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INFLUENCE OF BEAVER DAM DENSITY ON RIPARIAN AREAS AND RIPARIAN BIRDS IN SHRUBSTEPPE OF WYOMING

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ABSTRACT.—Through dam-building activity, beavers (*Castor canadensis*) play an important role in creating pond and wetland habitat for bird communities. Their impact may be intensified in semiarid landscapes and may increase with increasing dam density on a stream. Our objective was to examine relationships between dam density, riparian area characteristics, and the riparian bird community in a semiarid landscape. In 2002 and 2003 we surveyed riparian birds, riparian area characteristics, and the number of dams along 1.2-km sections of 11 streams in sagebrush steppe regions of Wyoming. We categorized the riparian bird community into 2 assemblages based on their affiliation with terrestrial or aquatic riparian habitats. Average width of the woody riparian zone, average riparian shrub height, and percent cover of emergent vegetation all had significant positive relationships with dam density, but percent cover of ponded water did not. Species richness and abundance of all riparian birds, and of the terrestrial assemblage, increased significantly with increasing woody riparian zone width. In contrast, richness and abundance of the aquatic assemblage were significantly positively influenced by cover of emergent vegetation and ponded water. When we accounted for riparian area characteristics, we found that total species richness, total abundance, and aquatic assemblage abundance were each positively correlated with dam density, suggesting that dam density is related to other riparian characteristics selected by birds. Our results suggest increasing dam-building activity may be important in creating favorable riparian conditions for a rich and abundant bird community in semiarid regions.

Key words: beaver dams, riparian habitat, riparian birds, riparian width, emergent vegetation, ponds, waterfowl, beaver reintroduction, shrubsteppe, Wyoming.

Beavers (*Castor canadensis*) are ecosystem engineers, constructing dams that impound water, trap sediment, and increase the productivity of riparian zones (Rosell et al. 2005). The value of beaver ponds and associated wetlands to riparian birds, particularly waterfowl, has been well documented for forested regions of eastern North America (e.g., Renouf 1972, Grover and Baldassarre 1995, Edwards and Otis 1999, Bulluck and Rowe 2006). Less is known about the impact of beaver dam-building on riparian birds in semiarid regions of western North America (but see Medin and Clary 1990, Brown et al. 1996, McKinstry et al. 2001). The paucity of studies examining the influence of beaver dams on riparian birds in semiarid landscapes of western North America is surprising given that riparian habitat in these regions is critical to a diverse group of birds and accounts for <1% of the landscape (Knopf et al. 1988).

Within the home range of a beaver colony, the density of dams increases as new dams are constructed yearly and as a growing colony requires a larger complex of ponds and canals (Grasse 1951, Novak 1987). Associated with an increase in dam density is an increase in retention of sediment and water, an expansion of the riparian zone, and an increase in heterogeneity of riparian vegetation (Naiman et al. 1988, Johnston and Naiman 1990, Rosell et al. 2005). The value of single beaver impoundments to birds has been well demonstrated (e.g., Renouf 1972, Medin and Clary 1990, Brown et al. 1996, Edwards and Otis 1999, Bulluck and Rowe 2006), yet no studies have examined the value of varying levels of dam density to the riparian bird community.

Our objective was to examine relationships between increasing dam density and characteristics of the riparian area and richness and abundance of the riparian bird community along streams in the sagebrush-steppe region of Wyoming. Given that riparian birds respond positively to increasing size and availability of ponds, wetlands, and riparian shrub patches in areas both with and without beaver activity (Grover and Baldassarre 1995, Sanders and Edge 1998, Edwards and Otis 1999, Scott et al. 2003), increases in dam density should be

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positively correlated with increases in the abundances of birds that are tied to both the aquatic and terrestrial components of riparian areas. We first examined the relationship between dam density and 4 characteristics of the riparian zone: emergent vegetation cover, pond cover, and width and height of the woody riparian zone. We expected each characteristic to be positively correlated with dam density. We then evaluated the separate effects of riparian characteristics and dam density on the richness and abundance of the riparian bird community. We did 2 levels of analysis: 1 included all species with riparian affiliations and the other distinguished 2 assemblages based on their terrestrial or aquatic affiliation for nesting and foraging. The former assemblage included landbirds classified as riparian-associated by Rich (2002). These species are dependent primarily on herbaceous and woody riparian vegetation during the breeding season. The latter assemblage included waterfowl, rails, and shorebirds that depend on herbaceous vegetation and/or ponds during the breeding season. We expected species richness and abundance of all riparian birds to increase with increases in emergent vegetation cover, ponded water, and width and height of the woody riparian zone. We expected the terrestrial assemblage to show a stronger response to differences in the width and height of the woody riparian zone and the aquatic assemblage to respond more to differences in the amount of ponded water and emergent vegetation.

