THESIS

IMPACTS OF ELK MANAGEMENT AND RIPARIAN CONDITION ON SONGBIRDS IN ROCKY MOUNTAIN NATIONAL PARK

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2015

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ABSTRACT

IMPACTS OF ELK MANAGEMENT AND RIPARIAN CONDITION ON SONGBIRDS IN ROCKY MOUNTAIN NATIONAL PARK

The widespread loss of apex predators from the western U.S. is having cascading effects on ecosystems. As in other western parks, riparian willow (*Salix* spp.) communities in Rocky Mountain National Park (RMNP) are declining as a result of a trophic cascade involving the local extinction of wolves (*Canis lupus*) and an exponential increase in elk (*Cervus elaphus*). In 2008, RMNP began installing elk exclosures to protect and restore willow communities and the diverse taxa that depend on riparian ecosystems from heavy browsing. Using point counts, I evaluated the effect of elk exclosures and riparian shrub condition on songbird density and occupancy. I found little support for a direct effect of elk exclosures on bird communities, with the exception of shrub nesting birds which occurred at higher densities within exclosures. However, the density and occupancy of some riparian bird species and guilds was positively correlated with particular vegetation conditions in this ecosystem. Shrub height positively related to both density and occupancy of Dusky Flycatcher. For the Lincoln Sparrow and shrub-nesting guild, occupancy also had a positive relationship with shrub height. The percent of shrub cover within 15 m of the survey point was an important positive predictor of density for Lincoln's Sparrows, Song Sparrows, and Wilson's Warblers, and foliage-gleaner and shrub-nesting guilds. The percent of riparian shrub cover within 300 m was an important positive predictor for the density of Wilson's Warblers. American Robin, a habitat generalist, and ground-nesting and foraging guilds did not respond strongly to shrub cover or height at any scale. These results

reflect the variable shrub conditions inside and outside exclosures, and affirm that managing for mid to high density shrub cover and height will be beneficial for some riparian specialists. My findings provide park managers critical information on bird communities in experimental elk exclosures, and insight into the conditions needed to support songbird communities in the park's riparian ecosystems.

ACKNOWLEDGEMENTS

Funding for this project was provided by the Colorado Mountain Club and the National Park Service. Past and present park managers at Rocky Mountain National Park contributed knowledge and encouragement. Judy Visty and Gary C. Miller served as a springboard for this research. Thank you to Therese Johnson, John Mack, and Ben Bobowski for the flexibility and support to see this project through, for making mentoring a priority, for empowering me to turn my passion into conservation, and for all the fun along the way.

I was privileged to wade through muck with enthusiastic, skilled, and dedicated colleagues and friends including Shelley Spear, Will Spear, Adam Miller, Alison White, and Sarah Garza. Phil Magistro showed bottomless patience and support in the field and at home. I appreciate Zach Szablewski's support in the writing of this thesis.

Dr. Paul Doherty, Dr. Richard Scherer, Dr. Viviana Ruiz-Gutierrez, and Sara Bombaci provided valuable technical assistance with along the way. My graduate committee members, Drs. Cameron Aldridge, Ben Bobowski, and Barry Noon greatly improved the quality of this manuscript through their thoughtful review and suggestions at every stage. My deepest appreciation goes to my advisor, Liba Pejchar, for believing in me when I did not believe in myself, continually showing me new perspectives, and giving me the confidence to take on future challenges.

Thanks to my parents for their continued support of my education. Thank you for all the days on the river and vacation out west.

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CHAPTER ONE

IMPACTS OF ELK MANAGEMENT AND RIPARIAN CONDITION ON SONGBIRDS IN ROCKY MOUNTAIN NATIONAL PARK

INTRODUCTION

Apex predators influence prey density and behavior, affecting community structure and ecosystem function (Hairston et al. 1960, Pace et al. 1999). Removal of predators and the subsequent release from predation experienced by primary consumers has cascading impacts on other trophic levels. Estes & Palmisano (1974) were one of the first to document the consequences of removing a top predator from a system driven by top-down control. Where sea otters (*Enhydra lutris*) were hunted to extinction off the pacific coast of North America, sea urchin (*Strongylocentrotus spp.*) populations exploded and kelp forests declined dramatically. Following the widespread decline of large carnivores (Ripple 2014), similar top-down trophic cascades have been observed in freshwater and terrestrial ecosystems globally (Pace et al. 1999), including those in parks and other protected areas.

Predators influence prey populations directly through consumption and by stimulating costly defensive behavior, or trait-mediated indirect interactions (Creel & Christianson 2008). In Yellowstone National Park, removal of wolves (*Canis lupus*) resulted in a five-fold increase in the elk (*Cervus elaphus*) population size over 25 years (Eberhardt et al. 2007), and wolf reintroduction demonstrated that elk use of areas occupied by predators was reduced (Altmann 1956, Ripple et al. 2001). In the absence of wolves, large herds of elk and other ungulates can remain for long periods of time and in high concentrations in areas rich in resources such as riparian willow communities (Singer et al. 1994, Roath & Krueger 1982). In Grand Teton National Park, Wyoming, USA, for example, Berger et al. (2001) demonstrated a trophic cascade brought about by the local extinction of grizzly bears and wolves that included an increase in moose (*Alces alces*), a subsequent change in riparian vegetation structure, and a reduction of avian neotropical migrants in the impacted willow communities.

Willow growth and height is determined by large ungulate and beaver browsing (Singer et al. 1994), as well as site conditions such as soil type, length of growing season, nutrient concentrations, and water table height (Cottrell 1995, Peinetti 2001). In the absence of wolves, elk have heavily impacted riparian vegetation by decreasing willow and aspen growth and recruitment directly through herbivory (Grimm 1939, Lovaas 1970, Singer et al. 2002, NRC 2002, Barmore 2003), and indirectly by out-competing and reducing beaver populations, which maintain surface and groundwater levels that are favorable to willow (Cooper et al. 2003).

Degradation to riparian willow communities threatens a number of critical ecological and economic functions for nature and society, including stabilizing stream banks (Wright et al. 2002), moderating water temperatures (Anbumozhi et al. 2005), purifying water for downstream communities (Vellidis et.al. 2002), and offering attractive recreational opportunities (Taylor et al. 1996). Riparian areas also provide important habitat for plants and animals (Naiman et al. 2005, Sabo et al. 2005). Although riparian corridors cover less than 1.0 percent of the landscape in western North America (Knopf et al. 1988), they support 80% of vertebrates during some stage of their life (Knopf et al. 1988) and avian density in riparian areas is often double that of adjacent uplands (Brinson et al. 1981).

