrow	*Melospiza melodia*	9	51	29
Mtn. White-crowned Sparrow	*Zonotrichia leucophrys oriantha*	0	1	1
Oregon Junco	*Junco hyemalis oreganus*	0	7	3
Black-headed Grosbeak	*Pheucticus melanocephalus*	15	16	16
Blue Grosbeak	*Guiraca caerulea*	4	0	2
Lazuli Bunting	*Passerina amoena*	14	7	11
Red-winged Blackbird	*Agelaius phoeniceus*	2	10	6
Western Meadowlark	*Sturnella neglecta*	1	6	3
Brewer's Blackbird	*Euphagus cyanocephalus*	1	38	18
Brown-headed Cowbird	*Molothrus ater*	22	35	28
Bullock's Oriole	*Icterus bullockii*	4	14	9
Cassin's Finch	*Carpodacus cassinii*	0	11	5
House Finch	*Carpodacus mexicanus*	3	1	2
Lesser Goldfinch	*Carduelis psaltria*	9	3	6

Table 3. Correlations between breeding bird species diversity (mean over 3 annual visits 1998-2000, square root transformed) and 21 habitat variables within 50m at point count stations among seven geographic or habitat types (*n* stations). All coefficients listed are significant ($P < 0.05$) after Bonferroni adjustment.

Habitat Variable	Entire Study Area (477)	Jepson Climate Zone 11: Entire Zone (253)	Water Birch (128)	Mixed Willow (77)	Jepson Climate Zone 2/3: Entire Zone (224)	Montane Wetland Shrub (99)	Aspen (56)
riparian width	+0.518	+0.599	+0.333	+0.618	+0.208		
percent riparian	+0.525	+0.609	+0.308	+0.663	+0.207		
forb cover	+0.355	+0.454		+0.617	+0.264		
grass cover	+0.406	+0.239			+0.256	+0.306	
shrub cover							
tree cover	+0.399	+0.374		+0.469	+0.322	+0.370	
tree height	+0.390	+0.200			+0.276	+0.484	
tree DBH	+0.415	+0.363		+0.354	+0.288	+0.408	
tree spp richness	+0.274				+0.372	+0.500	
shrub spp richness	-0.343	-0.377		-0.424			
herb spp richness	+0.258						
willow cover	+0.205	+0.290		+0.363			
water birch shrub cover	-0.192	-0.196				+0.340	
aspen cover	+0.428				+0.396		
black cottonwood cover							
Jeffrey pine cover	+0.207						
water birch tree cover	-0.154						
black willow tree cover	+0.152	+0.453		+0.531			
lodgepole pine cover	+0.207						
black oak cover				+0.245			
elevation	+0.475	-0.269			+0.547	+0.562	

positively correlated with 9 habitat features ($P < 0.05$, Table 3). The final model indicated a positive correlation between BSD and percent riparian, riparian width, and cover provided by both black willow trees and willow shrubs, and a negative correlation with shrub species richness ($P < 0.001$, Table 4B).

Percent riparian and riparian width were positively correlated with BSD at Water Birch stations in JCZ 11 ($P < 0.05$, Table 3), but only riparian width remained in the final model ($P = 0.0001$, Table 4C). BSD at Mixed Willow stations was positively correlated with 8 habitat variables and negatively correlated with 1 ($P < 0.05$, Table 3). Forb cover and percent riparian remained as positive correlates in the final model ($P < 0.001$, Table 4D).

BSD ranged from 1.25 – 13.3 per station for JCZ 2/3 and was positively correlated with 10 habitat features ($P < 0.05$, Table 3). Elevation, tree species richness and aspen cover remained as positive correlates with BSD in the final model. Tree cover was negatively correlated with BSD ($P < 0.001$, Table 4E).

BSD correlated positively with 7 habitat features at Montane Wetland Shrub sites in JCZ 2/3 ($P < 0.05$,

Table 4. Breeding bird species diversity in relation to habitat features within 50m of point count stations for (A) entire study area, (B) Jepson Climate Zone 11, (C) Water Birch habitat in Jepson Climate Zone 11, (D) Mixed Willow habitat in Jepson Climate Zone 11, (E) Jepson Climate Zone 2/3, and (F) Montane Wetland Shrub habitat in Jepson Zone 2/3. Multiple linear regression models (using stepwise, backward elimination procedure) presented. Breeding bird species diversity (transformed Shannon index, mean over 3 annual visits 1998-2000, square root transformed) as dependent term in all cases.

