

AVIAN NEST SUCCESS IN RELATION TO PAST GRAZING REGIMES IN A MONTANE RIPARIAN SYSTEM¹

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Abstract. One possible link between livestock grazing and bird population declines is variation in nest predation rates. To explore this possibility we documented vegetational differences in a montane riparian community subdivided by a fence, one side of which traditionally has been summer-grazed, and the other side rested from grazing for 30 years. We found that ground vegetation was more abundant, willows (*Salix* spp.) less abundant, and vertical vegetational diversity was lower on the grazed relative to the rested side. Predation rates on real nests were higher on the grazed side compared to the rested side. Artificial nests were placed (1) in mixed conifer vegetation to mimic the most common nest types currently present in the riparian zone, (2) in streamside willows that differed in abundance across the fence, and (3) in old-willow remnants distant from the stream, which were equally abundant on both sides of the fence. All artificial above-ground nests, and ground nests in the old-willow experiment, suffered greater predation rates on the grazed compared to the rested side. Thus, livestock grazing may not only affect availability of nesting substrates for riparian birds by reducing streamside vegetation, but could influence bird populations by facilitating nest predation, possibly by increasing detectability of nests or through changes in predator assemblage.

Key words: grazing, nest success, artificial nests, riparian birds, population declines.

INTRODUCTION

Livestock grazing in riparian ecosystems of western North America has been linked to reduced riparian vegetation (Szaro and Pase 1983, Schulz and Leininger 1990, Sedgwick and Knopf 1991), as well as decreased bird species diversity and abundance (Mosconi and Hutto 1982, Taylor 1986). In a recent review, 17 of 43 species of Neotropical migrants breeding in western riparian habitats were found to respond negatively to grazing (Bock et al. 1993). Similarly, DeSante and George (1994) listed "over-grazing" and "destruction of riparian habitat" as causes of population declines in 8 and 15 western species, respectively. Although numerous studies have documented negative effects of grazing on bird populations (for a review, see Saab et al. 1995), mechanisms that link grazing to population declines have been identified only at a general level, with destruction of breeding habitat through grazing impacts on the vegeta-

tion usually being regarded as the most important cause.

A more subtle mechanism that may connect habitat alterations by livestock to bird losses is reduced reproductive success. Reproductive failure of songbirds is most commonly a result of nest predation (Ricklefs 1969). Impacts on nest predation rates by other large-scale perturbations, such as forest clearcutting and other types of habitat fragmentation, have been studied in depth (e.g., Wilcove 1985, Andrén 1992). However, studies addressing effects of livestock grazing on nesting success are surprisingly scarce, considering the predominance of grazing as a land use practice in western riparian ecosystems and its reported impacts on bird populations (Ohmart 1994, Saab et al. 1995, Stacey 1995).

The first objective of our study was to determine differences in vegetation structure of a grazed plot and a plot that had been rested from grazing for 30 years in a montane riparian community in Nevada. Second, we determined differences in predation rates of active nests adjacent to the stream and of artificial nests that simulated those of species currently abundant in the riparian zone. Much of the meadow has

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been invaded by conifers in the last 30 years, probably due to fire suppression. As a result, the riparian zone is currently dominated by generalist and edge species of birds, including American Robin (*Turdus migratorius*), Chipping Sparrow (*Spizella passerina*), and Dark-eyed Junco (*Junco hyemalis*). To estimate nest success of potentially occurring riparian species, such as Song Sparrow (*Melospiza melodia*), Lincoln's Sparrow (*M. lincolnii*) and Warbling Vireo (*Vireo gilvus*), we placed additional artificial nests simulating those of willow-nesting species into two types of willows, those adjacent to the stream and old willow remnants far from the stream. Extensive old-willow stands existed distant from the stream on both sides of the fence. The old-willow experiment thus served to control for nest site availability which was expected to be reduced in the willows directly adjacent to the stream, because grazing is commonly associated with reduced willow cover along the stream (Knopf and Cannon 1982, Schulz and Leininger 1990).

Because livestock was absent during the year of the study, immediate effects of livestock on reproductive success, such as disturbance of ground nests, removal of cover of active nests, or attraction of nonresident predators or cowbirds (*Molothrus ater*) could be excluded in this study. Therefore, rather than examining such direct impacts of grazing, our study was designed to assess more permanent effects of livestock on habitat and bird populations.