In the mid 1900’s, gray wolves and grizzly bears (*Ursus arctos ssp.*) were extirpated from much of the western United States including Sequoia and Kings Canyon National Parks, CA, Yellowstone National Park, WY, and Rocky Mountain National Park, CO. At each of these parks, wolves preyed primarily on deer (*Odocoileus virginianus* and *Odocoileus hemionus*) and elk, which consume willow (*Salix spp.*) and aspen (*Populus tremuloides*) as a large portion of their winter diet (Monello et al. 2005). Research at each of these parks has shown that increased ungulate browsing following the local extirpation of wolves causes significant long-term impacts to riparian plant communities (Monello 2005, Beschta et al. 2008, Ripple et al. 2012).

In the early 1990's, Rocky Mountain National Park (RMNP) managers observed declines in riparian plant communities and began research on the causes of the decline, impacts to the ecosystem and park visitors, and potential restoration techniques. As part of this research, RMNP installed sixteen small experimental exclosures (0.13 ha) in 1994 and one larger-scale exclosure (12.26 ha) in 2007 to determine the cost, visual impact, and ecological impacts of using fencing to protect vegetation from elk browse. Based on observed patterns of elk browse and vegetation recovery, RMNP managers implemented an Elk and Vegetation Management Plan in 2008 to restore these degraded willow and aspen communities, using a combination of elk exclosures and culling. RMNP has since installed 1-3 additional exclosures per year (2.0-12.2 ha in size), with vegetation conditions varying within the fence at the time of installation. The exclosures are ~2 m tall with a 40 cm gap at the bottom, allowing smaller animals to enter. Each exclosure also has a gate to provide human access. RMNP monitors vegetation annually, but does not monitor other components of riparian ecosystem restoration as part of the Elk and Vegetation Management Plan.

Many agencies such as the National Park Service, lack funds for species-level monitoring that is essential to inform adaptive management. Instead land managers rely on a coarse-filter approach such as remote monitoring of vegetation communities to address the conservation of biological diversity (e.g., Haufler et al. 1996). To leverage this course-filter approach, agencies need to understand the role of species as indicators of changes to ecosystem processes (Simberloff 1998), the degree that proxy species serve as surrogates for unmeasured species (e.g., Wiens et al. 2008), and the limitations of these approaches.

The objective of my study is to evaluate how elk exclosures and the condition and extent of the riparian willow community in RMNP affect songbirds in the absence of an apex predator. Specifically, I address the following questions: How does the presence or absence of elk exclosures, and key characteristics of the riparian plant community (shrub height as well as local and landscape scale shrub cover) influence the density and occupancy of riparian bird species? If so, will monitoring trends in common riparian species over time also capture long-term effects on rare species that are more difficult to detect? Based on findings from the Greater Yellowstone Ecosystem (Beger et al. 2001; Olechnowski & Debinski 2008; Baril 2011), I predicted that riparian bird density and occupancy would respond positively to elk exclosures, shrub height, and local and landscape scale percent cover. I expected these relationships to be strongest for birds in guilds such as foliage gleaners and shrub nesters that rely on riparian vegetation for foraging and nesting. I also predicted that shrub height and percent cover would have a greater effect on riparian birds than the presence of an exclosure given the variation in shrub condition at the time the exclosures were installed.

METHODS

Study Area

Rocky Mountain National Park is situated in north central Colorado and consists of ~1075 km^2 of federally protected land. I established my study sites in eight valleys in RMNP's low-elevation montane riparian ecosystems (Figure 1). These valleys are between 2300-2800 m in elevation and have a mean annual precipitation of 41 cm (Singer et al. 1998b), with peak stream flow usually occurring in early to mid-June (USDA 1995, 1996, 1997) due to snow runoff. The 30-year average temperature ranges from 9 to 17°C during the 5-month growing season of May through September (Alstad et al. 1999).

My study areas consist of wet meadows dominated by willow (mainly *Salix monticola, S. geyeriana,* and *S. planifolia*), birch (*Betula spp.*), alder (*Alnus spp.*), sedges (*Carex spp.*), rushes (*Juncus balticus*), and grasses (*Phleum spp., Calamagrostis spp., Bromus spp., Poa spp.*). Adjacent to the riparian zone lie large, open grasslands bordered by lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudtsuga menziesii*) on north facing slopes and ponderosa pine (*Pinus ponderosa*) on south facing slopes with intermittent stands of trembling aspen.

Sampling Design

Fifty bird sampling sites were identified using a stratified random design that accounted for valleys, the presence or absence of an elk exclosure, willow height, and willow density, using data collected by RMNP between 2009-2011 as part of the EVMP monitoring plan (unpublished data; Appendix 1). Sites were at least 150 m apart to minimize the likelihood of counting the same individual twice at two sites. Territory widths for species commonly occurring in riparian plant communities are generally smaller than 150 m (Ammon 1995, Ammon & Gilbert 1999, Guzy & Ritchison 1999, Wheelwright & Rising 2008). Eleven sites were located within elk exclosures; seven of these exclosures were erected in 2007-2011 and they ranged in size from 1.98-12.26 hectares. The remaining four were established in 1994 as 0.13 ha experimental exclosures.

Bird Surveys

Birds were sampled at all 50 study sites using standard point count techniques (Hutto et al. 1986) during June-July 2013. Each site was sampled by one of two trained observers 3-4 times during the duration of the study. All visits were separated by at least seven days. After arriving at a site, I allowed a one minute rest period before beginning a five minute point count. For each bird seen or heard during the count, I recorded species, distance from the observer, and time observed. Birds that flew over a point without landing were not recorded. Surveys were conducted from one- half hour before sunrise until no later than 10:00. No sites were sampled in rain. I recorded wind speed on the Beaufort scale and all surveys exceeding 20 km/hr were removed from analysis (Anderson and Ohmart 1977).

To determine if elk exclosures and riparian shrub conditions affected birds with similar behaviors or resource requirements, I classified all observed species by nesting guild (BLM 2014) and foraging guild (DeGraaf et. al 1985; Appendix 2). I excluded guilds with less than 50 observations from the analysis. I also excluded the flycatching guild because the Dusky Flycatcher was the only species observed in this guild. Similarly, I did not include the hovering guild because the Broad-tailed Hummingbird was the only species observed in this guild. Thus, only ground foragers and foliage gleaners were included in the analysis.

Vegetation Surveys

At each site, I measured vegetation along a 30 m line transect. The middle of the transect was fixed on the bird sampling point and the line extended 15 m in either direction along a randomly selected bearing. For all live shrubs intersecting the line, including foliage projected downward onto the line, I recorded species name, canopy intercept length, and maximum height. A site's shrub height was calculated as the average height of all intersecting shrubs. Percent cover at a site was calculated as the sum of the intercepting shrub canopies divided by the total line length. To investigate the effects of larger scale vegetation patterns, I used land cover data from the RMNP GIS database (USBR 2005), which includes polygon coverage of vegetation (digitized from 1:12000 scale aerial photographs), to determine the percent of riparian shrub cover within a 300 m radius of each site.

