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Effects of proximity to riparian zones on avian species richness and abundance in montane aspen woodlands

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ABSTRACT. Riparian zones often provide more food or nesting resources than surrounding ecosystems and thus support more species or a greater abundance of birds. However, the extent to which the positive effects of riparian zones extend into adjoining habitats has rarely been investigated. We examined bird species richness and abundance in aspen (*Populus tremuloides*) woodlands of the upper East River Valley in Colorado, a region with extensive stands of aspen located upslope from riparian zones dominated by willows (*Salix* spp.). Our objective was to determine how species richness and abundance in aspen stands located closer to riparian zones compared to that of aspen stands farther away. To control for elevation effects, we conducted point counts for birds and examined the effects of riparian proximity on avian species richness and abundance in three elevation belts (low, 2840–2875 m; middle, 2940–2960 m; and high, 3040–3060 m). We determined riparian proximity by measuring distances from each census site to the nearest body of water and to the nearest patch of willow. Proximity to major willow patches (≥6500 m^2) had a stronger influence on species richness and abundance than did proximity to water or smaller patches of willows. Total species richness and abundance significantly increased with proximity to major willow patches at low elevation sites only. This relationship was driven by a greater prevalence of riparian-nesting species at lower elevation sites, where aspens were generally closer to riparian zones. The positive effects of willows diminished with abrupt changes in elevation. Our results highlight the importance of protecting willows around riparian zones in valley bottoms where habitat destruction caused by human land use is most prominent.

RESUMEN. **Efectos de la proximidad a la zona riparia sobre la riqueza y abundancia de especies de aves en bosques montanos de álamo**

En muchos casos las zonas riparias proveen una mayor cantidad de alimentos o recursos para la anidación que los ecosistemas circundantes. Por lo tanto tienen un mayor numero de especies o una mayor abundancia de aves. Sin embargo, la medida en que los efectos positivos de las zonas riparias se extiende hacia hábitats adjuntos ha sido raramente explorada. Examinamos la riqueza de aves y la abundancia en bosques de álamo (*Populus tremuloides*) en la parte alta del "East River Valley" en Colorado, una región con poblaciones extensas de álamo ubicadas en cerca de zonas riparias dominadas por sauces (*Salix* spp.). Nuestro objetivo era determinar el cambio en la riqueza y abundancia de especies de aves en los bosques de álamo de acuerdo con la distancia a la zona riparia. Para contralar por los efectos de la elevación, realizamos puntos de conteo para aves y examinamos los efectos de la proximidad a zonas riparias sobre la riqueza y abundancia de aves en tres franjas altitudinales (baja, 2840–2875 m, medio 2940–2960 m y alto, 3040–3060 m). Tomamos la distancia desde cada punto de censo hasta el cuerpo de agua mas cercano como la proximidad a la zona riparia. La proximidad a los parches de sauces grandes (≥6500 m^2), tuvo una mayor influencia en la riqueza y abundancia de especies que la proximidad a los cuerpos de agua o a los parches de sauces mas pequeños. La riqueza y abundancia total, incrementó significativamente con la proximidad a los parches de sauce grandes, solamente en sitios de baja elevación. Esta relación estuvo determinada por una mayor prevalencia de especies que anidan en zonas riparias en los sitios de baja elevación, donde los álamos están generalmente mas cerca de las zonas riaprias. El efecto positivo de los sauces disminuyo con los cambios abruptos en elevación. Nuestros resultados resaltan la importancia de proteger los sauces alrededor de regiones riparias en la base de los valles, donde la destrucción del hábitat causada a causa de efectos antrópicos es mas prominente.

Key words: Colorado, elevation, Red-naped Sapsucker, Rocky Mountains, willow, buffer zone

Riparian zones are widely recognized for their conservation value because they comprise a relatively small proportion of the landscape, yet support greater organismal diversity and abundance than surrounding areas (Naiman et al. 1993, Maisonneuve and Rioux 2001, Palmer and Bennett 2006). In the western United States, for example, deciduous riparian vegetation covers less than 1% of the region, but supports higher levels of bird species richness and abundance than any other habitat type (Knopf

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et al. 1988, Tewksbury et al. 2002). By creating heterogeneity in microclimate, geomorphology, and nutrient cycling, the interface between land and a fluvial system leads to enhanced growth and complexity of vegetation (Gregory et al. 1991, Naiman and Decamps 1997), providing a resource-rich habitat for wildlife, particularly birds (Maisonneuve and Rioux 2001, Scott et al. 2003, Bub et al. 2004).

Many studies have revealed greater bird species diversity and abundance in riparian zones than in surrounding habitats, but this pattern is most prominent in arid regions (Szaro and Jakle 1985, Woinarski et al. 2000). In mesic regions, the association is often weak or nonexistent (McGarigal and McComb 1992, Pearson and Manuwal 2001, Loehle et al. 2005, Lehmkuhl et al. 2007), especially where the transition between riparian and upland vegetation is indistinct (Wiebe and Martin 1998, Shirley 2005). Few investigators have examined the extent to which positive effects of riparian zones on bird species richness and abundance might extend into adjoining habitats. For example, at sites in the mesic Pacific Northwest where riparian zones were embedded in mature, unfragmented forests, Shirley (2005) observed little change in bird species richness and total abundance over a riparian-to-upland gradient. In central Arizona, Szaro and Jackle (1985) found that bird species residing in an isolated patch of riparian habitat accounted for 7–33% of bird abundance in adjacent habitats. In stands of mature forest in the Oregon Coast Range, McGarigal and McComb (1992) noted that bird species in upslope areas contributed more to total species richness and abundance than did streamside areas. Thus, the spatial extent of the influence of riparian zones depends on the characteristics of the surrounding landscape (Wiens et al. 1993, Woinarski et al. 2000).