	P	Direction of Effect	Partial R^2 (%)
A. Entire study area: (n = 477), $P < 0.001$, $R^2_a = 51\%$			
elevation	< 0.001	+	22.42
riparian width	< 0.001	+	13.58
tree DBH	< 0.001	+	8.58
black willow tree cover	< 0.001	+	2.61
forb cover	< 0.001	+	1.81
shrub species richness	0.006	-	0.77
aspen tree cover	0.002	+	0.60
Jeffrey pine cover	0.023	-	0.44
B. Jepson Climate Zone 11: (n = 253), $P < 0.001$, $R^2_a = 42\%$			
percent riparian	0.005	+	36.86
black willow tree cover	0.018	+	2.18
shrub species richness	0.016	-	1.83
willow shrub cover	0.016	+	1.37
riparian width	0.039	+	0.22
C. Water Birch habitat: (n = 128), $P < 0.001$, $R^2_a = 10\%$			
riparian width	< 0.001	+	10.38
D. Mixed Willow habitat: (n = 77), $P < 0.001$, $R^2_a = 46\%$			
percent riparian	0.001	+	43.27
forb cover	0.026	+	3.12
E. Jepson Climate Zone 2/3: (n = 224), $P < 0.001$, $R^2_a = 36\%$			
elevation	< 0.001	+	29.61
tree species richness	0.001	+	3.53
aspen tree cover	0.001	+	1.39
tree cover	0.029	-	1.13
F. Montane Wetland Shrub habitat: (n = 99), P < 0.001, $R^2_a = 40\%$			
elevation	< 0.001	+	30.92
tree species richness	< 0.001	+	9.06

Table 3). Elevation and tree species richness account for 40% variation in BSD in the final model ($P < 0.001$, Table 4F). No significant correlations were determined for BSD and any habitat variables at Aspen sites (Table 3).

Differences in breeding bird species diversity between habitat types

Within JCZ 11, BSD was lower at Water Birch sites than at either Black Cottonwood, Mixed Willow or Black Willow sites ($P < 0.005$). Black Willow sites had higher BSD than the other four habitat types ($P < 0.005$). BSD at Black Cottonwood and Mixed Willow sites was not significantly different, and BSD at Oak Riparian sites was not significantly different from BSD at habitat types other than Black Willow (Figure 2A).

Within JCZ 2/3, BSD was higher at Aspen sites than at Montane Wetland Shrub, Black Cottonwood and Water Birch sites ($P < 0.02$). BSD at Black Cottonwood and Montane Wetland Shrub sites were not significantly different and Water Birch sites had higher BSD than the latter ($P < 0.002$, Figure 2B).

Abundance and occurrence of riparian focal species

Numbers of Yellow Warblers detected were significantly correlated with 9 vegetation and environmental features (Table 5). A final logistic regression model incorporating elevation, grass cover and riparian width accurately predicted Yellow Warbler occurrence 74.6% of the time (Table 6A).

Warbling Vireo detections were significantly correlated with 12 vegetation and environmental variables (Table 5). A combination of higher elevation, aspen tree cover and tree height accurately predicted the occurrence of Warbling Vireos at 82.9% of stations (Table 6B).

Numbers of Song Sparrows detected were significantly correlated with 7 habitat variables (Table 5). Greater grass cover, willow shrub cover and riparian width, but fewer shrub species, predicted Song Sparrow occurrence 74.1% of the time (Table 6C).

Black-headed Grosbeak detections were significantly and positively correlated with elevation and tree species richness (Table 5). These features predicted the occurrence of Black-headed Grosbeaks 65.4% of the time (Table 6D).