Data Analysis

I assessed whether the continuous habitat variables (shrub height, local-scale percent shrub cover, 300 m riparian shrub cover) were correlated using Pearson's correlation coefficients. I used two-sided t-tests with unequal variances to examine potential correlations among the presence of an elk exclosure and shrub height, local-scale percent shrub cover, and 300 m riparian shrub cover.

Bird Density

I used Program DISTANCE 6.0 Release 2 (Thomas et al. 2006) to estimate detection probability and bird density for species with at least 50 observations (Buckland et al. 1993). I accounted for the uneven number of visits to each point transect by incorporating a survey effort multiplier in the analysis (Buckland et al. 2001). I right truncated observations at 50 m to remove large distance outliers (Buckland et al. 2001). For each species and guild, I manually selected distance intervals (Buckland et al. 2001), with cut points based on the distribution of observations at different distances, to identify the detection curves that fit best.

I modeled detection for each of the five species. Guild observations were comprised of a number of species and detection probability was modeled for the guild using pooled species data. I modeled detection probability by testing half-normal and hazard rate key functions using simple polynomial and cosine series expansions (Buckland et al. 2001). I used an information theoretic approach (Burnham & Anderson 2002) to select the top detection model based on

Akaike's Information Criterion (AIC) and assessed overall model fit using standard goodness of fit tests and visual plots of the data (Thomas et al. 2006). I then used the Multiple Covariate Distance-Sampling engine (Thomas et al. 2006) to model detection probabilities using covariates. I considered covariates on detection representing (1) time of day, (2) observer effect, and vegetation obstruction cover due to (3) shrub height or (4) local-scale shrub percent cover, and identified the best detection model using AIC.

DISTANCE 6.0 is designed to directly model continuous covariates on detection, but can only model categorical covariates on density. Therefore, prior to analysis of the factors associated with bird density, I categorized continuous habitat predictor variables into three categories. For local-scale percent cover, I defined cover categories relative to other sites surveyed, with the bottom 30% of observed values being classified as “sparse”, middle 40% as “medium”, and top 30% as “thick”. Local scale percent cover ranged from 0-100% therefore the categories were sparse: 0-29% (n=22), medium: 30-70% (n=16), and thick: 70-100% (n=12). Landscape scale riparian shrub cover (% cover within a 300 m radius of each site) ranged from 0.9-79.3%, thus categories were small: 0-23% (n=24), medium: 24-55% (n=24), and 56-80% large (n=2). The average shrub height at a site was categorized as short < 0.5 m (n=6), medium: 0.5 – 1.5 m (n=13), and tall >1.5m (n=30), with tall sites being defined by the height at which shrubs have been shown to tolerate elk browse (Gaffney 1941). These categories were incorporated into the DISTANCE analysis as strata to estimate mean habitat-specific density of songbirds within each vegetation type.

Using the best detection model, I estimated bird or guild density and 95% confidence intervals for each category of covariate. I express my results as estimates of density (birds/ha) and I interpret differences using 95% confidence intervals (density, 95% lower CL–upper CL)

(Sim & Reid 1999, Brand et al. 2010). Models that failed to converge or that contained nonsensical parameter estimates were eliminated from the model set for the appropriate species and were not used for inference.

Bird Occupancy

I modeled bird occupancy (Ψ) as a function of site characteristics affecting presence–absence, dependent on site and sampling covariates affecting detectability (MacKenzie et al. 2002), using the Unmarked package (Fiske et al. 2011) in R (R Development Core Team 2012). As with density, I modeled detection for each of the five species using data from repeat visits. Guild observations were comprised of a number of species and detection probability was modeled for the guild using pooled species data. I began by determining the best covariate structure on detection probability (p). I held the proportion of sites occupied constant, $\Psi(\cdot)$, and allowed species detection to vary with each covariate separately (time of day, observer, shrub height, local-scale shrub cover). Using the best detection model, I held detection constant and varied Ψ with each covariate on occupancy separately. I used my constant model, $\Psi(\cdot)p(\cdot)$, as a reference model. All models were ranked according to AIC values (Akaike 1973, Burnham & Anderson 1998) calculated within Unmarked. Models were chosen a priori to compare several factors I predicted to be likely to affect parameter estimates. As with bird density, I tested the influence of average shrub height, local-scale percent cover, 300 m riparian cover, and exclosure presence/absence. I ranked models based on AIC (Burnham & Anderson 2002), identifying top models (ΔAIC < 2.0) for each species and guild. The top model does not necessarily represent all of the environmental or biological processes that influenced the probability of occupancy or species detection probabilities.

To determine whether common riparian bird species could act as surrogates for species with relatively few detections, I assessed species co-occurrence using the Cooccur package version 1.2 (Griffith et al. 2014) for R. This R package applies the probabilistic model of species co-occurrence (Veech 2013) to a set of species distributed among a set of survey or sampling sites. Because sites were visited an uneven number of times, I pooled presence/absence data from two randomly chosen visits. I used Cooccur to calculate the observed and expected frequencies of co-occurrence between each pair of species. The expected frequency is based on the distribution of each species being random and independent of the other species. Species pairs that were expected have less than 1 co-occurrence were filtered from the analysis.

RESULTS

Bird and plant community composition

I observed 1264 individuals of 43 bird species. Five species were detected at least 50 times and thus met my criteria for analysis. These species were American Robin (*Turdus migratorius*), Lincoln's Sparrow (*Melospiza lincolnii*), Song Sparrow (*Melospiza melodia*), Dusky Flycatcher (*Empidonax oberholseri*), and Wilson's warbler (*Wilsonia pusilla*; Table 1).

Of the ten foraging guilds observed (Appendix 3), ground foragers were the most frequently detected (669). Ten of the 43 species observed were classified as foliage gleaners, which were observed 381 times. Wilson's Warblers constituted 186 (49%) of the 368 foliage gleaner observations. I observed 669 ground foragers, which consisted of nineteen species including American Robin, Lincoln's Sparrow, and Song Sparrow. These three species were observed 85 (13% of ground forager observations), 223 (33%), and 128 (19%) times, respectively, and collectively comprised 65% of ground foragers detected.

Of the six nesting guilds observed (Appendix 4), ground nesters were the most frequently detected (492). Seven species were classified as ground nesters. Lincoln's Sparrow (n = 223) and Wilson's Warblers (n = 186) were included in the ground nesting guild and accounted for 45% and 38%, respectively, of the 492 total observations of ground nesters. I recorded 404 observations of shrub nesters which was comprised of five species including Song Sparrows (n = 128, 25%) and Dusky Flycatchers (n = 68, 12%).