Recently, there has been considerable interest in quantifying the influence of landscape-scale factors on avian diversity and abundance in riparian zones (e.g., Rodewald and Bakermans 2006, Fletcher and Hutto 2008, Pennington et al. 2008). Most of these studies have focused on the negative effects of human land use on bird communities and often include recommendations on how to address these impacts in conservation and management plans. Such efforts are particularly important in the western United States where riparian habitats are facing increasing degradation and fragmentation from anthropogenic factors, such as livestock grazing, water diversions, logging, and housing developments (Goodwin et al. 1997, Miller et al. 2003, Smith and Wachob 2006). For example, in the East River Valley of western Colorado, housing development associated with a nearby ski resort has led to substantial fragmentation of aspen woodland and other montane habitats (Theobald et al. 1996).

We investigated the effect of riparian zone proximity on species richness and abundance of birds in adjacent aspen (*Populus tremuloides*) woodlands of the upper basins of the East River Valley (upper ERV) near Crested Butte, Colorado (Fig. 1). The upper ERV is a mesic, montane region with extensive aspen woodlands bordered by meadows located various distances (directly bordering to hundreds of meters away) from riparian zones that are typically dominated by patches of willows (*Salix* spp.). Approximately 80 species of birds breed in the upper ERV, with 13 species commonly nesting in aspen woodlands and 16 in riparian zones. In previous surveys in the upper ERV, Daily et al. (1993) found that proximity to willows was positively correlated with the abundance of cavity-nesting birds in aspen stands. These authors, however, did not consider the possible influence of elevation, and the positive effects they found were largely mediated by Red-naped Sapsuckers (*Sphyrapicus nuchalis*). These woodpeckers are considered a keystone species because they excavate nest cavities that are later used by other cavity-nesting birds, and they drill sap wells in aspens and willows, thus providing high energy food for many species that visit the wells (Daily et al. 1993). Sapsucker abundance increased with proximity to (i.e., decreased with distance from) willows, suggesting that sapsuckers preferred to nest near willows. Furthermore, abundance of secondary cavity-nesting species was enhanced where sapsuckers were more abundant. Daily et al. (1993), however, found no effect of sapsucker abundance or willow proximity on the abundance of bird species that were not cavity-nesters. We expanded on the work of Daily et al. (1993) by examining the effect of riparian zone proximity on the abundance and species richness of all birds in aspen woodlands of the upper ERV.

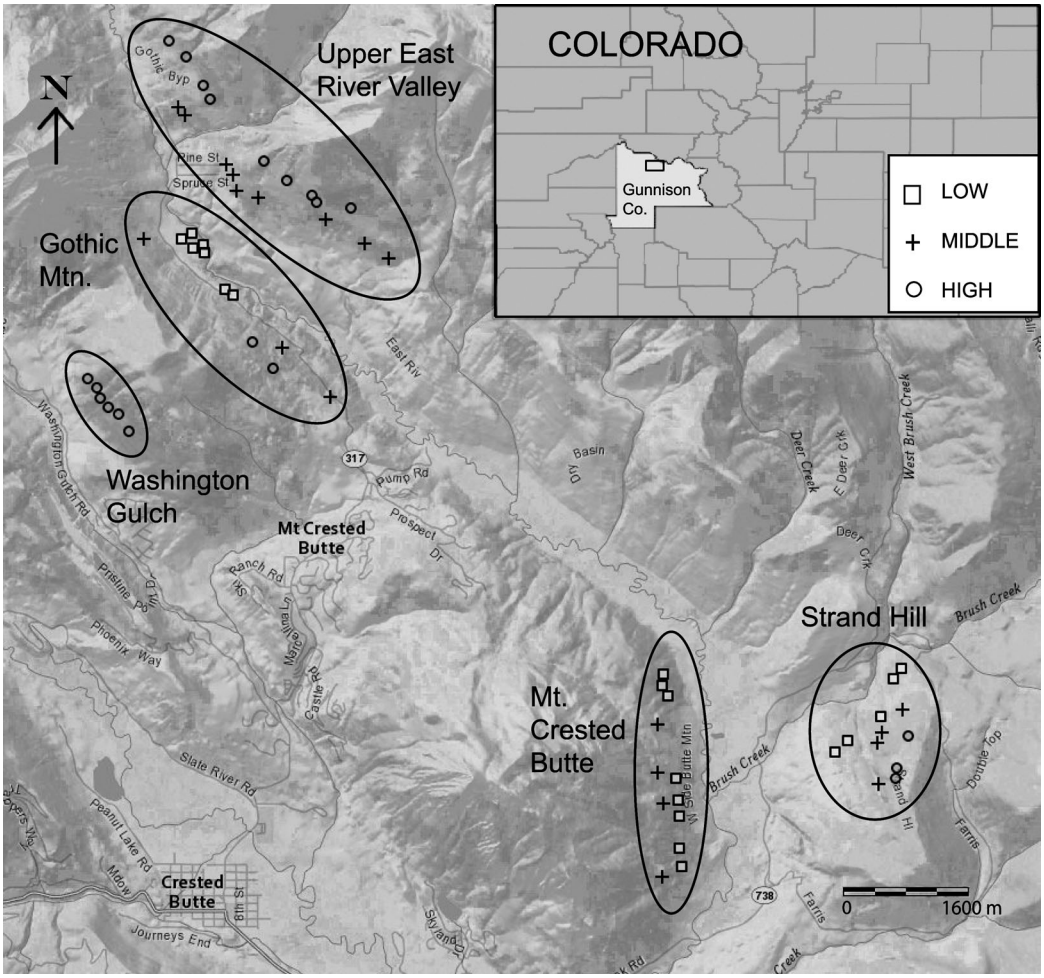

Fig. 1. Study area composed of aspen (*Populus tremuloides*) groves, montane meadows, and riparian zones in the East River Valley of Gunnison County, Colorado. Point-count censuses were conducted in aspen groves at 60 sites, 20 from three different elevations: low, 2840–2875 m, squares; middle, 2940–2960 m, crosses; and high, 3040–3060 m, circles. Each site was located ≥130 m from other sites. Image created using Esri ArcGIS Online (ESRI, Redlands, CA).