METHODS

Study Sites

Wyoming is a semiarid region with a climate characterized by long winters, short growing seasons, and low annual precipitation. Our study sites were located within the counties of Sweetwater, Carbon, and Fremont in central and southern Wyoming. At Rawlins, Wyoming (central to our study sites), for the period 1948–2006, the mean maximum temperature for June was 23.8°C, and the mean annual precipitation was 20.8 cm (Western Regional Climate Center, http://www.wrcc.dri.edu). Elevation within the study area ranged from 1750 to 2400 m.

We identified study sites with the assistance of land managers from the Bureau of Land Management and the Wyoming Game and Fish Department. We considered potential study sites to be perennial streams located in sagebrush (*Artemisia* spp.) steppe landscapes that either currently or historically supported beaver dam-building activity. We visited these sites in May of each year of the study to determine levels of dam-building activity. We were constrained logistically and financially in the number of sites we could sample each year. We therefore chose to maximize the efficiency of our sampling design by selecting sites exhibiting a gradient in the number of dams, thus ensuring sufficient variation in dam density to address our research objective (Guisan and Zimmermann 2000). As most of this region is or has been subject to grazing, we were unable to exclude sites based on grazing history and therefore assumed that the effect of livestock grazing was similar across sites.

We sampled 11 study sites: 4 in 2002 and 7 in 2003. All sites were on 1st- and 2nd-order streams, which ranged in width at unimpounded points from approximately 0.50 to 3.0 m. Woody riparian vegetation at all sites was predominantly willow (*Salix* spp.) but also included alder (*Alnus* spp.), trembling aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), rose (*Rosa* spp.), gooseberry (*Ribes* spp.), and chokecherry (*Prunus* spp.). These species occurred primarily as shrubs (0.5–5.0 m in height). Riparian trees (woody vegetation >5 m in height) accounted for <5% of cover on the 2 sites where they occurred. Herbaceous cover within the riparian zone was predominantly grasses followed by rushes, forbs, sedges, and cattails. Upland habitat was dominated by sagebrush.

At each study site, a 1200-m transect was positioned directly adjacent and parallel to the stream. Five sampling points were located 250 m apart along each transect. On streams that were accessed where a road crossed the stream, the 1st sampling point was randomly located at least 100 m from the road to avoid including the road in the study site. On streams without road crossings, the 1st sampling point was randomly located within the area of beaver activity and at least 100 m from a property boundary to ensure the transect did not cross from public to private lands. Two study sites (RCAN and DEEP) were located on 1 stream and separated by 2.5 km, and 2 sites (CURA and CURB) were located on 1 stream and separated by 3.5 km. The other sites all occurred on separate streams.

Bird Community

We surveyed the riparian bird community at each sampling point using point-count methods (Ralph et al. 1993). All birds observed by sight or sound within 50 m of the sampling point were counted during a 5-minute period. Surveys were initiated within 1 hour after sunrise and completed within 4 hours after sunrise. Surveys were repeated 2 times at least 7 days apart between 5 June and 15 June in each year. Bird surveys were conducted by 5 observers who were rotated among sites. We did not conduct surveys during rainy or windy conditions.

For the terrestrial bird assemblage, we excluded 2 species classified as riparian obligates by Rich (2002): the American Dipper (*Cinclus mexicanus*) because its affiliation with riparian areas is based on water condition, not vegetation (Kingery 1996), and the Bank Swallow (*Riparia riparia*) because its riparian affiliation is to banks, not vegetation (Garrison 1999). Killdeer (*Charadrius vociferus*) is affiliated with water, but we removed it from the aquatic assemblage because it may nest quite far from the riparian area and does not use water habitats directly (Jackson and Jackson 2000).