I recorded four woody plant genera along vegetation transects. Willow was the dominant plant, comprising 74% of shrubs observed at the sites. Other species observed included birch (*Betula spp.*; 16%), aspen (6%), and shrubby cinquefoil (*Dasiphora fruticosa*; 4%). Average shrub height ranged from 0.0-6.1 m with a mean of 2.2 m (SD=1.6). Local-scale percent cover ranged from 0.0-100.0% with a mean of 42.4% (SD= 33.9%), and 300 m riparian percent cover ranged from 0.9-79.3% with a mean of 25.7% (SD= 17.1).

Correlation among predictor variables

Using Pearson's correlation, I found a strong positive relationship (r = 0.68) between the number of years an exclosure was in place and local-scale percent cover of shrubs (Table 2). Local-scale shrub cover was also moderately correlated with shrub height (r = 0.48). Elk exclosure age was moderately correlated with shrub height (r =0.40). There was a weak relationship between 300 m riparian shrub cover and local-scale percent cover (r =0.26). I found no significant relationship between 300 m riparian cover and shrub height (r =0.08), or exclosure age (-0.12).

Detection probability

When modeling bird density, a half normal model with cosine adjustment was the best fit to the distance data for Wilson's Warbler (χ^2 = 0.9072, p = 0.92), Song Sparrow (χ^2 = 0.9136, p =

0.92), Dusky Flycatcher (χ^2 = 4.7331, p = 0.45), and American Robin (χ^2 = 2.3089, p = 0.68) detection. A hazard rate model with cosine adjustment was the best fit to model detection for Lincoln's Sparrow (χ^2 =3.90, p = 0.27).

When modeling occupancy, detection probability varied with observer for Wilson's warbler and American Robin. Dusky Flycatcher detection varied with shrub height. Detection probability of Song Sparrows and Lincoln's sparrows did not vary with any covariates tested. There was substantial model selection uncertainty for most species (Table 3).

Effects of elk exclosures and willow condition on bird communities

Elk exclosures did not influence the density ($\bar{x}$, 95% lower CL–upper CL) of any species or guild except for shrub-nesting birds; a significantly higher density of shrub nesters were observed within exclosures (3.12, 2.51-3.89) compared to unfenced sites (6.95, 4.15-11.62). The presence of elk exclosures did not appear in the top occupancy model for any bird species or guild (Table 3).

Shrub height was positively correlated with bird density for one of the five species modeled (Figure 2a). Due to too few detections at short-height sites (n=2), I was unable to estimate Dusky Flycatcher density at short sites; however, significantly more Dusky Flycatchers were observed in tall shrubs compared with sites with medium shrub heights. There was no relationship between bird density and shrub height for American Robin, Lincoln's Sparrow, Wilson's Warbler, Song Sparrow, or any of the guilds (Figure 2b). Shrub height was an important predictor of bird occupancy for Dusky Flycatcher and Lincoln's Sparrow (Table 3). For shrub-nesters, the top occupancy model included shrub height (Table 3).

Local-scale (15 m) percent shrub cover was an important predictor of bird density for three out of five species modeled (Figure 2c). I found significantly higher densities of Lincoln's

Sparrows, Song Sparrows and Wilson's Warblers in sites with thick shrub cover. Density of foliage gleaners and shrub nesters was also significantly greater at sites with greater shrub cover (Figure 2d). I found no relationship between density of American Robin, Lincoln's Sparrow, ground foragers, and ground nesters and percent shrub cover at local scales. Local-scale percent shrub cover did not appear in the top occupancy model for any species or guilds tested (Table 3).

Landscape-scale (300 m radius) riparian shrub cover was an important predictor of the density of Wilson's Warblers, with higher bird densities observed in areas with greater riparian shrub cover (Figure 2e). I found no relationship between landscape scale shrub cover and any other bird species, foraging or nesting guild (Figure 2f), and this habitat variable did not appear in the top occupancy model for any species or guild (Table 3).

Species co-occurrence

Of the 43 species observed during up to five visits to each sampling site, 40 species were observed during the two visits analyzed for co-occurrence. Of 780 species pair combinations, 467 pairs (59.87 %) were removed from the analysis because expected co-occurrence was < 1; thus, 313 pairs were analyzed. Seventeen associations were classified as positive, with the Yellow-rumped Warbler (*Setophaga coronate*) having the most positive associations (5). Two negative associations were found, 294 associations were random, and zero unclassifiable (Figure 3; Appendix 5).

DISCUSSION

Protecting and restoring habitat for riparian birds is important in the absence of apex predators (Berger 2001). Over-browsing by elk reduces the cover and structural complexity of riparian shrubs (Monello 2005), which compromises the availability of food, cover and nesting sites for avian species (Baril 2011). RMNP is using elk exclosures in an adaptive management framework restore riparian vegetation (USDOI 2012), with yet unknown consequences for bird communities and other taxa of conservation concern. My study reveals that the presence of elk exclosures has positive effects on the density of riparian shrub-nesting birds. I also found that Dusky Flycatcher, Song Sparrow and Wilson's Warbler, three species that depend on riparian vegetation for foraging or nesting (BLM 2014, DeGraaf et. al 1985), had strong positive associations with shrub height and cover both inside and outside exclosures.

Overall, I found that the exclosures, themselves, are not providing benefits such as protection from predators and that any observed differences in bird density or occupancy can be attributed to vegetation structure. However, birds in the shrub nesting guild were observed in greater densities in exclosure sites compared to unfenced sites. These results may reflect the finding that shrub cover increased with time since exclosure installation, and shrub nester density was more than three times greater at sites with high percent cover than in medium or low cover. The positive correlation between exclosure age and percent shrub cover, and weak correlation with shrub height, suggests that shrub cover may recover faster than shrub height within exclosures.

I found a greater density of foliage gleaning and shrub-nesting bird guilds, and a greater density of particular bird species that depend on these resources (Dusky Flycatcher, Song Sparrow and Wilson's Warbler) in riparian habitats with greater shrub cover and height. Complex vertical and horizontal structure provides a variety of foraging and nesting resources that can be partitioned among species and individuals, thus supporting greater bird density (MacArthur & MacArthur 1961). Studies in the Greater Yellowstone Ecosystem support these results, showing that willow height significantly influenced songbird richness and abundance (Olechnowski & Debinski 2008, Baril 2011). The two other species with sufficient detections for density models, American Robin and Lincoln’s Sparrow, do not utilize shrubs for foraging or nesting (BLM 2014, DeGraaf et. al 1985). The density of these species did not vary with shrub height or cover. Similarly, as expected, ground forager and ground nester density was not dependent on vegetation structure.

The extent of willow cover may be as or more important than local shrub cover and structure for some species. I found that the percent cover of riparian shrubs at a larger scale (300 m) was strongly predictive of Wilson's Warbler density. This result suggests that larger patches of riparian shrubs may be critical for providing high quality foraging habitat for warblers and other foliage gleaners.