METHODS

Study area. Our study was conducted from June to August 2009. The upper ERV is a mesic watershed with an area of ~600 km^2, ranging in elevation from 2400 to 4300 m and featuring large expanses of undisturbed alpine, subalpine, and montane vegetation. Our study focused on montane zones comprised largely of aspen groves and meadows that grew on slopes above and alongside streams. Stream banks were dominated by shrubby vegetation, especially three species of willows (*Salix brachycarpa*, *S. pseudocordata*, and *S. subcaerulea*; Daily et al. 1993) that grew in clumps covering areas ranging from 10 m^2 to >10,000 m^2. Each individual willow was made up of dozens of stems, the most mature of which generally reached 1.5–2.5 m in height. Most willow patches (and most riparian zones in the upper ERV) were surrounded by meadows. These meadows also formed the borders of aspen groves located ~5 to 600 m from the willow patches. Most aspen groves in the upper ERV were pure,

mature stands that covered areas ranging from 1500 m^2 to >240,000 m^2. Groves were irregular in size and shape, and were often diffusely connected with other groves. The glacier-carved valleys of the upper ERV made for steep transitions between riparian zones and the matrix of meadow and aspen woodlands upslope, such that a bird flying 500 m upslope from a willow to an aspen grove would generally experience an elevation gain of at least 100 m (C. Floyd, unpubl. data). The steep elevation gradients and tight association between willows and streams created abrupt transitions between riparian and upland vegetation. The same combination of riparian zones, meadow, and aspen habitats extended from the mouth of the valleys at ~2400 m elevation to locations up-valley at ~3000 m. Because valleys in the upper ERV became progressively narrower toward their headwaters, distances between riparian zones and habitats upslope became correspondingly reduced. Thus, for birds nesting in aspen woodlands, there was often a negative relationship between elevation of the site and distance to riparian areas, making it essential to control for elevation as much as possible.

Study site selection. We controlled for elevation by conducting point counts within three elevation belts and examined the effect of riparian proximity on bird abundance and species richness within each belt. We selected 60 census sites, 20 from each of three elevation belts, labeled low (2840–2875 m), middle (2940–2960 m), and high (3040–3060 m). These belts were chosen to represent variability of the landscape and maximize the number of independent census sites. Sites were located in aspen woodlands on the slopes of Gothic Mountain, Snodgrass Mountain, Mount Crested Butte, Strand Hill, Washington Gulch, and unnamed ridges in the upper ERV (Fig. 1). To qualify for selection, sites had to be ≥130 m from any other site and ≥30 m from the nearest meadow edge. We chose this minimum separation distance because it would leave at least 100 m between surveyed areas (30-m radius circles). Our preliminary observations suggested that a 100-m interval would make it unlikely that the same individual bird would be detected at two different sites, and the requirement that sites fall within a minimum of 30 m from the nearest meadow ensured that each site was composed primarily of aspen woodland cover. We selected sites by overlaying a grid composed of squares representing 0.65 km^2 onto an aerial photo of the study area (30 cm/pixel resolution) in Google Earth and randomly selecting numbered cells using a random number generator, given they met our elevation and spacing criteria. The aspen tree nearest to the center of grid cells (determined in the field) was designated as the center of the point count, from which all distance measurements were recorded.

Bird censuses. One of us (J. Glass) conducted all censuses using 10-min fixed-radius point counts during the period from 29 June to 24 July 2009. All birds within 30 m detected by sight or sound were recorded (Sutherland 2006). On days when censuses were conducted, six sites were visited between 06:30 and 10:30, with the first count starting 1 h after sunrise. Each site was censused twice. To determine the order of sites visited, we created 10 clusters composed of six sites each, based on the proximity of those sites to one another and the feasibility of sampling all six in a 4-h period. Adjoining clusters were not sampled on consecutive days. We chose the order within each cluster based on the walking distance from each site to the starting point. For the initial census, we visited sites closest to the starting point (e.g., a trailhead) first, and then reversed the order in the second census to eliminate systematic bias in the elevation of the starting point. Not every cluster of six included sites from all three elevation belts. Censuses were not conducted in rain or high wind (>11 knots).

Spatial measurements. Because the potential effects of riparian zones on bird communities were presumably related to water or willow availability, we measured distances to the nearest body of water (river, creek, brook, or pond) and the nearest patch of willow. Larger areas of riparian zones potentially provide more resources than smaller areas, so we categorized water bodies and willow patches as major or minor. Major willow patches were those with aerial coverage ≥6500 m^2 (our estimated median size of willow patches in the upper ERV) measured in ArcGIS. Minor willow patches ranged in size from ~10 m^2 (clusters of a few shrubs) to patches less than 6500 m^2. Major water bodies were the five largest streams in the upper ERV, including East River, Copper Creek, Washington Gulch Creek, Verzuh Young Bafand Ditch, and Brush Creek. Minor water bodies included those depicted by blue lines

on U.S. Geological Survey topographical maps from 1971. Water bodies not depicted by blue lines were not included because they were either ephemeral brooks or seeps. We measured the minimum distance of our point count sites to the edge of the nearest minor willow patch (minor willow), major willow patch (major willow), minor water body (minor water), and major water body (major water). We measured distances to willows <200 m away with a tape or laser range finder. Distances to willows ≥200 m away, as well as distances to water bodies, were estimated from aerial photos (~15 cm/pixel resolution). Major willow patches were easily identifiable and measurable using aerial photos due to the small amount of overlap with other vegetation types. We did not measure willow height, although this variable has been shown to be an important contributor to avian richness (Baril et al. 2011). However, all willows in our study were mature clumps with at least one stem taller than 1.5 m. In addition, we measured distance to the nearest meadow, defined as a continuous area of at least 100 m^2 not containing any aspen trees >5 cm DBH, because meadow proximity or availability is an important predictor of nest site choice for some species that nest in aspens (Dobkin et al. 1995, Lawler and Edwards 2002).