Riparian Area Characteristics

We measured 4 characteristics of the riparian zone at each sampling point: average distance that woody riparian vegetation extended across the floodplain perpendicular to the stream channel (hereafter woody riparian zone width), average height of the riparian shrub layer, percent cover of emergent vegetation, and percent cover of ponded water. Emergent vegetation was defined as woody and herbaceous riparian vegetation emerging from the water surface. Ponded water was classified as open water (i.e., without emergent vegetation) located upstream of a dam and extending out into the floodplain beyond the width of the unimpounded stream channel. Woody riparian zone width and riparian shrub height were measured within a sampling area that encompassed the riparian zone 50 m upstream and downstream of each sampling point. To measure woody riparian zone width, the observer first used a Bushnell Yardage Pro 500 range finder to measure width at 3–5 random locations within the sampling area. These measurements were then used to calibrate a visual estimate of average width for the entire sampling area. We calibrated the visual estimate with measurements made using the range finder in order to minimize any bias in a visual estimate that could occur due to observer knowledge of dam density. In the same manner, we visually estimated average riparian shrub height for the sampling area and calibrated this estimate using a 3-m PVC pipe marked at 0.25-m intervals. We visually estimated percent cover of ponded water and emergent vegetation within a 50-m radius of each sampling point. A single observer made all measurements.

We determined dam density by searching for all intact dams (active and inactive) along the stream and within the floodplain of each study site. Incomplete or degraded dams, which were not impounding water, were not included. Dams were considered active if newly cut vegetation, fresh mud, or fresh beaver trails were observed on them. The total number of dams per site was recorded from a section of stream with a straight-line distance of 1200 m, regardless of the sinuosity or braiding of the stream channel.

Data Analyses

Ponded water cover, emergent vegetation cover, riparian shrub height, and woody riparian zone width were averaged across sampling points for each study site. Since both active and inactive intact dams function similarly to impound water, we combined counts of both and used the total number of dams on a study site in all analyses. We calculated bird species richness for each study site as the total number of species observed in each assemblage across all sampling points and for both visits. We calculated bird abundance for each study site as the sum of the maximum number of detections of each species at each sampling point over both visits. Differences in detectability of birds due to behavior (e.g., singing rates) and environmental conditions (e.g., vegetation structure) can result in biased estimates of abundance (Rosenstock et al. 2002). Distance methods are used to calculate probability of detection of a species but were not feasible for any species in our study, as they require large sample sizes ($n > 40$). Our point counts were not divided into time intervals and thus we could not use removal models to calculate detection functions (Farnsworth et al. 2002). However, our use of a fixed-radius

TABLE 1. Mean, standard deviation (*s*), minimum (min) and maximum (max) abundance of birds detected on point-count surveys of 1.2-km sections of 11 streams in a shrubsteppe region of Wyoming. See text for description of assemblages.