In contrast to bird density, the probability of occupancy did not depend on vegetation structure for most species and guilds. Estimates of occupancy and detection for all five species of birds modeled did not meet standards of ‘good precision’ used in other studies (SE(est)/est < 0.30; Bailey et al. 2004).

The striking difference in the relationships between bird density and occupancy and riparian structure has important implications for long-term monitoring in RMNP and other areas where active ecological restoration monitoring is underway. Because detection/non-detection data can often be collected with much less effort, site occupancy may be a less expensive alternative to density (Noon et al. 2012). Density and occupancy measure different but related aspects of population dynamics—the number of individuals of the target species in the landscape and the proportion of the landscape occupied by the target species, respectively (MacKenzie & Nichols 2004). While occupancy and abundance are positively related (Royle & Nichols 2003, MacKenzie & Nichols 2004), changes in abundance may not always be reflected as occupancy changes depending on the scale, life history, and environmental conditions (Nielsen et al. 2005, Royle & Dorazio 2008). Despite the greater effort required to estimate density, my results suggest that when the objective is to observe small changes to populations, density estimation may detect important trends that occupancy may miss. I consistently detected relationships between vegetation condition and birds more frequently using density as state variable compared with occupancy. My results support other findings that environmental factors influencing abundance may differ from those limiting distribution (Nielsen et al. 2005). Thus, the density of riparian obligate birds may be the most accurate metric for long-term monitoring of riparian habitat condition in areas altered by anthropogenic change.

Only the most frequently observed species in my study, however, had sufficient observations to estimate density. The number of observations required makes density or abundance estimation difficult or impossible for rare species, which are often of particular interest to agencies such as NPS. For instance, the MacGillivray's Warbler may be of particular interest to RMNP due to its designation by Partners in Flight as one of four species identified as high priority in high-elevation riparian habitats in Colorado (Beidleman 2000). With only twenty-six observations, modeling density is not possible. In these cases, occupancy modeling may provide valuable information on long-term trends (Noon et al. 2012).

Alternatively, measuring species co-occurrence may allow land managers to rely on "surrogate" species to serve as proxies for measuring the effects of a conservation intervention on a broader sets of species (Wiens et al. 2008). Support for surrogate or indicator species is mixed, and studies suggest that relationships between species or taxa must be demonstrated rather than assumed (Simberloff 1998, Roberge & Angelstam 2004, Cushman et al. 2010). My co-occurrence analysis demonstrated associations between a limited number of bird species that could be used as surrogate species by RMNP; however, the majority of species showed no positive or negative associations.

I also caution that this study occurred over a single season, and does not provide any information on changes in population density or occupancy over time as function of elk exclosures and vegetation condition. Longer-term monitoring would enable managers to more accurately attribute differences in bird density and occupancy to changing vegetation characteristics within the exclosures. Furthermore, long-term monitoring of conditions within the exclosures may identify other factors that may be hindering ecosystem recovery such as changes to hydrology. Loss of riparian shrubs has led to destabilization of river banks, and changes to hydrologic regimes as well as a reduction in beaver populations (Cooper et al. 2003). Natural hydrological processes may be too altered to recover without additional human intervention. Beaver may find streams too wide or incised to recolonize. Long-term monitoring of hydrological flow and other ecosystem functions in riparian ecosystems should complement monitoring of bird and plant communities.

Many parks and protected areas such as Rocky Mountain National Park provide suitable habitat for diverse plant and animal communities, while also providing recreational and educational opportunities for millions of visitors annually. RMNP visitors reported a serious negative response to potential losses of water, riparian vegetation, or riparian-dependent wildlife, and a willingness to pay 70% more in entrance fees to protect these resources (Taylor et al. 1996). Because density has been shown as one of the greatest influences on detection probability (Royle & Nichols 2003), restoring riparian vegetation increases the chances of visitors encountering birds and other riparian-dependent wildlife.

In plant and animals communities altered by the loss of apex predators, and subject to the deleterious effects of over grazing by herbivores, conservation interventions may be critical to restoring habitat for birds. My results suggest that a top-down trophic cascade may be at least locally mitigated using a bottom-up approach such as fenced exclosures, if those exclosures restore the vegetation structure and cover required for food, shelter and reproduction for the species that inhabit these communities.