METHODS

STUDY AREA

The study was conducted along Franktown Creek in Little Valley, located at 1,920 m in the Carson Range 35 km south of Reno, Nevada. The valley contains a single 70–80 ha meadow that traditionally had been summer-grazed with cattle and sheep. Thirty years ago, roughly half of the site was obtained by the University of Nevada and has been rested since, while the other half continued to be grazed (typically 24 cow-calf units from 8 June to 7 August). The grazed and the rested side are about 25–30 ha in size and surrounded by mature lodgepole pine (*Pinus contorta*), Jeffrey pine (*P. jeffreyi*), and white fir (*Abies concolor*) forest. The woody vegetation along Franktown Creek consists of willows (*Salix* spp., predominantly *S. geyeri-*

ana), whereas the ground cover in the surrounding meadows is interspersed with sagebrush (*Artemisia* spp.) in dry areas and willows in wet areas. In addition, possibly as a result of fire suppression, the entire site has been invaded by lodgepole pine in the past 30 years, which now dominates large parts of the valley. The bird assemblage consisted of, in descending order of abundance, Chipping Sparrow, Dark-eyed Junco, American Robin, Warbling Vireo, Cassin's Finch (*Carpodacus cassinii*), Yellow-rumped Warbler (*Dendroica coronata*), Song Sparrow, Brown-headed Cowbird, Brewer's Blackbird (*Euphagus cyanocephalus*), Red-winged Blackbird (*Agelaius phoeniceus*), and Lincoln's Sparrow. Nest predators were identified by tooth and bill imprints on artificial eggs, which were compared to bill and teeth of specimens of potential nest predators seen in the study area, and by direct observations. Predators documented in this way included small rodents (probably mostly yellow pine chipmunk, *Tamias amoenus*), red squirrel (*Tamiasciurus hudsonicus*), and Steller's Jay (*Cyanocitta stelleri*). Other potential predators observed at the site were House Wrens (*Troglodytes aedon*), garter snakes (*Thamnophis* spp.), coyotes (*Canis latrans*), black bears (*Ursus americanus*), long-tailed weasels (*Mustela frenata*), Belding's ground squirrels (*Spermophilus beldingi*), and domestic dogs (*Canis familiaris*).

DATA COLLECTION

We sampled the riparian vegetation (0–50 m from the stream) in July 1994. We used a 1 m² frame that was subdivided into 25 squares. In each square we estimated the predominant vegetation type at ground level, categorized into "bare ground," "ground vegetation" (i.e., graminoids and forbs), "willows," "conifers," and "other." In addition, we categorized the top vegetation layer at one corner of the vegetation frame as follows: ground cover (<50 cm), shrub layer (50–300 cm), and overstory (>300 cm). Ninety-five samples were taken on both the grazed and the rested side at 0, 10, 20, and 50 m from the stream in 100 m increments (0–600 m on one side and 50–550 m on the other side of the stream) from the fence, which subdivided the meadow across the stream.

Nest searches were conducted throughout the summer of 1994, starting in early May. We located nests of American Robin, Dark-eyed

Junco, Chipping Sparrow, Brewer's Blackbird, Song Sparrow, Lincoln's Sparrow, and Warbling Vireo by following adults returning to the nest and searching the vegetation. All natural nests were monitored during visits every 3–5 days until they either failed or the young fledged. In the artificial nest experiments we placed a total of 240 artificial nests at 0–650 m from the fence using the following three designs.

First, 30 ground and 30 above-ground nests were placed on the grazed and on the rested plot within 50 m of the stream simulating natural placements of Dark-eyed Junco, American Robin, and Chipping Sparrow nests (generalist and edge species currently dominating the community). Second, to measure nest success of potential riparian breeders, an additional 15 ground and 15 above-ground nests were placed in willows on the bank within 15 m of the stream on the grazed and on the rested plot (streamside-willow experiment). Finally, to determine if predation patterns can be attributed exclusively to streamside vegetation loss, an additional 15 ground and 15 above-ground nests were placed in old willow stands (>4 m in height) located >100 m from the stream on the grazed and the rested plot (old-willow experiment). In this experiment, nests were paired across the fence based on similarity of the substrate patch. In both willow experiments we simulated nest placements of riparian species, such as Song Sparrow and Warbling Vireo; sample sizes and densities of nests used in these two experiments were low in order to minimize density-dependent effects on predation in the existing narrow riparian zone.