Habitat categories. We conducted separate analyses on four data subsets composed of species categories based on habitat nesting preferences, including riparian, non-riparian, aspen, and cavity-nesters (Table 1). These data subsets were determined using published information on the nesting-habitat preferences of each species (Ehrlich et al. 1988, Poole 2005), as well as 15 years of field observations by one of us (C. Floyd) in the upper ERV. Species in the riparian category nested primarily in riparian zones (e.g., Wilson's Warbler, *Wilsonia pusilla*) or in both riparian zones and aspen woodlands (e.g., American Robin, *Turdus migratorius*). Non-riparian species were those nesting infrequently or not known to nest in riparian habitats in our study area; most of these species nest predominantly in aspen woodlands, but a few also nest in conifers (e.g., Pine Siskin, *Carduelis pinus*) or dry meadows (e.g., Green-tailed Towhee, *Pipilo chlorurus*). We also separately analyzed non-riparian species nesting only in aspens and those nesting only in aspen cavities. Broad-tailed Hummingbird (*Selasphorus platycercus*) and Rufous Hummingbird (*Selasphorus rufus*) were both observed, but could not be reliably identified during point counts so were recorded as *Selasphorus* spp.

We created the category of riparian species to determine if any positive effects of riparian proximity might be due to increased overlap with the foraging range of riparian-nesting birds, for example, MacGillivray's Warblers (*Oporornis tolmiei*) feeding in nearby aspens, rather than the greater presence of aspen-nesting birds, for example, numbers of Warbling Vireos (*Vireo gilvus*) increasing with availability of benthic invertebrate prey. Cavity-nesting species included Red-naped Sapsuckers and species that nest in aspen cavities originally excavated by these woodpeckers. Hairy Woodpeckers (*Picoides villosus*) were not included in the cavity-nesting category because they were uncommon (J. Glass, pers. observ.), do not feed in willows, and do not use sapsucker nest cavities (Jackson et al. 2002). We analyzed cavity-nesting species separately because we suspected that some of the perceived positive effects of riparian proximity might be indirectly caused by sapsuckers (Daily et al. 1993), that is, abundance of sapsuckers and thus availability of cavities for secondary cavity-nesting species might be higher in aspens closer to willows because sapsuckers feed extensively in willows.

Data analyses. We calculated species richness as the cumulative number of unique species observed at each site over the two visits. We calculated an index of the total relative abundance at each site by summing the number of individuals observed at each site over the two visits and dividing the sum by the total number of birds observed at all sites (e.g., if we recorded two Warbling Vireos at a site on the first visit and one on the second visit, we summed the observations as three observations of that species). Similarly, we calculated an index of relative abundance for each habitat category (i.e., including only observations of species in that category) and for Red-naped Sapsuckers. This was defined as the number of birds in each nesting habitat category at a site divided by the total number of individuals of that habitat category over all sites. Correlations between the environmental variables (minor willow, major willow, minor water, major water, and meadow) were calculated using Pearson's correlation coefficients.

We analyzed relationships between environmental variables (e.g., proximity to major

Table 1. Abundances of bird species recorded in point-count censuses conducted in aspen woodlands in the East River Valley, Colorado, from 29 June to 24 July 2009. The number of individuals observed during point counts are given for all 33 species (plus hummingbirds) summed over the first and second visits.

Common name	Scientific name	Abundance by elevation		
		Low	Middle	High
Dusky Grouse[a]	*Dendragapus obscurus*	0	1	0
Hummingbird[a,b]	*Selasphorus* spp.	6	2	8
Red-naped Sapsucker[a,c,d]	*Sphyrapicus nuchalis*	13	2	1
Hairy Woodpecker[a,c]	*Picoides villosus*	7	12	2
Northern Flicker[a,c,d]	*Colaptes auratus*	9	13	5
Olive-sided Flycatcher[a]	*Contopus cooperi*	3	0	0
Western Wood-Pewee[a,c]	*Contopus sordidulus*	20	22	4
Dusky Flycatcher[e]	*Empidonax oberholseri*	6	3	5
Cordilleran Flycatcher[a]	*Empidonax occidentalis*	10	2	0
Warbling Vireo[a,c]	*Vireo gilvus*	36	38	25
Tree Swallow[a,c,d]	*Tachycineta bicolor*	4	0	0
Black-capped Chickadee[a,c,d]	*Poecile atricapillus*	2	18	3
Mountain Chickadee[a,c,d]	*Poecile gambeli*	2	0	0
White-breasted Nuthatch[a,c,d]	*Sitta carolinensis*	1	1	0
Brown Creeper[a]	*Certhia americana*	0	0	1
House Wren[a,c,d]	*Troglodytes aedon*	53	47	31
Ruby-crowned Kinglet[a]	*Regulus calendula*	6	1	4
Mountain Bluebird[a,c,d]	*Sialia currucoides*	2	0	1
Swainson's Thrush[e]	*Catharus ustulatus*	5	0	0
Hermit Thrush[a]	*Catharus guttatus*	2	1	2
American Robin[e]	*Turdus migratorius*	23	14	5
Orange-crowned Warbler[e]	*Vermivora celata*	1	0	2
Yellow Warbler[e]	*Dendroica petechial*	10	2	0
Yellow-rumped Warbler[a]	*Dendroica coronata*	14	14	4
Macgillivray's Warbler[e]	*Oporornis tolmiei*	1	4	2
Wilson's Warbler[e]	*Wilsonia pusilla*	2	0	0
Western Tanager[a,c]	*Piranga ludoviciana*	4	1	1
Green-tailed Towhee[a]	*Pipilo chlorurus*	2	5	18
Fox Sparrow[e]	*Passerella iliaca*	1	0	0
Lincoln's Sparrow[e]	*Melospiza lincolnii*	6	9	3
White-crowned Sparrow[e]	*Zonotrichia leucophrys*	0	1	0
Dark-eyed Junco[a]	*Junco hyemalis*	37	27	25
Lazuli Bunting[e]	*Passerina amoena*	1	0	0
Pine Siskin[a]	*Spinus pinus*	10	10	2

[a]Non-riparian-nesting species.
[b]Hummingbirds were either Broad-tailed or Rufous hummingbirds that could not be distinguished from each other in the field.
[c]Aspen-nesting species.
[d]Cavity-nesting species. All cavity-nesting species also nested in aspens.
[e]Riparian-nesting species.