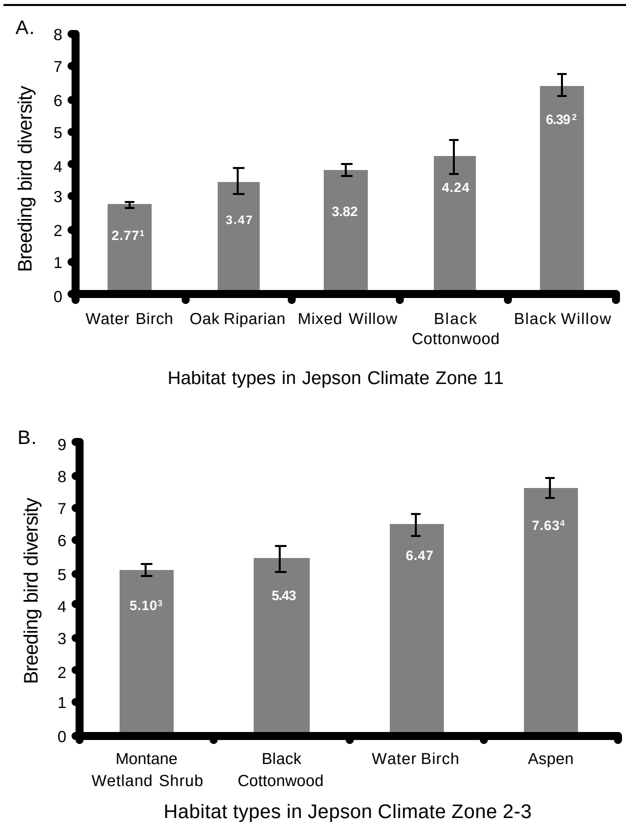
DISCUSSION

The importance of examining BSD at several spatial scales has been well documented, especially in western riparian habitats (e.g. Knopf and Samson 1994; Saab 1999). Some of the habitat features we examined influenced BSD at all three spatial scales (entire study area, JCZ, and habitat types), while the importance of others was only obvious after bracketing our analysis to specific climate zones or habitat types. We will first discuss the variables that significantly correlated with BSD at more than one spatial scale, and describe the importance of these variables in predicting focal species occurrence across the entire study area. We will then discuss our results of models predicting BSD within specific climate zones and habitat types. Throughout, we will discuss the implications that our results have for management and restoration of riparian habitats in the region.

Factors that influence BSD at multiple scales and focal species occurrence across the entire study area

Vegetation. Habitats dominated by aspen and black willow trees proved to be bioregionally important, supporting the most diverse riparian breeding pop-

Figure 2. Comparisons of breeding bird species diversity between habitat types for (A) Jepson Climate Zone 11 and (B) Jepson Climate Zone 2/3. Standard error bars and mean breeding bird species diversity displayed for each habitat type. Breeding bird species diversity is mean of Shannon index within 50m of point count stations for each habitat type and over 3 annual visits 1998-2000.



[1] Water Birch BSD < all other habitat types ($P < 0.005$) except Oak Riparian ($P = 0.10$), [2] Black Willow BSD > all other habitats ($P < 0.005$), [3] Montane Wetland Shrub BSD < Water Birch and Aspen ($P < 0.002$), [4] Aspen BSD > all other habitats ($P < 0.02$).

ulations in the study area. This was evident at all spatial scales we examined: for the entire study area, within the two climate zones, and in comparisons between habitats within each climate zone (Table 4, Figure 2). Aspen tree cover was also highly predictive of the occurrence of Warbling Vireo (Table 6B): a CalPIF focal species known to be declining in other regions of California (Gardali et al. 2000).

The importance of Aspen and Black Willow habitats should be considered in the context of documented degradation to each. For example, Li and Martin (1991) documented an extremely diverse cavity-nesting bird community in aspen groves of central Arizona, where aspens provided 88% of all nest sites, but comprised only 12% of all trees at random plots. They also documented a decrease in aspen tree regeneration, and warned that cavity nesters may decrease locally with the decreasing future availability of nest sites. In the Sierra Nevada, Burton (2000) reported declines in condition and lack of regeneration for a significant number of aspen stands. He cited several potential contributing factors, including fire suppression, livestock grazing, wild ungulate browsing and conifer succession.

Encroachment on remaining Black Willow habitat types along the Owens River by Russian olive and salt cedar, and the degradation of this habitat due to water diversions (Brothers 1984) is also of concern, since these sites tended to have high BSD in our study. However, non-native plant removal projects are underway (ICWD 2000) as are plans to return water to a 62-mile section of the Lower Owens River (LORP 1999).