TABLES AND FIGURES

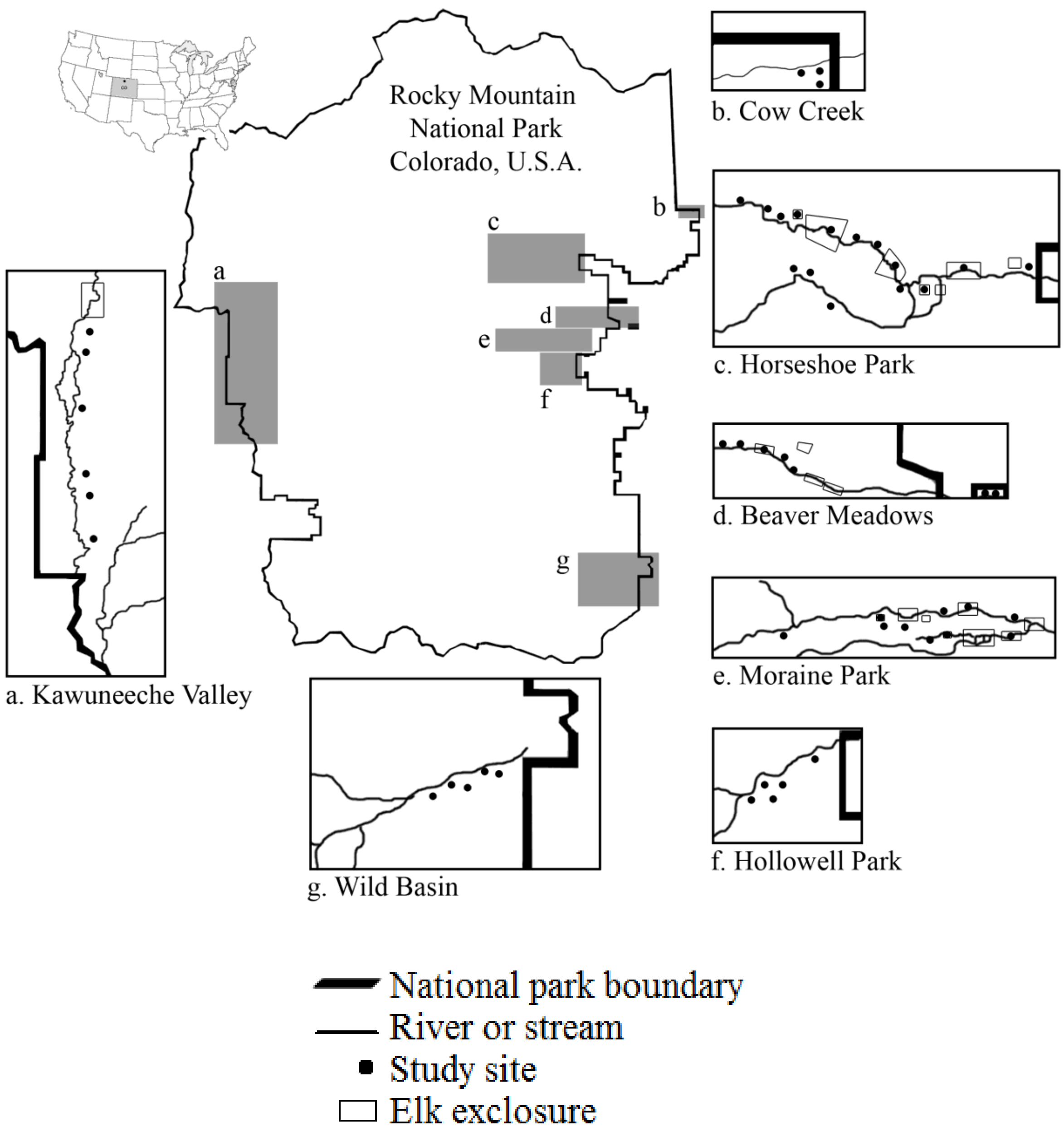

FIG. 1. Map of 2013 bird and vegetation study sites, including exclosures and unfenced sites, in Rocky Mountain National Park, Colorado, USA.

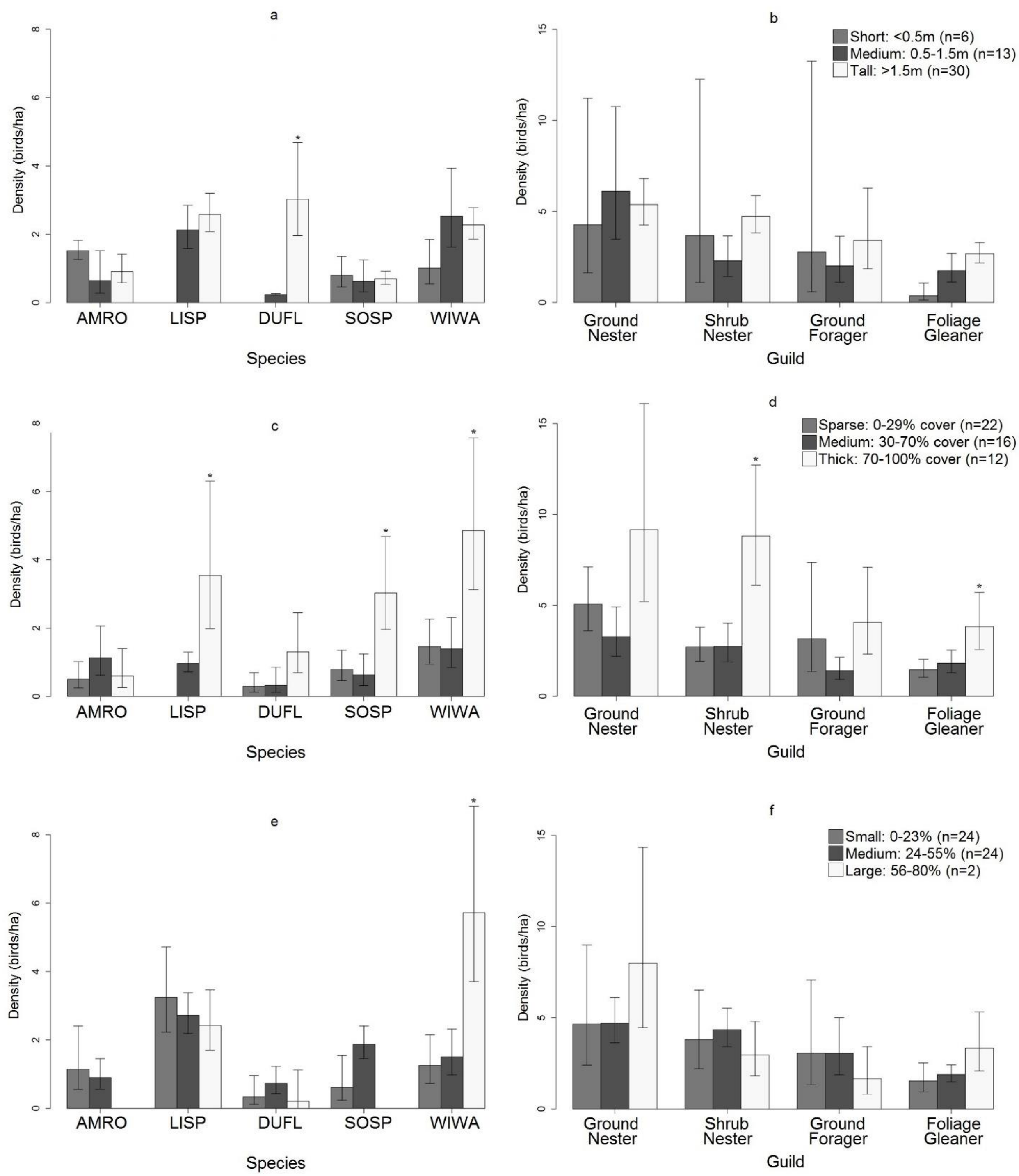

FIG 2. Bird density in RMNP riparian willow communities in 2013 varied by 'height' (a, b), 'local scale shrub cover' (c, d) and '300 m shrub cover (e, f). Figures report estimates ± 95% CI and significant differences (*) within species or guild groups. See appendix 2 for full species names associated with each four letter code.