willows) and species richness and abundance using generalized additive modeling (GAM). GAMs are useful for ecological analyses because they accommodate nonlinear relationships between predictor and response variables by fitting linear smoothing terms, thus allowing for a more flexible characterization of the response (Fewster et al. 2000, Guisan et al. 2002, Wood 2006). We modeled the effects of the environmental variables separately for species richness and abundance and limited the basis of all smoothing functions to four dimensions (i.e., four maximum possible degrees of freedom) to avoid over-fitting. After analyzing initial models for an overall effect, we constructed additional models for each elevation belt (high, middle, and

low) to investigate the effects of environmental variables on species richness and abundance independent of elevation effects. We repeated these procedures for the habitat categories (riparian, non-riparian, aspen-nesting, and cavity-nesting). Red-naped Sapsuckers were examined within the cavity-nesting category, as well as independently across all elevations, due to their importance as a keystone species. We examined characteristics of model fit (deviance explained, R^2 values, and generalized cross validation score) to evaluate which environmental variables contributed significantly ($\alpha = 0.05$) to the models. All analyses were conducted using R version 3.1.1 in the package mgcv, with the default option selected for calculating α values (R Development Core Team 2011, Wood 2011).

RESULTS

During the census period, 703 individuals and 35 species of birds were observed. We classified 11 species as riparian and 24 as non-riparian. The non-riparian category included 12 aspen-nesting species, eight of which were also cavity-nesters (Table 1). Average proximity to nearest minor willow, major willow, minor water, and major water decreased with higher elevations, but proximity to meadow did not (Table 2). Models incorporating major willow patches and major water bodies had lower generalized cross validation scores, higher R^2 values, and explained a larger percentage of the deviance compared to the models incorporating minor willow and minor water bodies, indicating a better fit (Table 3). Therefore, after performing these comparisons for the overall dataset, we conducted the remainder of the analyses (those for elevation belts and habitat categories) considering only major willow patches and major water bodies (Table 4).

Correlations among predictor variables. Model results across all elevations revealed weak, positive correlations between willow proximity and water proximity ($r = 0.56$, $P < 0.001$), willow proximity and major water proximity ($r = 0.34$, $P = 0.01$), major willow proximity and water proximity ($r = 0.38$, $P < 0.01$), and major willow proximity and major water proximity ($r = 0.45$, $P < 0.001$).

Species richness. Total mean species richness, as well as mean species richness for each habitat category, declined with increasing elevation (Table 5). Analyzed across all elevation belts, significant predictors of total species richness were proximity to major willow patches ($F_{2,2} = 5.6$, $P = 0.004$, Fig. 2) and major water bodies ($F_{1,1} = 4.0$, $P = 0.05$, Fig. S1). We observed this relationship across all elevations until ~350 m, after which the effect of major willows became null (Fig. 2). Beyond 500 m, the effect of major water bodies became null (Fig. S1). Within elevation belts, however, total species richness increased only with proximity to major willows at low-elevation sites ($F_{1,1} = 8.3$, $P = 0.01$, Fig. 3). These effects extended to ~200 to 300 m (Fig. 3). No effect of major water proximity on total species richness was found within any elevation belt (Table 4).

For riparian birds, species richness increased significantly with proximity to major willows at low elevations ($F_{2,2} = 6.3$, $P = 0.008$) and high elevations ($F_{1,1} = 5.9$, $P = 0.026$, Fig. 3). Meadow proximity was the only environmental variable that significantly predicted species richness of non-riparian birds, but only in the high elevation model ($F_{3,3} = 5.2$, $P = 0.011$, Table 4). This relationship showed a distinct nonlinear trend, with richness decreasing until ~150 m away from meadows, then increasing until 200 m, which was the maximum distance to any meadow from any high-elevation site (Fig. 3). At low elevations, species richness of cavity-nesting birds increased with proximity to major willows, but the relationship was just marginally significant ($F_{1,1} = 3.8$, $P = 0.051$). We found no effects of willow, water, or meadow proximity on species richness of aspen-nesting birds at any elevation.

Abundance. Across all elevations, relative abundance increased with proximity to major willows ($F_{2,3} = 12.5$, $P < 0.001$, Fig. 2) and meadows ($F_{1,1} = 6.2$, $P = 0.015$, Fig. S2). The effect of major willows extended to ~350 m (Fig. 2), but diminished with meadows at ~75 m (Fig. S2). Analyses by elevation revealed significant associations with predictor variables only at low-elevation sites (Table 4). These effects extended to ~200 to 300 m (Fig. 4). At those sites, proximity to major willows had a positive effect on abundance of all species ($F_{2,2} = 5.4$, $P = 0.013$, Fig. 4) and the abundance of riparian species ($F_{2,2} = 10.4$, $P < 0.001$, Fig. 4). At low-elevation sites, proximity to major willows ($F_{1,1} = 5.3$, $P = 0.035$) and meadows ($F_{1,1} = 5.8$, $P = 0.029$) were significant, positive predictors of abundance of aspen-nesting

Table 2. Average distance (m) from the center of the point count site to the nearest willow patch, water body, and meadow. Confidence intervals are reported in parentheses, and were calculated using $\alpha = 0.05$.

Elevation	Minor willow	Major willow	Water	Major water	Meadow
High	264 (83)	508 (97)	398 (82)	802 (118)	89 (25)
Middle	149 (34)	412 (53)	340 (65)	648 (74)	76 (30)
Low	80 (51)	241 (93)	254 (61)	298 (138)	86 (19)

Table 3. Comparative results of general additive models (GAMs) using major and minor environmental variables (willow patches and water bodies) for (a) total species richness and (b) total relative abundance. For each model, the generalized cross validation (GCV) score, R^2 value, and the percent deviance explained are provided.