Assemblage	Species	Mean	*s*	Min	Max
Aquatic	Cinnamon Teal (*Anas cyanoptera*)	0.18	0.60	0	2
Aquatic	Wilson's Snipe (*Gallinago delicata*)	0.45	0.93	0	3
Aquatic	Gadwall (*Anas strepera*)	0.09	0.30	0	1
Aquatic	Green-winged Teal (*Anas crecca*)	0.73	2.10	0	7
Aquatic	Mallard (*Anas platyrhynchos*)	2.27	3.61	0	12
Aquatic	Sora (*Porzana carolina*)	0.09	0.30	0	1
Terrestrial	American Goldfinch (*Carduelis tristis*)	1.00	1.90	0	6
Terrestrial	Bank Swallow (*Riparia riparia*)	0.09	0.30	0	1
Terrestrial	Black-capped Chickadee (*Poecile atricapillus*)	0.27	0.65	0	2
Terrestrial	Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.18	0.60	0	2
Terrestrial	Blue Grosbeak (*Passerina caerulea*)	0.18	0.40	0	1
Terrestrial	Bullock's Oriole (*Icterus bullockii*)	0.36	0.81	0	2
Terrestrial	Common Yellowthroat (*Geothlypis trichas*)	0.82	1.08	0	3
Terrestrial	Fox Sparrow (*Passerella iliaca*)	0.27	0.65	0	2
Terrestrial	Gray Catbird (*Dumetella carolinensis*)	0.18	0.40	0	1
Terrestrial	House Wren (*Troglodytes aedon*)	0.18	0.60	0	2
Terrestrial	Lazuli Bunting (*Passerina amoena*)	0.45	0.69	0	2
Terrestrial	MacGillivray's Warbler (*Oporornis tolmiei*)	0.64	1.43	0	4
Terrestrial	Song Sparrow (*Melospiza melodia*)	6.73	3.80	1	14
Terrestrial	Warbling Vireo (*Vireo gilvus*)	1.55	2.07	0	6
Terrestrial	Western Wood-Pewee (*Contopus sordidulus*)	0.36	0.92	0	3
Terrestrial	Willow Flycatcher (*Empidonax traillii*)	0.27	0.65	0	2
Terrestrial	Wilson's Warbler (*Wilsonia pusilla*)	0.09	0.30	0	1
Terrestrial	Yellow-breasted Chat (*Icteria virens*)	1.00	1.84	0	6
Terrestrial	Yellow Warbler (*Dendroica petechia*)	7.09	4.76	0	13
Non-riparian	American Crow (*Corvus brachyrhynchos*)	0.09	0.30	0	1
Non-riparian	American Dipper (*Cinclus mexicanus*)	0.09	0.30	0	1
Non-riparian	American Robin (*Turdus migratorius*)	3.27	2.69	0	7
Non-riparian	Barn Swallow (*Hirundo rustica*)	0.18	0.60	0	2
Non-riparian	Black-billed Magpie (*Pica hudsonia*)	0.55	1.81	0	6
Non-riparian	Brown-headed Cowbird (*Molothrus ater*)	3.45	3.05	0	9
Non-riparian	Brewer's Blackbird (*Euphagus cyanocephalus*)	1.36	1.86	0	5
Non-riparian	Brewer's Sparrow (*Spizella breweri*)	1.91	2.02	0	6
Non-riparian	Chipping Sparrow (*Spizella passerina*)	0.09	0.30	0	1
Non-riparian	Clark's Nutcracker (*Nucifraga columbiana*)	0.09	0.30	0	1
Non-riparian	Cordilleran Flycatcher (*Empidonax occidentalis*)	0.09	0.30	0	1
Non-riparian	Common Raven (*Corvus corax*)	0.27	0.65	0	2
Non-riparian	Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.09	0.30	0	1
Non-riparian	Dusky Flycatcher (*Empidonax oberholseri*)	1.18	1.89	0	5
Non-riparian	Green-tailed Towhee (*Pipilo chlorurus*)	3.27	3.07	0	9
Non-riparian	Killdeer (*Charadrius vociferus*)	0.18	0.60	0	2
Non-riparian	Mountain Bluebird (*Sialia currucoides*)	0.27	0.90	0	3
Non-riparian	Mourning Dove (*Zenaida macroura*)	0.55	0.69	0	2
Non-riparian	Northern Flicker (*Colaptes auratus*)	0.18	0.40	0	1
Non-riparian	Northern Harrier (*Circus cyaneus*)	0.18	0.40	0	1
Non-riparian	Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	0.64	1.21	0	3
Non-riparian	Dark-eyed Junco (*Junco hyemalis*)	0.18	0.60	0	2
Non-riparian	Pine Siskin (*Carduelis pinus*)	0.45	1.51	0	5
Non-riparian	Rock Wren (*Salpinctes obsoletus*)	0.27	0.47	0	1
Non-riparian	Red-winged Blackbird (*Agelaius phoeniceus*)	3.36	4.78	0	13
Non-riparian	Spotted Towhee (*Pipilo maculatus*)	1.36	3.04	0	8
Non-riparian	Vesper Sparrow (*Pooecetes gramineus*)	0.18	0.60	0	2
Non-riparian	Violet-green Swallow (*Tachycineta thalassina*)	0.64	0.92	0	2
Non-riparian	White-crowned Sparrow (*Zonotrichia leucophrys*)	1.27	3.13	0	10
Non-riparian	Western Meadowlark (*Sturnella neglecta*)	0.82	1.83	0	6
Non-riparian	Western Tanager (*Piranga ludoviciana*)	0.27	0.65	0	2
Non-riparian	White-throated Swift (*Aeronautes saxatalis*)	0.09	0.30	0	1

TABLE 2. Parameter estimate and standard error (b [$s_{\bar{x}}$]), odds ratio with 95% confidence interval (C.I.), and ANOVA results for univariate linear regressions of each characteristic of riparian habitat against density of beaver dams along 11 streams in a shrubsteppe region of Wyoming.