Landscape. Two landscape features, elevation and riparian-width/percent riparian, contributed to most models predicting BSD and single species occurrence in our study. Abiotic factors such as elevation, climate, topography, and soil type have been demonstrated to influence bird habitat relationships, and the inclusion of these factors should improve the reliability of bird habitat models (Irwin 1998). On a continental scale, James et al. (1996) suggested that landbird populations might be regulated by correlates associated with elevation. Knopf (1985) found that riparian bird communities tended to be more diverse at both ends of an elevational continuum. Physical landscape characteristics contribute strongly to vegetative structure of riparian systems in the eastern Sierra (Kondolf et al. 1987).

Table 5. Number of individuals detected (mean over 3 annual visits, 1998-2000, log transformed) of Yellow Warbler, Warbling Vireo, Song Sparrow and Black-headed Grosbeak within 50m, at point count stations in transects where they occur (*n* stations), correlated with 21 habitat variables. All coefficients are significant ($P < 0.05$) after Bonferroni adjustment.

Habitat variable	Yellow Warbler (350)	Warbling Vireo (330)	Song Sparrow (191)	Black-headed Grosbeak (429)
riparian width	+0.456	+0.231	+0.292	
percent riparian	+0.463	+0.278	+0.231	
forb cover				
grass cover	+0.379	+0.219	+0.283	
shrub cover				
tree cover		+0.430		
tree height		+0.442		
tree DBH		+0.350		
tree spp richness		+0.352		+0.158
shrub spp richness	-0.391	-0.167	-0.414	
herb spp richness	+0.196	+0.246		
willow cover	+0.385		+0.266	
water birch shrub cover				
aspen tree cover	+0.206	+0.523		
black cottonwood tree cover				
Jeffrey pine cover			-0.218	
water birch tree cover	-0.186			
black willow tree cover			+0.254	
lodgepole pine cover		+0.240		
black oak cover				
elevation	+0.498	+0.480		+0.150

Table 6. Probability of species occurrence in relation to habitat features within 50 m of point count stations for (A) Yellow Warbler, (B) Warbling Vireo, (C) Song Sparrow and (D) Black-headed Grosbeak. Multiple logistic regression models (using stepwise, backward elimination) presented with occurrence of each species (over 3 annual visits, 1998-2000) as the dependent term in all cases. Models built using odd-numbered stations (n = 251) and tested on even stations (n = 228), results expressed as % correctly classified.

	P	Direction of Effect
A. Yellow Warbler: *P* < 0.001		
Correctly classified: 74.6%		
elevation	< 0.001	+
grass cover	0.012	+
riparian width	< 0.001	+
B. Warbling Vireo: *P* < 0.001		
Correctly classified: 82.9%		
elevation	< 0.001	+
aspen tree cover	< 0.001	+
tree height	< 0.001	+
C. Song Sparrow: *P* < 0.001		
Correctly classified: 74.1%		
grass cover	0.007	+
willow shrub cover	0.001	+
riparian width	0.005	+
shrub species richness	0.014	-
D. Black-headed Grosbeak: *P* < 0.001		
Correctly classified: 65.4%		
elevation	0.003	+
tree species richness	0.011	+

Elevation contributed to variation in BSD and the probability of occurrence of Yellow Warblers, Warbling Vireos and Black-headed Grosbeaks across the entire study area. Elevation was also positively correlated with BSD in JCZ 2/3 and Montane Wetland Shrub habitat (Table 4, Table 6). Across the entire study area, sites located within JCZ 2/3 are generally at higher elevations and had more diverse breeding populations than those within JCZ 11. Similarly, both Yellow Warblers and Warbling Vireos were absent as abundant breeders among most of our sites in JCZ 11, but were relatively abundant at higher elevation sites in JCZ 2/3 (Table 2; also see Heath et al. 2001). In the Mono Basin of JCZ 2/3 and Montane Wetland Shrub habitat types, sites had higher BSD on the upper reaches versus the lower reaches of the same creeks (Heath et al. 2001).