	GCV score	R^2	% Deviance explained
(a) Total species richness			
Major willow, major water bodies, meadow	4.73	0.34	38.5
Minor willow, minor water bodies, meadow	5.71	0.20	26.8
(b) Total relative abundance			
Major willow, major water bodies, meadow	0.32	0.43	47.5
Minor willow, minor water bodies, meadow	0.43	0.21	26.0

Table 4. Results of general additive models (GAMs) for (a) species richness and (b) relative abundance incorporating the following predictor variables: major willow patches ($\geq$6500 m^2), major water bodies, and meadows. The elevation category, generalized cross validation (GCV) score, R^2 value, and the percent deviance explained are provided for each model. Only models where significant predictors were identified are shown.

	Elevation	GCV score	R^2	% Deviance explained	Significant predictor
(a) Species richness					
Total	Low	4.66	0.28	31.7	Major willow
Riparian	Low	1.41	0.40	45.0	Major willow
Riparian	High	0.38	0.20	24.6	Major willow
Non-riparian	High	1.51	0.41	49.7	Meadow
(b) Relative abundance					
Total	Low	0.348	0.37	43.0	Major willow
Riparian	Low	3.091×10^{-4}	0.56	60.8	Major willow
Aspen	Low	6.223×10^{-5}	0.23	34.9	Major willow, major water, and meadow

Table 5. Mean species richness for all species (total) and each habitat category (riparian, non-riparian, aspen- and cavity-nesters) across elevation belts (high, 3040–3060 m; middle, 2940–2960 m; low, 2840–2875 m). Confidence intervals are provided in parentheses and were calculated using $\alpha = 0.05$.

Elevation	Total	Riparian	Non-riparian	Cavity	Aspen
High	4.65 (0.67)	0.70 (0.29)	3.95 (0.63)	1.05 (0.26)	2.00 (0.51)
Middle	6.70 (1.02)	1.20 (0.56)	5.50 (0.81)	1.50 (0.39)	3.55 (0.56)
Low	7.86 (1.06)	1.70 (0.62)	6.45 (0.64)	1.90 (0.37)	3.50 (0.66)

species (Fig. 4). In contrast, abundance of aspen-nesting species decreased with proximity to major water bodies ($F_{1,1} = 5.2$, $P = 0.037$, Fig. 4). Abundance of non-riparian and cavity-nesting species was not affected by proximity to major willow, major water, or meadow. Integrated over all elevations, abundance of Red-naped Sapsuckers increased

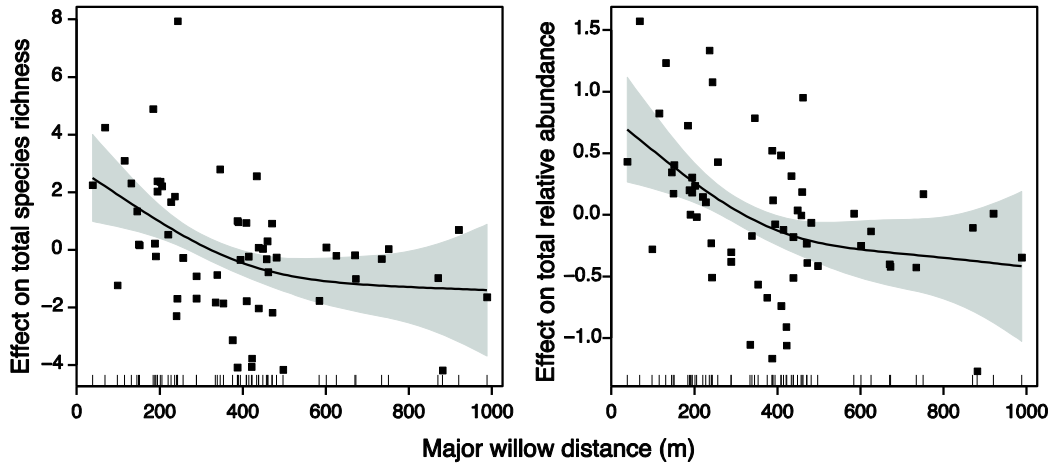

Fig. 2. Effect of major willow patches (≥6500 m^2) on species richness and abundance of birds across all elevations. The *y*-axes represent changes in the dependent variables relative to their means. Gray shading around the solid line represents standard errors, and residuals are plotted as solid squares. Vertical hash marks on the bottom of the plot represent distances of each of the 60 sampling sites from major willows.

with proximity to major willow ($F_{2,2} = 3.5$, $P = 0.03$).

DISCUSSION

We found largely positive effects of riparian zone proximity on avian species richness and abundance in montane aspen woodlands. These effects diminished at distances beyond 200–350 m from riparian zones, reflecting a transition to higher elevations. Proximity to water was less important than proximity to willows in its influence on species richness and abundance, suggesting that the positive effects of riparian zones were mostly due to resources provided by willows. Our results corroborate previous findings of the significance of willows in shaping avian communities in similar habitats (Daily et al. 1993, Baril et al. 2011). Further evidence for the importance of willows comes from our finding that larger patches (≥6500 m^2) had a greater influence on avian species richness and abundance than smaller patches.

As expected, the effect of riparian proximity varied with elevation. When analyzed by elevation zone, the strongest effects (and, in some cases, the only significant effects) were found at low-elevation sites. One explanation for this is that the largest patches of willows were generally in the bottoms of valleys. Furthermore, low-elevation sites were on average closer to willows than were middle- and high-elevation sites. Our results show the importance of considering the effects of elevation, particularly in montane regions where changes in elevation cause a rapid alteration of environmental conditions over short distances (Ruggiero and Hawkins 2008). Globally, species richness typically decreases with elevation, although attempts to model this decrease suggest that factors other than elevation, such as habitat area, temperature, and water availability, often play a role (Rahbek 1997, Herzog et al. 2005, McCain 2009). Quantifying environmental variables associated with increasing elevation would provide insight into how to tease apart elevation from other environmental components.

