The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
M.L. BEAN LIFE SCIENCE MUSEUM
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 59 | 31 JULY 1999 | NO. 3

Great Basin Naturalist 59(3), ©1999, pp. 205–212

EFFECTS OF HABITAT TYPE AND DEGRADATION ON AVIAN SPECIES RICHNESS IN GREAT BASIN RIPARIAN HABITATS

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ABSTRACT.—The overwhelming majority of bird species in the Great Basin region are found in riparian habitats. However, most previous research on the impact of change in habitat condition through degradation on these bird communities failed to account for the large intersite differences in both habitat type and extent of degradation. We examined songbird communities in 4 riparian habitat types (meadows, willow-, birch-, and aspen-dominated forest stands) during summers 1994 (last year of a 7-yr drought) and 1995 (following the 6th wettest winter recorded) in the Toiyabe Mountain Range of central Nevada. Habitat degradation significantly influenced bird species richness in riparian areas, but the impact was dependent upon habitat type. While meadow bird communities were affected adversely by habitat degradation, with significant drops in species richness on degraded sites, bird species richness in forested riparian habitats was consistently greater on degraded sites. Data for the 6 most common species seen during our study indicated that degradation may have influenced distribution of American Robins (*Turdus migratorius*) and Yellow Warblers (*Dendroica petechia*), but habitat type was the best predictor of abundance for House Wrens (*Troglodytes aedon*), Red-naped Sapsuckers (*Sphyrapicus nuchalis*), Warbling Vireos (*Vireo gilvus*), and Brewer's Blackbirds (*Euphagus cyanocephalus*). Avian species diversity in meadow habitats may be linked to moisture levels during specific times of the year. Diversity increased during the pre-migratory period of the dry year (1994) when compared with that of the breeding season, but was unchanged in the wet year (1995).

Key words: riparian woodland, meadow, grazing, breeding, songbird, Nevada.

Riparian woodlands in western United States support some of the highest densities of breeding landbirds in the United States and Canada (Carothers et al. 1974, Knopf et al. 1988). Although such habitats cover <1% of the total regional landmass, 2/3 to 3/4 of regional, nongame landbird species are associated primarily with these riparian areas during the breeding season (reviewed in Saab et al. 1995). Riparian habitats are attractive to birds for a variety of reasons. Streams produce invertebrates that are the primary prey of many of these birds, and adjacent vegetation provides nest sites not otherwise available in the surrounding landscape (Ryser 1985).

Due to their strong dependence upon riparian areas, landbird communities in the Great Basin region may be affected by any activities

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altering habitat condition. Over the last decade concern about these limited riparian habitats has attracted increasing attention; one focal point has been the potential impact of livestock grazing (e.g., Knopf et al. 1988, Fleischner 1994, Knopf and Samson 1994, Brown and McDonald 1995, Saab et al. 1995). Water, shade, and diverse succulent vegetation of these riparian areas attract not only wildlife (e.g., Johnson et al. 1977, Thomas et al. 1979) but also grazing livestock (Gillen et al. 1984). Problems arise because riparian areas are highly susceptible to degradation by the concentrated activities of domesticated animals. Grazing livestock can substantially alter essential characteristics of streams by changing surrounding vegetative structure and species composition, altering soil structure and porosity, and modifying stream bank morphology (e.g., Smith 1940, Ellison 1960, Brown 1978, Platts 1981, Kauffman and Krueger 1984, Milchunas et al. 1988, Baker and Guthery 1990, Smith et al. 1994).

Generalizing anticipated impacts of activities, such as grazing, on native flora and fauna can be difficult because riparian areas differ greatly among sites in such characteristics as plant community structure and extent of habitat degradation (Carothers et al. 1974, Rice et al. 1983). Summaries such as those of Saab et al. (1995), which pool data from numerous studies, are useful as an initial approximation of the impact of grazing on riparian avifauna across a wide range of habitat and degradation types, but must be applied with caution to specific sites.