Riparian width and/or percent riparian was positively correlated with BSD for the entire study area, within JCZ 11, both habitat types investigated within Zone 11, and with the occurrence of Yellow Warblers and Song Sparrows across the entire study area (Table 4, 6). In cases where riparian width and percent riparian were highly correlated, only one of the two variables remained in the model. The model where these variables were not correlated (Table 4B) probably reflects sites with patchy riparian vegetation, where the total riparian area was wide, but vegetation such as willow or cottonwoods was interspersed with large areas of grass, water or forb cover. This situation is especially characteristic of the wide but patchy Owens River valley bottom sites.

The importance of riparian width for the entire study area and for JCZ 11 is not surprising. These models incorporated riparian widths ranging from 0 to 100 m and sites across different geophysical settings including glacial valleys, narrowly incised alluvial fan drainages and a river floodplain (Kondolf et al. 1987). Additionally, habitat types with high BSD (e.g. Aspen and Black Willow) were generally wider than those with low BSD in JCZ 11 (e.g. Water Birch).

We were surprised, however, by the significance of riparian width in models for Water Birch and Mixed

Willow habitat types in JCZ 11. Sites dominated by water birch and willow shrub in JCZ 11 are characteristically narrow, incised riparian strips with low flow rate (Taylor 1982). Our Water Birch sites, for example, range in width from 1-35m. It is interesting that BSD significantly increased with riparian width within these habitats, even though they had relatively low BSD and geomorphologically-limited potential increase of riparian width (Taylor 1982; Kondolf et al. 1987). We therefore urge managers to maintain riparian width even within these relatively narrow habitats.

Factors that influence breeding bird species diversity within climate zones and habitat types

Jepson Climate Zone 11. In addition to black willow tree cover, willow shrub cover was correlated with high BSD in JCZ 11 (Table 4B). The importance of willow shrub cover is of particular interest because it is structurally similar to water birch, and it co-occurs with water birch as one of the most prevalent alluvial fan riparian vegetation types in the region (Taylor 1982). Yet water birch cover was eliminated from all models by the stepwise regression procedure (Table 4), and BSD at Mixed Willow sites was significantly higher than at Water Birch sites (Fig 2B). Forb cover was positively correlated with BSD in the Mixed Willow model (Table 4D), and this may account for the differences with Water Birch, where forb cover is generally lower than at willow sites. It has been noted that arroyo willow (*Salix lasiolepis*) is out-competed by water birch in the alluvial fan region (Taylor 1982), and therefore should be of interest when managing for BSD.

Wiens and Rotenberry (1981) warn against using low bird diversity indices and associated habitat features as a means to determine the relative importance of particular habitat types. Knopf and Samson (1994) caution that unique elements of a riparian avifauna may be overlooked when managing for site specific BSD. We recognize this advice and point out that water birch is unique in California as it reaches its southwestern distributional limit in the eastern Sierra (Taylor 1982). Additionally, water birch provides the majority of the nesting substrate for rather dense populations of breeding Calliope and Black-chinned hummingbirds (Heath et al. 2001) – species that often go undetected by point counts. Further, Water Birch sites at higher elevations (i.e., in JCZ 2/3) had relatively high BSD (Figure 2B).

Jepson Climate Zone 2/3. In addition to aspen tree cover, BSD was correlated positively with tree species richness and negatively with tree cover in JCZ 2/3 (Table 4E). The negative correlation with tree cover is probably driven by sites with very high cover of Jeffrey pine and lodgepole pine, which had relatively little other riparian vegetation (SKH, pers. obs.). In addition to these two pine species, sites with high tree species richness also had non-conifer species such as black cottonwood, water birch, willow and aspen, as well as small numbers of white fir (*Abies concolor*), juniper (*Juniperus occidentalis*), or piñon pine (*Pinus monophylla*). Sites with high tree species richness in this area were typified by trees of different heights and patchy canopies, and do not necessarily have high overall percentages of tree cover. Managing the over-encroachment of pines, while maintaining tree species richness, should benefit BSD.