The positive influence of riparian zones in our study was largely a function of greater prevalence of riparian-nesting, not aspen-nesting, species. This suggests that individuals nesting in riparian zones were making feeding forays into aspen woodlands, such that sites closer to willows were more likely to be within their home ranges. The use of adjacent habitats by riparian-nesting birds has been observed in other systems (Szaro and Jakle 1985, McGarigal and McComb 1992, Shirley 2005). An interesting question is whether aspen woodlands closer to willows are more favorable foraging habitats

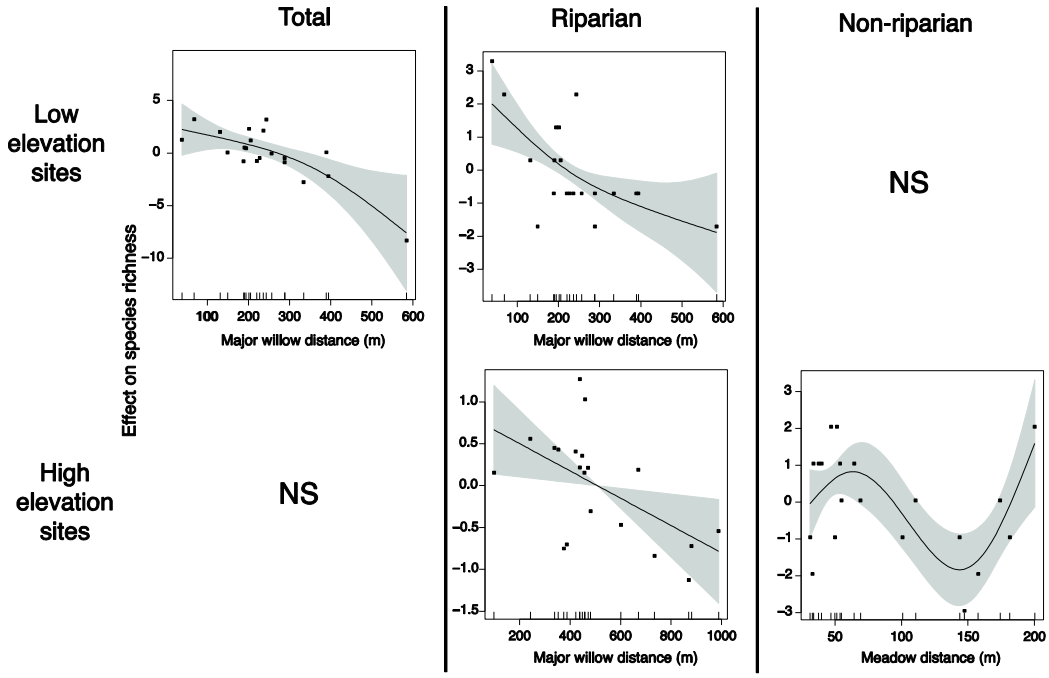

Fig. 3. Effect of major willow or meadow proximity on bird species richness. Species richness was measured for all species (Total) and those split into riparian or non-riparian categories. The *y*-axes represent changes in the dependent variable (species richness) relative to its mean for each category. Gray shading around the solid lines represents standard errors, and residuals are plotted as solid squares. Vertical hash marks on the bottom of the plot represent distances of each of the 20 sampling sites at that elevation from the independent variables. Missing panels are due to non-significant (NS) results for that particular habitat category and elevation.

for reasons other than reduced travel distance. Aspen groves closer to riparian habitats may have a greater abundance of resources that flow from neighboring riparian habitats, or they may have greater habitat complexity (McGarigal and McComb 1992).

Consistent with the findings of Daily et al. (1993) in the upper ERV, we found that sites closer to willows tended to have a greater abundance of Red-naped Sapsuckers and more species of secondary cavity-nesters. This result suggests that aspen groves closer to willows were more likely to attract nesting sapsuckers and thus had greater availability of tree cavities for secondary cavity-nesters. In contrast to Daily et al. (1993), however, we did not find a greater abundance of secondary cavity-nesters at sites closer to willows.

Total species richness declined as elevation increased, a finding that is probably linked to decreasing proximity to willow at sites farther upslope from riparian areas. Sites more than 300 m from willow patches were generally at middle or high elevations, equating to a 100 m gain (middle sites) and 200 m gain (high sites) in elevation from low sites. Past 300 m (laterally), the effects of elevation and other associated factors may have outweighed any benefits provided by willows. A distance of 300 m is a potential "threshold distance" beyond which riparian areas no longer benefit avian species in our study area. This distance might also represent a limit to the home range sizes of riparian species. Previous studies of the extent to which the home ranges of riparian birds extended into adjacent habitat types have revealed a wide range of distances, from ~75 m in Michigan hardwood forests (Bub et al. 2004) to 500 m in Arizona desert-wash habitats (Szaro and Jakle 1985). The concept of a threshold distance as it relates to avian species richness and abundance has been studied in the context of urban development (e.g., Palomino