	b ($s_{\bar{x}}$)	$F_{1,9}$	P	R^2	Odds ratio	95% C.I. of odds ratio
Woody riparian zone width	0.692 (0.211)	10.79	0.01	0.55	1.99	1.59–2.41
Riparian shrub height	0.021 (0.006)	14.43	0.01	0.62	1.02	1.01–1.03
Ponded water cover	0.101 (0.066)	2.35	0.16	0.21	1.11	0.98–1.24
Emergent vegetation cover	0.175 (0.065)	7.34	0.02	0.45	1.19	1.06–1.32

(50 m) point count reduced differences in detectability due to vegetation structure (Schieck 1997, Hutto and Young 2003), and our calculation of species richness and maximum abundance from 2 visits increased the likelihood of detecting individuals (Tozer et al. 2006).

We addressed 3 objectives with our data analysis. We examined (1) relationships between dam density and each riparian characteristic, (2) relationships between all riparian characteristics and the bird community, and (3) relationships between dam density and the bird community. For all analyses of the bird community, we examined species richness and abundance for each assemblage separately and combined. For the 1st objective, we used univariate linear regression to examine the relationship between each riparian characteristic (dependent variables) and total number of dams (independent variable). Data for all riparian characteristics met assumptions of normality so were not transformed for this analysis. For the 2nd objective we first examined Pearson's correlation coefficients for all pairs of riparian characteristics and excluded 1 variable from future analyses when $r > 0.70$ (Quinn and Keough 2002). We modeled all bird-riparian characteristic relationships using generalized linear models (GLM) with a quasi-likelihood function. We used quasi-likelihood estimation because species richness and abundance are count data and the dispersion parameter for our models ranged between 0.5 (underdispersed) and 5.5 (overdispersed; Quinn and Keough 2002). We included year as a categorical covariate in all models to account for variation in species richness or abundance due to regional population trends associated with the year in which a site was surveyed. To identify riparian characteristics that contributed significantly to each model, we used likelihood ratio (G^2-statistic) tests to compare the deviance of the full model (all riparian characteristics) to the deviance of a model with each characteristic removed in turn. After removing nonsignificant variables, we used Wald tests to evaluate the significance of parameter coefficients in the final model, and we evaluated the strength of each model using D^2, which is a measure of the percent deviance explained (D^2 = [null deviance – residual deviance]/null deviance; Guisan and Zimmermann 2000). For the 3rd objective, we used partial correlation coefficients to examine correlations between dam density and each bird community measurement while accounting for the effects of any significant riparian characteristics. All analyses were conducted using S-Plus 2000 (Mathsoft, Inc. 2000) and NCSS (Hintze 2001) software.

RESULTS

We observed 59 species across all study sites, of which 6 were classified in the aquatic riparian assemblage and 19 were classified in the terrestrial riparian assemblage (Table 1). The total number of riparian species per study site ranged between 4 and 14, with abundances ranging from 10 to 59. The number of terrestrial riparian species per study site ranged between 2 and 12, with abundances ranging between 10 and 46. The number of aquatic riparian species per study site ranged between 0 and 4, with abundances ranging between 0 and 13. The total number of beaver dams per study site ranged between 0 and 62. Total number of dams was a significant predictor of woody riparian zone width, riparian shrub height, and percent cover of emergent vegetation (Table 2).

Woody riparian zone width and riparian shrub height were highly correlated ($r = 0.79$) and therefore only width, ponded water, and emergent vegetation were included in the bird-riparian characteristic models. In the models for both total riparian species richness and total riparian abundance, woody riparian zone width was the only variable that contributed

TABLE 3. Results of G^2 (likelihood ratio) tests examining the relative importance of each riparian variable in 3-variable models for the riparian bird community along 11 streams in a shrubsteppe region of Wyoming.