Livestock grazing, one agent of change in these riparian systems, is the general context for this study. However, disturbance through grazing by native wildlife, droughts, floods, insect outbreaks, and wildfires also may alter habitat conditions. In this study we used techniques developed by the U.S. Forest Service (Weixelman et al. 1996; see Methods) to quantify the general condition of riparian forested habitats and meadows on the basis of soil and understory vegetation characteristics. We examined how habitat conditions, created by various disturbances listed above, affected bird communities in riparian habitats of central Nevada compared with communities found in relatively undisturbed riparian habitats of the same region. Although livestock grazing may have led to substantial change in parts of the study area, our main interest lay in the correlation between the general condition of riparian habitats and bird communities found in them, rather than a direct link between cattle grazing intensity and avian species richness.

We present results of census data for songbird communities from 4 different riparian habitat types, at known levels of habitat degradation, within a limited geographic area, in a replicated study conducted over 2 yr. Our objectives were to (1) determine whether observed levels of habitat degradation affected bird species composition (and abundance of the 6 most common species), and (2) determine if these effects differed among habitat types. In the case of meadow habitat, we also were interested in variation by period within the summer season.

STUDY AREA AND METHODS

Censuses were conducted over 2 summers in the Toiyabe Mountain Range, which is part of the Humboldt-Toiyabe National Forest located 240 km east of Reno in central Nevada, USA (Lander and Nye counties; 39°N, 117°W). This narrow, 200-km-long range is oriented north–south with peaks ranging in elevation from 2100 to 3600 m. Along its length are a large number of deep canyons with riparian areas seldom exceeding 30–50 m wide at stream level. Dominant vegetation in the canyons includes quaking aspen (*Populus tremuloides*), water birch (*Betula occidentalis*), willow (*Salix* spp.), and meadow plant assemblages (e.g., characterized by dense cover of *Carex nebrascensis*, *C. aquatilus*, *Poa secunda*, *Juncus balticus*, or *Deschampsia cespitosa*). Seasonal precipitation typically is less than 250 mm in basins on either side of the range, with about 60% falling in autumn and winter (Weixelman et al. 1996). Summer 1994 was the last year of a 7-yr drought, and summer 1995 followed the 6th wettest winter recorded for this region (data for Austin, NV, from the Western Regional Climate Center, Reno, NV). Indirect human disturbance of these canyons through cattle and sheep grazing at varying intensities has led to significant changes in vegetative structure and composition over recent times. Human recreational activities and natural disturbances such as droughts, floods, and wildfires also have resulted in some habitat degradation. We assessed the degradation level at each census

site on the basis of soil and understory plant characteristics (see below).

General Censuses

We established 42 transects in 19 drainages along the range. The transects represented 4 riparian habitat types (meadow, willow, aspen and birch) at 2 levels of degradation (high and low). They included 9 moist meadows (5 on highly degraded sites and 4 on minimally degraded sites), 15 willow habitats (9 high and 6 low), 10 aspen habitats (7 high and 3 low), and 8 birch habitats (5 high and 3 low). These transects were assigned to plant communities and degradation types by the Humboldt-Toiyabe National Forest Ecology Team, using criteria described in detail by Weixelman et al. (1996). Soil, water, climate, and plant species present determined community assignment. Criteria for degradation level included factors such as seral stage association of plant species present, groundcover, extent of water infiltration, root depth and abundance, and soil temperature. Values for sites of each habitat type were compared with those of the potential natural community to determine habitat degradation level (high, medium, and low). Three values were calculated for habitat degradation at each site based on the aggregated characteristics of soil, vegetation, and the 2 data sets combined. We selected only those sites classified as having high- or low-degradation levels for these analyses.