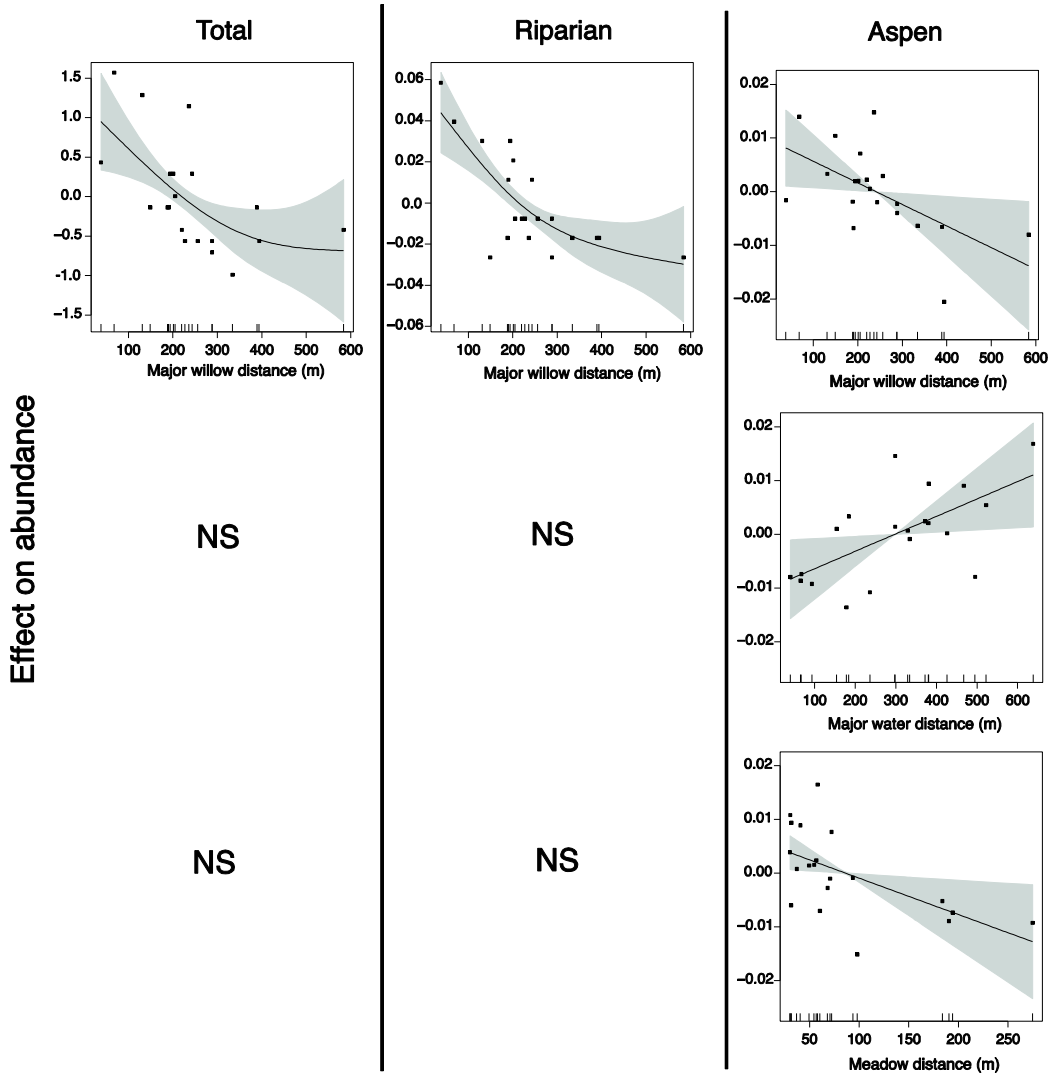

Fig. 4. Effect of major willow, major water, or meadow proximity on bird abundance at low elevation sites. Bird abundance was measured for all species (Total) and for those split into riparian- and aspen-nesting habitat categories. The *y*-axes represent changes in the dependent variable (relative abundance) relative to its mean for each category. Gray shading around the solid lines represents standard errors. Residuals are plotted as solid squares. Vertical hash marks on the bottom of the plot represent distances of each of the 20 low elevation sampling sites from the independent variables. Missing panels are due to non-significant (NS) results for that particular habitat category.

and Carrascal 2007) and in creating buffer zones around riparian areas for conservation purposes (Naiman and Decamps 1997, Pearson and Manuwal 2001). A review of buffer zones in the United States and Canada revealed that most were insufficiently wide to protect terrestrial communities (Lee et al. 2004). In the Rocky Mountain region, including Colorado and surrounding states, the average buffer distance for large permanent streams (>5 m wide) is 24.4 m, though this varies based on factors such as type of desired land use and presence of fish in streams (Lee et al. 2004). Although we did not compare buffer widths, our results suggest

that conservation efforts in the upper ERV should consider the importance of this variable, particularly given that the mean distance to major willow patches at low-elevation sites was >200 m (Table 2). In Pacific Northwest conifer forests of western Washington, a 45-m buffer was recommended as appropriate to conserve avian species communities (Pearson and Manuwal 2001), whereas similar coniferous forests in British Columbia supported riparian species up to 250 m from second-order streams (Wiebe and Martin 1998). Proper consideration of upland habitat structure on a region-specific basis should be given when determining buffer zones.

Our results illustrate the importance of riparian zones and surrounding habitat in mesic, montane regions. Studies in other habitats with these characteristics have shown a lesser impact of riparian areas on avian species richness and abundance (Whitaker and Montevecchi 1997, Shirley 2005), especially compared to arid regions where riparian zones are of substantial importance to avifaunal communities (Woinarski et al. 2000, Schneider and Griesser 2009). The complexity and uniqueness of riparian habitats across regions make it difficult to develop generalized models explaining patterns of variation in avian species richness and abundance. In this high-altitude region of the Rocky Mountains, where valleys are tightly confined by mountains, the changes in microclimate and topography that come with rapid increases in elevation create abrupt transitions between riparian and upland habitats. An abrupt transition between habitats may be one reason for the importance of riparian zones in desert habitats (McGarigal and McComb 1992).

Riparian areas tend to attract high levels of use by humans. Livestock grazing in the western United States has negatively impacted avian species richness and abundance (Dobkin et al. 1998, Miller et al. 2003, Scott et al. 2003). Development tends to fragment riparian habitats, leading to changes in the resource availability and territory size of birds residing in these areas (Fleischner 1994, Saab 1999, Smith and Wachob 2006). Although riparian vegetation in the western United States makes up only a small part of the landscape (Knopf et al. 1988), these areas can serve as habitat refuges for birds from nearby development (Skagen et al. 2005). For example, Knopf (1985) found that 82% of bird species breeding in northern Colorado used riparian areas. Our results highlight the importance of protecting riparian zones in the Rocky Mountains, especially in valley bottoms where habitat destruction from human land use tends to be concentrated (Theobald et al. 1996, Miller et al. 2003).

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Fig. S1. Effect of riparian proximity on total species richness of birds across all elevations. Riparian proximity was measured as distance to the nearest major water body. The y-axes represent changes in the dependent variables relative to their means. Gray shading around the solid line represents standard errors, and residuals are plotted as solid squares. Vertical hash marks on the bottom of the plot represent distances of each of the 60 sampling sites from major willows.

Fig. S2. Effect of meadow distance on total relative abundance of birds across all elevations. The y-axes represent changes in the dependent variables relative to their means. Gray shading around the solid line represents standard errors, and residuals are plotted as solid squares. Vertical hash marks on the bottom of the plot represent distances of each of the 60 sampling sites from major willows.