	Woody riparian zone width		Ponded water cover		Emergent vegetation cover	
	G^2	P	G^2	P	G^2	P
Total species richness	5.91	0.02	0.04	0.84	0.16	0.69
Total abundance	45.27	<0.01	2.57	0.11	2.02	0.16
Terrestrial assemblage species richness	14.56	<0.01	1.59	0.21	1.71	0.19
Terrestrial assemblage abundance	44.8	<0.01	0.53	0.47	0.15	0.7
Aquatic assemblage species richness	0.41	0.52	4.75	0.03	6.35	0.01
Aquatic assemblage abundance	10.74	<0.001	7.19	0.01	12.05	<0.001

significantly to model deviance (Table 3). Thus, final models for total richness and abundance included width as the only variable, and it explained 53% of the deviance in total richness and 81% of the deviance in total abundance among sites (Table 4). Similarly, woody riparian zone width contributed significantly to model deviance for both richness and abundance of the terrestrial assemblage, but cover of ponded water and emergent vegetation did not (Table 3). Thus, the final models for both terrestrial assemblage species richness and abundance included only riparian zone width; these models explained 49% and 90% of the variation in terrestrial species richness and abundance, respectively (Table 4). Ponded water and emergent vegetation cover contributed significantly to model deviance in the aquatic assemblage species richness model (Table 3). Together these variables explained 63% of the variation in aquatic species richness across sites, but neither had significant effects based on Wald tests (Table 4). All 3 riparian variables contributed significantly to model deviance in the aquatic assemblage abundance model. Together these variables explained 64% of the variation in aquatic species abundance across sites, but none had significant results for Wald tests (Table 4). The nonsignificant results for the Wald tests in the aquatic assemblage models are likely due to large coefficient standard errors resulting from small sample size.

After we accounted for the effect of woody riparian zone width, number of dams had a significant positive correlation with total riparian species richness (r = 0.71, df = 9, P = 0.01) and abundance (r = 0.66, df = 9, P = 0.03) and had a positive but nonsignificant correlation with terrestrial assemblage species richness (r = 0.47, df = 9, P = 0.14) and abundance (r = 0.50, df = 9, P = 0.12). After we accounted for the effects of ponded water and emergent vegetation cover, aquatic assemblage species richness was not correlated with number of dams (r = 0.07, df = 9, P = 0.84). When all 3 variables were accounted for, aquatic assemblage abundance was positively correlated with the number of dams (r = 0.57, df = 9, P = 0.07).

DISCUSSION

In a semiarid shrubsteppe region of Wyoming, we observed dam densities up to 52 dams · km^{-1} in 1.2-km sections of stream. This length of stream is within the range of North American beaver colony home ranges summarized by Novak (1987), but the density of dams observed on our sites was greater than that described for boreal streams in Quebec (8.6–10.0 dams · km^{-1}; Naiman et al. 1986). As would be expected given that the direct effect of a beaver dam is to impound water and force it into the adjacent floodplain, we found cover of emergent vegetation to be positively related to the number of dams. Our measurement of emergent vegetation did not differentiate vegetation that had been flooded due to dam creation from emergent vegetation that was recruited following dam creation. However, in either circumstance the result was the creation of a new riparian condition. The nonsignificant relationship between cover of ponded water and dam density likely results from variability in dam size, stream flow, and channel depth, which would all affect the volume of water behind each dam more than they would affect surface extent of water alone. Thus, a more appropriate measure of the relationship between dam density and degree of ponding would account for the total volume of ponded water behind each dam. Of all the measured riparian characteristics, width and

TABLE 4. Parameter estimate and standard error (b [$s_{\bar{x}}$]), Wald statistic (t) and associated *P*-value, and odds ratio with 95% confidence interval (C.I.) for variables included in final riparian models for the terrestrial and aquatic riparian bird community along 11 streams in a shrubsteppe region of Wyoming.

	Woody riparian zone width					Ponded water cover					Emergent vegetation cover				
	b ($s_{\bar{x}}$)	t	*P*	Odds ratio	95% C.I. of odds ratio	b ($s_{\bar{x}}$)	t	*P*	Odds ratio	95% C.I. of odds ratio	b ($s_{\bar{x}}$)	t	*P*	Odds ratio	95% C.I. of odds ratio
Total species richness	0.018 (0.006)	3.03	0.02	1.02	1.007–1.030										
Total abundance	0.029 (0.006)	5.27	0.00	1.03	1.019–1.040										
Terrestrial species richness	0.188 (0.007)	2.72	0.03	1.21	1.193–1.220										
Terrestrial abundance	0.026 (0.003)	7.62	0.00	1.03	1.019–1.033										
Aquatic species richness						0.265 (0.172)	1.54	0.17	1.30	0.967–1.639	0.131 (0.078)	1.69	0.13	1.14	0.988–1.293
Aquatic abundance	0.030 (0.027)	1.13	0.30	1.03	0.978–1.083	0.176 (0.179)	0.98	0.36	1.19	0.841–1.544	0.146 (0.119)	1.23	0.26	1.16	0.924–1.391