Because of the discontinuous nature of the habitats being sampled with various types of vegetation interspersed along the length of these canyons, transects varied from 120 to 200 m long and 8 to 40 m wide depending upon available habitat. High elevations and late snowmelt generally delayed onset of breeding at these sites; hence, transects to census breeding birds were walked once each year during a 10-d block in 1994 (26 June–5 July) and 1995 (27 June–6 July). Sites were visited between 05:30 and 09:30 h by 2 people, an observer and a recorder, walking at a constant pace (maximum 10 m per min). Start and finish times were recorded so that data from transects of different lengths could be standardized. All songbirds seen or heard were recorded as occurring within the specified riparian area or in the adjacent sagebrush (*Artemisia* spp.) or pinyon pine–juniper (*Pinus monophyla–Juniperus* spp.) habitat. Only those individuals within the riparian habitat, or actively foraging in the air above the riparian area (e.g., Violet-green Swallows, *Tachycineta thalassina*), were included in this analysis.

We analyzed species richness and species richness values standardized to account for the amount of time spent on each transect. Although correcting time-standardized species richness values for unequal sampling effort may be required under some circumstances (Elphick 1997a), examination of residual values for the linear model of species richness = time revealed a normal distribution for our data. In addition, we calculated species diversity for each transect. Because of the potential for differential attraction to riparian habitats among the species examined, we followed Magurran (1988) and used Brillouin's index (1962):

$$\mathrm{HB} = \frac{1nN! - \Sigma 1nn_i!}{N}$$

For statistical analyses, each of these 3 measurements (species richness, time-standardized species richness, and species diversity) formed the dependent continuous variable in a general linear model (PROC GLM; SAS Institute Inc. 1988), with the independent categorical variables being degradation level (based on aggregate characteristics of soil, vegetation, or the 2 combined), habitat type, year, and all possible interaction terms for the 3 variables. Because each possible response variable gave the same qualitative pattern of results for each degradation measure, we report only those values for species richness and the combined degradation measure. Brillouin's index takes into account both evenness and species richness in a composite measure; therefore, we also assessed species overlap within and between sites of the 2 degradation levels for each habitat type by calculating Sorenson's index (Southwood 1978):

$$C_s = \frac{2j}{(a + b)}$$

In addition, we examined the rarity of those species encountered on the basis of Gaston's (1994) definition, which uses the arbitrary cutoff of the least common 25% of bird species.

To examine how individual species reacted to degradation level in the 4 habitat types, we conducted analyses similar to that above but

substituted abundance in place of species richness for each of the 6 most common species observed (American Robin, *Turdus migratorius*; House Wren, *Troglodytes aedon*; Red-naped Sapsucker, *Sphyrapicus nuchalis*; Warbling Vireo, *Vireo gilvus*; Yellow Warbler, *Dendroica petechia*; and Brewer's Blackbird, *Euphagus cyanocephalus*).

Meadow Watches

Preliminary censuses indicated that meadows had substantially lower species richness when compared with the other 3 habitats. To ensure that this was an accurate reflection of circumstances, we expanded our examination of meadow habitat. Ten moist meadow sites adjacent to sagebrush or pinyon pine–juniper habitat (the 9 mentioned above plus 1 additional site) were selected for observation of avian activity in a 30 × 20-m section of each meadow, which typically was the entire meadow. Meadow use was assessed at each site during a 10-d period in the breeding season (26 June–5 July 1994 and 27 June–6 July 1995), and repeated during a 10-d period in the premigratory season (29 July–7 August 1994 and 25 July–3 August 1995) to test for seasonal change in meadow use. For both seasons, one 30-min sample was collected for each meadow by 2 observers during a 3-h period (06:00–09:00 h). Although birds were not individually marked, observers attempted to monitor movements in and out of the meadow to avoid counting the same individual more than once. Therefore, our data reflect only a minimum estimate of species diversity. Birds flying over the meadow were not included in the data, with the exception of swallows searching for prey. Meadow watch data were converted to indices of species diversity based on Brillouin's measure (1962). These data then were used as the basis for subsequent analyses to test for differences in species diversity at meadow sites between and within years using Wilcoxon's matched-pairs test (Zar 1996:167).