All artificial nests were made from hardware mesh and dry sedge material from the study site and were baited with one Japanese Quail (*Coturnix japonica*) egg and one plasticine egg sprayed with paint to resemble the quail egg. Because of generally high predation rates, exposure times of the artificial nests were 10 days for the first experiment and 8 days for the two willow experiments. Although incubation in most passerines lasts slightly longer than the exposure periods used here, and many untested assumptions must be made when using artificial nests to measure avian nest success (e.g., absence of attending adults, no nestling period, etc.), the purpose of using artificial nests in our study was not to provide

an accurate quantitative measure of predation on real nests, but rather to explore patterns of nest predation in presence and absence of grazing.

Artificial and real nests in which eggs or young were damaged or disappeared were considered "preyed upon." All nests were visited in 3–4 day intervals, and predation events were assumed to occur at the midpoint in time between two visits. Nests were considered "successful" when, in real nests, offspring fledged after no losses to predators and, in artificial nests, when the nest was undisturbed at the end of the exposure period.

DATA ANALYSIS

To compare the vegetation of the grazed and rested plots, logistic regression was performed using all vegetation-type variables, except for the category "other," as predictor variables and "grazed"/"rested" as the response variable. In addition, pairwise comparisons between treatments were made for each vegetation-type variable using Wilcoxon two-sample tests. Frequency distributions of vegetation height categories were compared between the grazed and rested side using a 2×3 contingency table. All of the above procedures were performed using the SAS statistical package (SAS Institute 1988). As the setting of the study entailed an unreplicated design, statistical comparisons were performed primarily for description of the plots used in this study rather than for rigorous hypothesis testing or for generalizing across different study areas.

Nest success of artificial and real nests was measured using the Mayfield (1975) method, in which the probability of nest survival per day is calculated based on the number of nests preyed upon and the number of days nests were exposed to predation. Of the real nests, only those which were either successful or lost to predation were included (abandoned nests were excluded). All nests were combined into two nesting guilds: ground nests ($n = 19$) and above-ground nests ($n = 21$). Separate analyses were performed for each nest type and experiment. Pairwise comparisons of nest success between grazed and rested plots were conducted using the variance estimate for daily survival probability and hypothesis testing according to Hensler and Nichols (1981).

TABLE 1. Vegetation differences between grazed and rested portions of Little Valley. Listed are mean numbers of 20 × 20 cm squares in a 1 m² frame predominantly covered by the vegetation type, sampled at 0, 10, 20, and 50 m from the stream.

Distance from stream (<i>n</i> _{grazed} ; <i>n</i> _{ungrazed})	Vegetation type	Mean number of squares (±SE)		Probability of across-fence difference ^a
		grazed	rested	
at stream (12; 12)	bare ground	3.4 ± 1.9	1.6 ± 1.0	0.61
	ground vegetation	19.7 ± 1.8	17.2 ± 1.7	0.18
	willows	0.6 ± 0.4	1.7 ± 0.5	0.03
	conifers	0.1 ± 0.1	0.0 ± 0.0	0.36
10 m (11; 12)	bare ground	2.2 ± 1.6	2.3 ± 1.4	0.85
	ground vegetation	21.2 ± 2.3	15.5 ± 2.8	0.08
	willows	0.0 ± 0.0	0.0 ± 0.0	0.99
	conifers	0.0 ± 0.0	0.0 ± 0.0	0.99
20 m (12; 12)	bare ground	0.2 ± 0.1	1.2 ± 0.6	0.49
	ground vegetation	21.4 ± 1.8	17.2 ± 2.3	0.16
	willows	0.0 ± 0.0	0.0 ± 0.0	0.99
	conifers	0.0 ± 0.0	0.0 ± 0.0	0.99
50 m (12; 12)	bare ground	0.7 ± 0.4	1.9 ± 0.9	0.35
	ground vegetation	22.9 ± 0.8	14.6 ± 2.5	0.02
	willows	0.0 ± 0.0	0.0 ± 0.0	0.99
	conifers	0.0 ± 0.0	0.5 ± 0.4	0.17

^a according to Wilcoxon two-sample test.