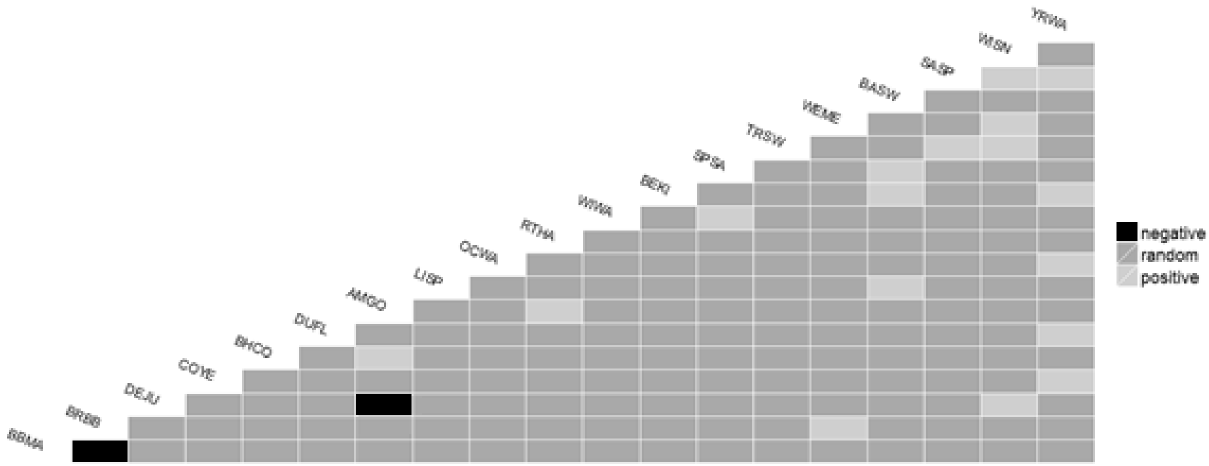

FIG 3. Bird species co-occurrence patterns in RMNP riparian willow communities in 2013 show negative associations with two species pairs (black blocks) and positive associations with 17 species pairs (light gray blocks). All other associations are random. Species pairs that are expected have less than 1 co-occurrences were filtered from the analysis.

TABLE 1. Bird species observed in RMNP riparian willow communities in 2013 with sufficient detections to estimate density, their foraging and nesting guilds, and the number of observations.

Species	**Scientific Name**	**Foraging Guild**	**Nesting Guild**	**Number Observed**
Lincoln's Sparrow	*Melospiza lincolnii*	Ground forager	Ground	223
Wilson's Warbler	*Cardellina pusilla*	Foliage gleaner	Ground	186
Song Sparrow	*Melospiza melodia*	Ground forager	Shrub	128
American Robin	*Turdus migratorius*	Ground forager	Tree	85
Dusky Flycatcher	*Empidonax oberholseri*	Flycatching	Shrub	68

TABLE 2. Pearson’s correlation coefficients for covariates.

	Shrub height	Shrub cover (15m radius)	Exclosure age
Shrub height	x	x	0.40
Shrub cover (15m radius)	0.48	x	0.68
Shrub cover (300m radius)	0.08	0.26	-0.12

TABLE 3. Models predicting bird species occupancy (ψ) in RMNP riparian willow communities in 2013, using the top ranked model for detection (*p*), and ranked by ΔAIC. *K* is the number of parameters; ΔAIC is the difference in AIC in relation to the most parsimonious value; w_i is Akaike weight.

Species Occupancy		*K*	ΔAIC	w_i
American Robin	ψ(.)*p*(observer)	3	0.00	0.33
	ψ (AveHeight)*p*(observer)	4	0.06	0.32
	ψ(LocalCover)*p*(observer)	4	1.96	0.12
	ψ(Exclosure)*p*(observer)	4	1.98	0.12
	ψ(300mCover)*p*(observer)	5	2.38	0.10
Lincoln's Sparrow	ψ(.)p(.)	2	0.00	0.39
	ψ(AveHeight)*p*(.)	4	1.12	0.23
	ψ(Exclosure)*p*(.)	3	1.16	0.22
	ψ(LocalCover)*p*(.)	3	2.70	0.10
	ψ(300mCover)*p*(.)	4	3.83	0.06
Song Sparrow	ψ(.)*p*(.)	2	0.00	0.40
	ψ(Exclosure)*p*(.)	3	1.29	0.21
	ψ(300mCover)*p*(.)	3	1.59	0.18
	ψ(LocalCover)*p*(.)	4	2.00	0.15
	ψ(AveHeight)*p*(.)	3	3.85	0.06
Dusky Flycatcher	ψ(.)*p*(AveHeight)	3	0.00	0.34
	ψ(AveHeight)*p*(AveHeight)	4	1.10	0.19
	ψ(LocalCover)*p*(AveHeight)	4	1.18	0.19
	ψ(300mCover)*p*(AveHeight)	5	1.53	0.16
	ψ(Exclosure)*p*(AveHeight)	4	1.92	0.13
Wilson's Warbler	ψ(.)*p*(observer)	3	0.00	0.29
	ψ(300mCover)*p*(observer)	5	0.45	0.23
	ψ(Exclosure)*p*(observer)	4	0.98	0.18
	ψ(LocalCover)*p*(observer)	4	1.29	0.15
	ψ(AveHeight)*p*(observer)	4	1.56	0.14
Guild Occupancy		*K*	ΔAIC	w_i
Ground Foragers	ψ(.)*p*(.)	2	0	0.498
	ψ(Exclosure)*p*(.)	3	2	0.183
	ψ(LocalCover)*p*(.)	3	2	0.183
	ψ(300mCover)*p*(.)	4	4	0.067
	ψ(AveHeight)*p*(.)	4	4	0.067

Foliage Gleaners	ψ(LocalCover)*p*(observer)	4	0	0.811
	ψ(AveHeight)*p*(observer)	4	4.51	0.085
	ψ(.)*p*(observer)	3	5.82	0.044
	ψ(300mCover)*p*(observer)	5	6.51	0.031
	ψ(Exclosure)*p*(observer)	4	6.72	0.028
Shrub Nesters	ψ(.)*p*(.)	2	0	0.365
	ψ(Exclosure)*p*(.)	3	0.88	0.235
	ψ(300mCover)*p*(.)	4	1.53	0.17
	ψ(LocalCover)*p*(.)	3	1.77	0.151
	ψ(AveHeight)*p*(.)	4	3.05	0.079
Ground Nesters	ψ(.)*p*(observer)	3	0	0.446
	ψ(LocalCover)*p*(observer)	4	1.99	0.165
	ψ(Exclosure)*p*(observer)	4	1.99	0.165
	ψ(AveHeight)*p*(observer)	4	1.99	0.165
	ψ(300mCover)*p*(observer)	5	3.99	0.061

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APPENDIX 1

Sampling points and covariates.