RESULTS

General Censuses

Analysis of species richness indicated a significant interaction effect between habitat type and degradation level (Table 1). Examining these data graphically (Fig. 1) revealed that among minimally degraded (i.e., high-quality) sites, there were similar levels of species richness for all 4 habitat types. Comparing highly degraded sites for each habitat, however, revealed that avian species richness values were lower in meadows and higher in aspen-, willow-, and birch-dominated habitats (although not statistically significantly so; Table 1) than values obtained for minimally degraded sites. The latter result suggested that observed levels of degradation of forested riparian habitats created opportunities for new species, normally not found in minimally degraded habitats, to move into aspen-, willow-, and birch-dominated stands.

Across habitat types, species overlap values in low-degradation sites were greater in birch than any other habitat type (Table 2). Within habitat type, however, the amount of overlap was greater in low-degradation than high-degradation sites, with the exception of aspen where the trend was reversed. Other than meadows, values of overlap between low- and high-degradation sites were intermediate to those of within-degradation level values. Some caution must be used when interpreting these species overlap data due to the generally low number of species encountered at many sites during the study (see average values reported in Fig. 1).

At a species-specific level, we identified 6 species that were encountered at ≥2 sites in highly, but not minimally, degraded forested habitats during our transects. These species may act as indicators of habitat degradation in riparian forested areas of the Toiyabe Mountain Range: Downy Woodpecker (*Picoides pubescens*) and Lazuli Bunting (*Passerina amoena*) occurred in highly degraded birch and willow, Plumbeous Vireo (*Vireo plumbeus*) in highly degraded willow and aspen, and Green-tailed Towhee (*Pipilo chlorurus*), Dark-eyed Junco (*Junco hyemalis*), and Pine Siskin (*Carduelis pinus*) in highly degraded aspen.

When we examined changes in abundance of the 6 most common species observed during the study, we detected no degradation effect, but habitat was a useful predictor of species abundance for 4 of 6 species. Aspen was used more often than other habitats by House Wrens (Habitat: $F_{3,68} = 22.71$, $P = 0.0001$), Red-naped Sapsuckers (Habitat: $F_{3,68} = 4.61$, $P = 0.0092$), and Warbling Vireos (Habitat: $F_{3,68} = 10.67$, $P = 0.0001$); individuals of the latter species also frequently were

TABLE 1. Analysis of variance test of the effects of degradation, habitat, and year on species richness of riparian birds for 4 habitat types in the Toiyabe Mountain Range, Nevada.

Source[a]	SS[b]	df	F	P
Degradation	0.05	1	0.00	0.949
Habitat	190.88	3	5.55	0.002
Year	8.41	1	0.73	0.395
Degradation × Habitat	108.06	3	3.14	0.031
Degradation × Year	6.46	1	0.56	0.455
Habitat × Year	31.39	3	0.91	0.439
Degradation × Habitat × Year	43.55	3	1.27	0.292
Error	779.39	68		

[a]Model $F_{15,68} = 2.73$, $P = 0.0025$
[b]Type III sums of squares

TABLE 2. Comparison of Sorensen's index values (mean ± $s_{\bar{x}}$, n) for riparian birds at 42 sites representing high- and low-degradation levels for 4 habitat types in the Toiyabe Mountain Range, Nevada.

	Birch	Willow	Aspen	Meadow
Low degradation	0.459 ± 0.078 (3)	0.362 ± 0.032 (15)	0.229 ± 0.019 (3)	0.150 ± 0.080 (6)
High degradation	0.175 ± 0.057 (10)	0.249 ± 0.033 (36)	0.554 ± 0.031 (21)	0.050 ± 0.050 (10)
High v. Low	0.194 ± 0.040 (15)	0.301 ± 0.023 (54)	0.394 ± 0.033 (21)	0.031 ± 0.022 (20)

encountered in birch, while Brewer's Blackbirds rarely were observed outside of meadows (Habitat: $F_{3,68} = 2.91$, $P = 0.0405$). The interaction of habitat type and degradation level was significant for both American Robins (Degradation × Habitat: $F_{3,68} = 5.63$, $P = 0.0023$) and Yellow Warblers (Degradation × Habitat: $F_{3,68} = 3.45$, $P = 0.0213$). Each of these 2 species was found more often in highly degraded birch and either intact willows (American Robins) or intact meadows (Yellow Warblers).