RESULTS

VEGETATION

Pairwise comparisons of vegetation variables showed a greater abundance of stream-side willows (0–15 m from stream) on the rested side than the grazed side of Little Valley (Table 1). Sample plots at all distances from the stream showed a trend toward greater cover of ground vegetation on the grazed than on the rested side. Logistic regression indicated a significant overall difference in vegetation structure between the grazed and rested plot (likelihood ratio $\chi^2_4 = 18.8$, $P < 0.001$; 70.6% concordance of the observed responses with the model's predicted probabilities). A larger proportion of sample plots had the shrub layer or overstory as the highest vegetation layer on the rested

TABLE 2. Frequency distribution and percent of vegetation samples on the grazed and rested portion of Little Valley in three vegetation height classes: ground cover, shrub layer, and overstory.

Plot	Vegetation height			Total
	<50 cm	50–30 cm	>300 cm	
Rested	25 (52%)	7 (15%)	16 (33%)	48 (100%)
Grazed	41 (80%)	6 (12%)	4 (8%)	51 (100%)
Total	66	13	20	99

compared to the grazed side (Table 2; $\chi^2_1 = 11.1$, $P < 0.01$).

NEST PREDATION

Success of both ground and above-ground real nests was overall lower on the grazed than on the rested portion of Little Valley (Table 3). Of the above-ground nests, 83% ($n = 6$) were preyed upon on the grazed side compared to 36% ($n = 14$) on the rested side. Of the ground nests, 67% ($n = 12$) were lost on the grazed side compared to 43% ($n = 7$) on the rested side. Artificial above-ground nests of the generalist and edge species types and above-ground nests in streamside willows simulating nests of riparian species had significantly lower survival on the grazed than on the rested plot, whereas artificial ground nests on the two plots showed no difference in survival. In the old willow remnants, both above-ground and ground nests simulating nests of riparian species had lower survival on the grazed than on the rested plot (Table 3). The artificial nests, particularly in above-ground placements, indicated a larger difference in nest success between the grazed and the rested plot than did the real nests. However, the direction of the trend (higher predation on the grazed than the rested side) was the

TABLE 3. Daily survival probability of artificial and real nests, according to Mayfield (1975), on the grazed and rested side of Little Valley.

Nest type and location	$(n_1; n_2)^b$	Daily survival probability (v^2)		z-value	Probability ^a
		Grazed	Rested		
Real nests					
ground	(12; 7)	0.923 (0.000677)	0.965 (0.000383)	1.29	n.s.
above-ground	(6; 14)	0.935 (0.000779)	0.977 (0.000104)	1.39	n.s.
combined	(18; 21)	0.928 (0.000364)	0.974 (0.000085)	2.13	*
Artificial nests					
generalist and edge sites					
ground	(30; 30)	0.939 (0.000290)	0.953 (0.000212)	0.61	n.s.
above-ground	(30; 30)	0.780 (0.001513)	0.955 (0.000212)	4.23	***
stream willows					
ground	(15; 15)	0.947 (0.000437)	0.967 (0.000264)	0.74	n.s.
above-ground	(15; 15)	0.659 (0.005485)	0.864 (0.001338)	2.48	**
old willows					
ground	(15; 15)	0.908 (0.000960)	0.977 (0.000175)	2.04	*
above-ground	(15; 15)	0.548 (0.007989)	0.773 (0.003305)	2.12	*

^a n.s. = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

^b n_1 = number of nests on grazed side; n_2 = number of nests on rested side.

same for all nest types across all comparisons (Table 3).

DISCUSSION

Because of the interdependence of communities along riparian corridors and the large geographic scale entailed in responses of bird populations to a disturbance, studies of grazing effects on riparian birds often lack the usual desired degree of replication (e.g., Mosconi and Hutto 1982, Schulz and Leininger 1990). Our study is not different in this respect. However, we believe that under these circumstances, case studies such as ours are indispensable for determining general impacts of large-scale perturbations, such as grazing, by using accumulated evidence from independent studies. Recent reviews of grazing effects on bird populations (e.g., Bock et al. 1993, Ohmart 1994, Saab et al. 1995) show that general patterns can be derived using such an across-study approach.

Streamside willow cover was significantly reduced on the grazed side compared to the rested side of Little Valley, corroborating findings of other studies on the effects of grazing (Schulz and Leininger 1990, Elmore 1992). Because cattle forage on willows (Knopf and Cannon 1982, Kauffman and Krueger 1984) and spend a disproportionately greater amount of time at the streamside than in upland sites (Van Vuren 1982), willow reduction through browsing,

trampling, and erosion is expected as a result of long-term grazing regimes. Strictly riparian birds, such as Lincoln's Sparrow, Willow Flycatcher (*Empidonax traillii*), and Wilson's Warbler (*Wilsonia pusilla*), have indeed been found to respond negatively to grazing (Taylor 1986, Schulz and Leininger 1990), although this is true of all riparian species (Knopf et al. 1988). The negative impact of grazing could be a direct response to the loss of nesting and foraging habitat (i.e., willows) and, at least in part, a result of indirect effects such as increased nest predation.