height of the riparian shrub layer had the strongest relationships with dam density. Riparian condition at beaver colonization and changes that have occurred since colonization are unknown, precluding us from differentiating correlative from causative relationships between dam density and riparian characteristics. However, other studies of beaver activity in semiarid regions report wider riparian zones, greater wetland area, more ponding, and taller shrubs on streams with beaver dams compared to streams without beavers, suggesting increasing dam density may contribute to increasing availability of these riparian features (Brayton 1984, Medin and Clary 1990, Albert and Trimble 2000, McKinstry et al. 2001). Relationships between dam density and characteristics of the riparian zone may be confounded by stream-channel incision, which was present on several of our sites. Incision can occur adjacent to the stream or any distance into the floodplain and can result in disjunct floodplains with discontinuous vegetation. Depending on the degree of incision, dams may have a stronger influence on riparian characteristics in a lower floodplain than they would in a higher floodplain. We could not evaluate this as we did not differentiate vegetation occurring on different floodplain levels.

When evaluating all riparian birds together, we found width of the woody riparian zone to be the most important characteristic for describing variation in species richness and abundance. This result concurs with other studies of riparian birds in semiarid regions both without beaver activity (Sanders and Edge 1998, Rottenborn 1999, Cooke and Zack 2008) and with beaver activity (McKinstry et al. 2001). Riparian width and riparian shrub height, which are strongly correlated, likely reflect both availability and heterogeneity of woody vegetation, since wider and taller riparian zones tend to have higher diversity and structural complexity of vegetation (Dobkin and Wilcox 1986, Rottenborn 1999). When we examined terrestrial riparian birds separately from birds associated with aquatic habitats, we found differences in the importance of the riparian characteristics. As expected, the terrestrial riparian assemblage responded to increases in availability of woody riparian vegetation, whereas ponded water and emergent vegetation cover explained more variation in the aquatic assemblage. Although the coefficient tests for ponded water and emergent vegetation in the aquatic assemblage models did not have significant results, these characteristics explained over 60% of the variation in the aquatic assemblage, suggesting that a significant effect may be detected with a larger sample size.

After accounting for the effects of riparian characteristics, we found a significant correlation between number of dams and total species richness, total abundance, and aquatic assemblage abundance. As it is unlikely that riparian birds are responding to the number of dams per se, this result suggests that dam density correlates with riparian characteristics that were not measured in our study but that are positively associated with habitat use by riparian birds. The availability of other riparian characteristics may be positively associated with dam density if their availability is enhanced by increasing levels of water impoundment and extended exposure to favorable growing conditions. For example, cover of herbaceous riparian vegetation, which is preferred by Sora (*Porzana carolina;* Melvin and Gibbs 1996), may be positively associated with dam density (Rosell et al. 2005) but was not differentiated from woody riparian vegetation in our measurement of emergent vegetation cover.

Although many North American beaver populations have recovered from near extirpation (Naiman et al. 1988), beavers remain absent from two-thirds of their historical range in Wyoming (Olson and Hubert 1994). McKinstry et al. (2001) estimated that the removal of beaver from 1st- to 3rd-order streams across Wyoming may have reduced up to 275,000 ha of wetland habitat for over 240,000 waterfowl. With habitat losses due to anthropogenic disturbances as high as 90% in some western states, riparian areas are priorities for restoration (Krueper 1993). Beaver reintroductions have been used with success to restore riparian functions and improve habitat conditions in semiarid regions (Brayton 1984, Albert and Trimble 2000, McKinstry et al. 2001). Given the strong positive correlations between dam density, riparian area characteristics, and the riparian bird community that we observed in Wyoming, beaver reintroductions may be an effective tool for restoring riparian bird habitat in semiarid regions. Future research should include long-term, replicated before-and-after studies of beaver reintroductions that clearly document riparian and avian conditions prior to and following beaver reintroductions. Future research should also incorporate detailed measurements linking changes in riparian characteristics associated with dam-building activity to productivity and survival of riparian-associated birds.

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