Tree species richness was also correlated with BSD in the model for Montane Wetland Shrub habitat of JCZ 2/3 (Table 4F). Sites within this habitat type are mostly located at higher elevation, moist alluvial outwash meadows (Taylor 1982) and along the lower reaches of Mono Lake's tributary creeks, some of which are undergoing restoration. Our results suggest that within this willow shrub dominated habitat, managing for or restoring a variety of slightly encroaching, but not dominant, tree species may be important for maintaining BSD. Tree species richness also predicted the occurrence of Black-headed Grosbeaks over the entire study area.

Black Cottonwood and Montane Wetland Shrub habitats had lower BSD than Aspen sites but relatively high BSD compared with most habitat types in JCZ 11 (Figure 2). This is an important consideration for restoration efforts on the lower reaches of Mono Lake's tributary creeks, where these two habitat types are common. Different bird species may utilize the distinct niches the two habitats provide, therefore restoration efforts and hydrological processes that maintain the characteristics of both habitat types should theoretically maintain higher BSD.

BSD for Water Birch sites in JCZ 2/3 was higher than for Water Birch sites in JCZ 11. It was also significantly higher than BSD in Montane Wetland Shrub habitat (Figure 2). Water Birch sites in JCZ 2/3 differ geomorphologically and hydrologically from their lower elevation counterparts. Most of these sites in JCZ 11 are characterized by stream flows less than about 0.3m^3 sec^{-1} (Taylor 1982). Water birch in JCZ 2/3 is predominantly found along creeks with higher flow rate, and co-occurs with Jeffrey pines, black cottonwoods and occasionally aspens (Taylor 1982; Kondolf et al. 1987; Stromberg and Patten 1992). These factors may contribute to higher BSD at Water Birch sites in JCZ 2/3.

Riparian characteristics in relation to stream flow in the eastern Sierra Nevada

Most streams within our study area are diverted for either hydroelectric projects, livestock forage pasture, or the Los Angeles Aqueduct (Stine et al. 1984; Brothers

1984; Kondolf et al. 1987). We did not directly investigate the effects of water diversions on BSD or species occurrence. However, several previous eastern Sierra studies have assessed the impacts of stream diversions on the same vegetation features that we have demonstrated important for riparian breeding songbirds.

Taylor (1982) found that average flow, gradient and degree of channel incision accounted for 68% of the variation in riparian width and that average flow alone accounted for 44% of the variance. Harris et al. (1987) argued that riparian width was correlated with floodplain width rather than directly with changes in stream flow. This study also suggested that vegetative thinning or loss of near-stream plants may result from stream diversion and that sites downstream from diversions had significant decreases in shrub and herbaceous cover. Smith et al. (1991) suggested that stream flow diversions, and the subsequent elimination of floods and high flows, may cause long-term selective mortality of juvenile plants. Stromberg and Patten (1990) demonstrated a strong relationship between growth rates of riparian trees and annual and prior-year flow volumes, and pointed out the importance of seasonal distribution of flows to riparian tree growth.

These authors have demonstrated the effects of stream flow reduction on riparian width, shrub and herbaceous cover, tree DBH and the vegetative structure resulting from the combination of these features. We have demonstrated the importance of these same characteristics for riparian breeding songbirds in the eastern Sierra Nevada. Incorporating stream flow management with ongoing restoration and management efforts can maximize the benefits for riparian breeding songbirds.

CONCLUSIONS

We have produced a series of riparian bird habitat models for the eastern Sierra Nevada, incorporating a variety of habitat types, spatial scales and bird indices including breeding bird species diversity and single species occurrence. This geographically broad and multiple scale effort represents the first of its kind for the region and can serve as a baseline for future and more in-depth investigations. We acknowledge the demonstrated limitations of bird habitat models (Rotenberry 1986), and the use of bird numbers and diversity indices to determine habitat suitability (Van Horne 1983; Wiens and Rotenberry 1981; Knopf and Samson 1994). We also acknowledge the importance of understanding the demographic parameters that most directly influence songbird fitness (such as productivity and survival) and the biological processes that may limit these parameters (e.g. predation and parasitism; Martin 1989; DeSante and Rosenberg 1998). Nonetheless, our findings contribute to the current state of knowledge and will assist riparian habitat management and songbird conservation efforts. The accuracy and utility of these models (and proactive conservation in general) can improve with increased communication among researchers and managers (Toth and Baglien 1986; Martin 1995), and continual re-evaluation over time.

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