Based on Gaston's (1994) definition of rarity, among the individuals encountered during these censuses, 12 species comprised 75% of all individuals sighted, and 32 species could be classified as rare. However, previous work by one of us (Reed 1996) suggests that there can be substantial difficulties in ascertaining the actual absence of rare species from a census site. As a consequence, rare species probably make the poorest indicators of habitat impact, and we will not address the issue of rarity any further.

Meadow Watches

Species diversity indices from meadow watches varied seasonally and annually (Table 3), with substantial differences in number of individuals and species encountered. No significant difference in species diversity was found in meadow sites during breeding seasons of 1994 and 1995 (Wilcoxon's matched pairs test; $Z = 0.0$, $n = 10$, $P = 1.0$). However, activity (as reflected in diversity measures) in these meadows increased sharply during the post-breeding, pre-migratory period of the dry

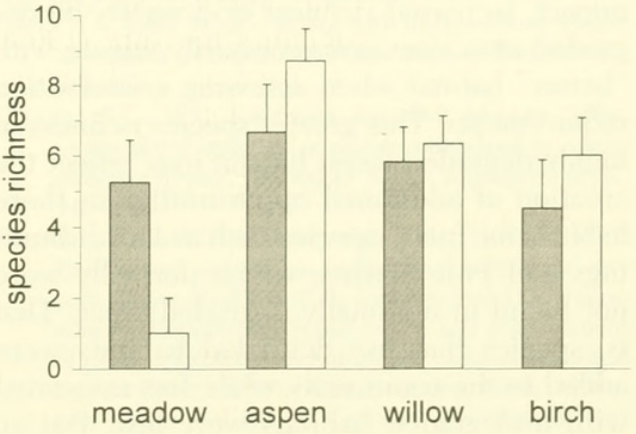

Fig. 1. Mean bird species richness (± $s_{\bar{x}}$) for 4 riparian habitats in the Toiyabe Mountain Range, Nevada. Shaded bars represent values for minimally degraded sites; open bars represent highly degraded sites.

TABLE 3. Comparison of Brillouin's species diversity index values (mean ± $s_{\bar{x}}$) for riparian birds at 10 meadow sites in the Toiyabe Mountains of central Nevada.

Year	Season	Diversity
1994	Breeding	0.062 ± 0.042
	Pre-migratory	0.254 ± 0.080
1995	Breeding	0.056 ± 0.030
	Pre-migratory	0.088 ± 0.054

year (1994; $Z = 2.201$, $n = 10$, $P = 0.0277$), while it rose marginally but not significantly in the wet year (1995; $Z = 0.534$, $n = 10$, $P = 0.5929$).

DISCUSSION

Previous studies (primarily focusing on grazing) show no single effect of change in habitat condition on riparian bird communities; even studies of the same bird species in different locations differ in their conclusions regarding the impact of change in habitat condition (Saab et al. 1995 and citations therein). In part, this ambiguity comes from comparing studies from different habitat types and with different levels of habitat degradation. We controlled for both factors *a priori* in our study area and found that habitat degradation did affect avifaunal communities, but its impact differed among habitats examined. While bird communities in meadows were strongly and adversely affected by increased degradation, species richness in forested riparian habitats was consistently higher on degraded sites. We note, however, that while lowered species richness on high-quality areas would be an adverse impact, increased richness or diversity on degraded sites does not necessarily equate with "better" habitat when assessing conservation requirements. This greater species richness in highly degraded forest habitat may reflect the creation of additional opportunities in these habitats for "new" species such as Lazuli Buntings and Pine Siskins, which normally were not found in minimally degraded areas. That is, species that use degraded habitats were added to the community while few associated with undegraded habitats were lost. But an increase in species richness with increased habitat degradation is not necessarily monotonic. Birds will disappear from forests in which the structure has been too drastically altered to continue meeting their habitat requirements, whereas intermediate levels of disturbance may increase species richness in a variety of habitats (Connell 1978).