Vertical diversity of vegetation was reduced on the grazed side of Little Valley compared to the rested side; in 80% of the samples of the grazed plot the vegetation was below 50 cm and only 8% had an overstory of >300 cm (Table 2). This finding suggests a possible link between grazing and bird populations, because vegetational diversity is not only an important predictor of avian diversity (MacArthur and MacArthur 1961), but also of nest predation rates in birds (Bowman and Harris 1980, Martin and Roper 1988).

Success of real and artificial nests was overall lower on the grazed side of Little Valley compared to the rested side. Previous studies have reported that grazing affected foraging guilds of birds differentially, suggesting that grazing impacts may depend upon the

foraging ecology of birds (Mosconi and Hutto 1982). Our results indicate an additional mechanism, i.e., increasing predation pressure, through which bird populations may be negatively affected by long-term grazing regimes.

Because livestock was not present on the grazed plot in the year of the study, the herbaceous layer had one year to recover from grazing. As a result, ground vegetation cover near the stream was more abundant on the grazed compared to the rested plot. Ground nests did not suffer greater losses on the grazed relative to the rested plot of Little Valley in two of the artificial nest experiments. Greater cover by ground vegetation on the grazed plot may best explain this finding, because concealment and structural heterogeneity at the nest should be greater where ground vegetation is dense. However, in the old-willow experiment, nest success of both nest types was reduced on the grazed compared to the rested plot, suggesting that other mechanisms that determine nest predation rates also are affected by livestock grazing. These mechanisms may include changes in the presence and abundance of predator species due to the traditional use of the sites by livestock and changes in predator behavior, such as search behaviors and incidental nest detection, in response to habitat modifications from grazing. For example, as willow patches may be more clumped as a result of livestock grazing (Knopf and Cannon 1982), nesting substrates of riparian birds should become more accessible to predators.

Our results suggest that the effects of grazing on nest success of riparian birds may be at least two-fold. First, by reducing the willow cover adjacent to the stream (Table 1), grazing may lead to greater predation rates by decreasing the availability of suitable microhabitats for nests of strictly riparian species (e.g., Song Sparrow and Yellow Warbler, *Dendroica petechia*). Second, we found that nest success remained lower on the grazed compared to the rested side in the old-willow experiment, in which we controlled for the effect of nest site availability by pairing nests across the fence based on substrate similarity. This suggests that additional factors contributed to a reduction in nest success on the grazed plot, such as differences in macrohabitat structure that lead to higher incidental predation, changes in the com-

position of the predator assemblage, or changes in predator search strategies.

The discrepancy between the findings for real and artificial nests, the latter showing a greater treatment effect on above-ground nest success than in real nests, suggests that caution must be exercised in the exclusive use of artificial nests for the study of avian nest success (see also Willebrand and Marström 1988, Ammon 1995). If nest predation patterns ascertained with artificial nests are not corroborated using samples of real nests, then false conclusions may be drawn about predation regimes in natural communities (for a review, see Ammon 1995). Nevertheless, although the artificial nests did not provide a quantitative estimate of predation on real nests, they did serve as a general index for predation differences, as the direction of the trends was consistent among all groups of real and artificial nests.

In conclusion, nest predation is one of the potential causal links between long-term grazing regimes and population declines in western riparian birds. We therefore propose that, in addition to documenting effects on foraging and nesting habitat availability, parameters important to predation, e.g., habitat variables involved in nest detection, composition and abundance of predators, and predator behaviors, also should be examined in studies of grazing effects on bird populations. The implications of our findings for management of riparian habitats include: (1) natural nest predation patterns are altered by livestock grazing and may not be immediately restored after livestock removal. Long-term changes in vegetation structure and possibly in the predator assemblage may reduce nest success even in the absence of livestock. (2) In addition to preserving suitable nesting and foraging habitats for riparian birds, management of riparian communities also should include consideration of nest predation patterns, which could be altered by livestock grazing to a similar degree as documented for other large-scale disturbances.

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