Within meadow habitat, degradation had strong adverse effects on bird communities, likely due to the susceptibility of meadow vegetation and stream bank morphology to cattle grazing (see introductory paragraphs for references). However, we also identified for meadows a seasonal effect on species diversity that was of a larger magnitude in the dry year (1994) than the wet year (1995). The significantly higher species diversity found during the pre-migratory period of 1994 suggests that birds are constrained more in their choices of habitat during dry than wet years by lack of moist meadows and other water sources. We presume that availability of suitable foraging or resting locations along water courses differs between years, being more restricted in drier years. During dry years, especially late in the season, low-lying wet meadows (such as those studied here) may be the only places where water is available.

Bock et al.'s (1993) review of literature on the impact of grazing on birds suggested that American Robins, Brewer's Blackbirds, and House Wrens would be positively affected by grazing (i.e., have increased population densities), while studies of Red-naped Sapsuckers, Warbling Vireos, and Yellow Warblers provided only mixed or uncertain results. In our analyses there was no significant impact of habitat degradation on numbers encountered for 4 of 6 species. Interaction effects that we uncovered indicate that degradation's impact differs among habitat types but, in this study, led to increased numbers of both American Robins and Yellow Warblers in certain habitats.

Sedgwick and Knopf (1991) expressed concern about the short duration of most studies on grazing impacts in terms of how long-term grazing may alter the plant community. We share this concern about study duration, but from the standpoint of missing the years in which impacts are most noticeable. We had 2 very different years in our sample. Our overall results suggest that single-year studies can provide misleading results when examining impacts of habitat degradation. Years during which conditions are the most extreme may be the most useful in identifying critical habitat.

Also, the importance of certain sites (here, meadows) can be overlooked if surveyed during the wrong season (breeding season versus pre-migratory period).

The majority of studies on potential impacts of grazing (or some other factor affecting habitat condition) have no replication and often lack controls. Resource managers need to use appropriate experimental designs when testing hypotheses such as those assessing potential impacts of grazing (Romesburg 1981, MacNab 1983, Gavin 1989, Murphy and Noon 1991). However, large-scale experimental studies are uncommon, in part because of limited resources and in part due to logistical inconvenience of such studies. With appropriate planning, experimental approaches often are possible (cf. Elphick 1997b). In our study we had 4 habitat treatments and 2 levels of degradation, with replication for each treatment combination. If we had been able to assign which plots received each level of degradation, rather than using already treated areas, such assignments would have increased the strength of our study. However, our experimental design is a good example of using space for time, and we recommend it for conservation-related studies that do not have time as a resource.

ACKNOWLEDGMENTS

Assistance was provided by J. Bury, L. Butcher, S. Dunham, S. Fleury, G. Guscio, S. Martin, C. Mutembi, and N. Olson. Thanks to C. Campbell, C. Elphick, R. Glinski, and T. Knight for their thoughtful comments on the manuscript. This research was funded by the U.S. Forest Service, the Center for Conservation Biology of Stanford University, a grant from the Wells Family Foundation, the Biological Resources Research Center of the University of Nevada–Reno, and the Principal's Research Fund of Sir Wilfred Grenfell College, Memorial University of Newfoundland. Monetary support was increased and/or aided by C. Boggs, G. Grevsted, and M. Schwalbach. We are indebted to D. Weixelman, D. Zamudio, and K. Zamudio (U.S. Forest Service) for developing habitat degradation scoring methods in the Toiyabe Mountain Range for estimating habitat condition at our study sites, and for facilitating our understanding and use of site scores. Thanks also to the Yomba Shoshone Tribal Council, staff from the Austin Ranger District Office of the U.S. Forest Service, and the people of Austin, Nevada, for their assistance and cooperation.

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Received 9 March 1998
Accepted 30 September 1998