Site	Valley	Exclosure	Shrub Percent Cover	Average Shrub Height
1	Hollowell Park	N	Dense	Tall
2	Moraine Park	N	Dense	Tall
3	Beaver Meadows	N	Dense	Tall
4	Hidden Valley	N	Dense	Tall
5	Wildbasin	N	Dense	Tall
6	Kawuneeche	N	Medium	Medium
7	Kawuneeche	N	Medium	Medium
8	Horseshoe Park	N	Medium	Medium
9	Kawuneeche	N	Medium	Short
10	Cow Creek	N	Medium	Tall
11	Horseshoe Park	N	Medium	Tall
12	Hollowell Park	N	Medium	Tall
13	Moraine Park	N	Medium	Tall
14	Hollowell Park	N	Medium	Tall
15	Hollowell Park	N	Medium	Tall
16	Hidden Valley	N	Medium	Tall
17	Wildbasin	N	Medium	Tall
18	Wildbasin	N	Medium	Tall
19	Wildbasin	N	Medium	Tall
20	Wildbasin	N	Medium	Tall
21	Kawuneeche	N	Sparse	Medium
22	Beaver Meadows	N	Sparse	Medium
23	Beaver Meadows	N	Sparse	Medium
24	Cow Creek	N	Sparse	Medium
25	Cow Creek	N	Sparse	Medium
26	Horseshoe Park	N	Sparse	Medium
27	Horseshoe Park	N	Sparse	Medium
28	Kawuneeche	N	Sparse	Medium
29	Kawuneeche	N	Sparse	Medium
30	Moraine Park	N	Sparse	Short
31	Hidden Valley	N	Sparse	Short
32	Beaver Meadows	N	Sparse	Short
33	Hondius	N	Sparse	Tall
34	Beaver Meadows	N	Sparse	Tall
35	Horseshoe Park	N	Sparse	Tall
36	Mill Creek	N	Sparse	Tall
37	Moraine Park	N	Sparse	Tall
38	Moraine Park	N	Sparse	Tall

39	Beaver Meadows	N	Sparse	Tall
40	Horseshoe Park	Y	Dense	Medium
41	Horseshoe Park	Y	Dense	Tall
42	Horseshoe Park	Y	Dense	Tall
43	Horseshoe Park	Y	Dense	Tall
44	Horseshoe Park	Y	Dense	Tall
45	Moraine Park	Y	Dense	Tall
46	Moraine Park	Y	Dense	Tall
47	Horseshoe Park	Y	Medium	Tall
48	Moraine Park	Y	Sparse	Short
49	Moraine Park	Y	Sparse	Short
50	Beaver Meadows	Y	Sparse	Tall

APPENDIX 2

All bird species observed in RMNP riparian willow communities in 2013, the number of detections for each species, and the foraging and nesting guild in which they were categorized.

Species Code	**Species**	**Scientific Name**	**Foraging Guild**	**Nesting Guild**	**Number Observed**
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	Ground forager	Ground	223
WIWA	Wilson's Warbler	*Cardellina pusilla*	Foliage gleaner	Ground	186
SOSP	Song Sparrow	*Melospiza melodia*	Ground forager	Shrub	128
AMRO	American Robin	*Turdus migratorius*	Ground forager	Tree	85
DUFL	Dusky Flycatcher	*Empidonax oberholseri*	Flycatching	Shrub	68
BBMA	Black-billed Magpie	*Pica hudsonia*	Ground forager	Shrub	46
RWBB	Red-winged Black Bird	*Agelaius phoeniceus*	Ground forager	Shrub	46
BTHU	Broad-tailed Hummingbird	*Selasphorus platycercus*	Hovering	Tree	45
YEWA	Yellow Warbler	*Setophaga petechia*	Foliage gleaner	Shrub	45
WAVI	Warbling Vireo	*Vireo gilvus*	Foliage gleaner	Tree	44
HOWR	House Wren	*Troglodytes aedon*	Foliage gleaner	Cavity	36
BRBB	Brewer's Blackbird	*Euphagus cyanocephalus*	Ground forager	Shrub	35
MAWA	MacGillivray's Warbler	*Geothlypis tolmiei*	Foliage gleaner	Shrub	26
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*	Ground forager	Tree	19
RCKI	Ruby-crowned Kinglet	*Regulus calendula*	Foliage gleaner	Tree	17
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	Ground forager	Ground	17

AMCR	American Crow	*Corvus brachyrhynchos*	Ground forager	Tree	15
WISN	Wilson's Snipe	*Gallinago delicata*	Probing	Ground	15
SPSA	Spotted Sandpiper	*Actitis macularius*	Probing	Ground	13
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	Foliage gleaner	Tree	13
TRSW	Tree Swallow	*Tachycineta bicolor*	Aerial forager	Cavity	11
CHSP	Chipping Sparrow	*Spizella passerina*	Ground forager	Shrub	10
DEJU	Dark-eyed Junco	*Junco hyemalis*	Ground forager	Ground	9
NOFL	Northern Flicker	*Colaptes auratus*	Ground forager	Cavity	9
PISI	Pine Siskin	*Sitta pygmaea*	Foliage gleaner	Tree	9
COYE	Common Yellowthroat	*Geothlypis trichas*	Ground forager	Tree	7
MADU	Mallard Duck	*Anas platyrhynchos*	Seeds	Ground	7
BCCH	Black-capped Chickadee	*Poecile atricapillus*	Ground forager	Cavity	6
SASP	Savannah Sparrow	*Passerculus sandwichensis*	Ground forager	Ground	6
VESP	Vesper Sparrow	*Pooecetes gramineus*	Ground forager	Ground	6
BASW	Barn Swallow	*Hirundo rustica*	Aerial forager	Tree	4
MOCH	Mountain Chickadee	*Poecile gambeli*	Foliage gleaner	Cavity	4
MOBL	Mountain Bluebird	*Sialia currucoides*	Flycatching	Cavity	3
WEME	Western Meadowlark	*Sturnella neglecta*	Ground forager	Ground	2
AMGO	American Goldfinch	*Spinus tristis*	Foliage gleaner	Shrub	1
BEKI	Belted Kingfisher	*Megaceryle alcyon*	Fish	Burrow	1
COGR	Common Grackle	*Quiscalus quiscula*	Ground forager	Tree	1
CORA	Common Raven	*Corvus corax*	Ground forager	Cliff	1
HAWO	Hairy Woodpecker	*Picoides villosus*	Bark forager	Cavity	1

OCWA	Orange-crowned Warbler	*Leiothlypis celata*	Foliage gleaner	Ground	1
PYNU	Pygmy Nuthatch	*Sitta pygmaea*	Bark forager	Cavity	1
RTHA	Red-tailed Hawk	*Passerculus sandwichensis*	Small animals	Tree	1
VGSW	Violet-green Swallow	*Tachycineta thalassina*	Aerial forager	Cavity	1

APPENDIX 3

All bird foraging guilds observed in RMNP riparian willow communities in 2013, and the number of detections for each guild.

Foraging Guild	**Number Observed**
Aerial forager	11
Bark forager	2
Flycatching	71
Foliage gleaner	368
Ground forager	669
Hovering	105
Probing	28
Seeds	8
Small animals	1
Fish	1

APPENDIX 4

All bird nesting guilds observed in RMNP riparian willow communities in 2013, the number of detections for each guild.

Nesting Guild	**Number Observed**
Burrow	1
Cavity	49
Cliff	1
Ground	492
Shrub	404
Tree	317

APPENDIX 5

Bird species co-occurrence patterns in RMNP riparian willow communities in 2013 listed in order of number of negative associations (n = 2 pairs), then number of positive associations (n = 17 pairs). See Appendix 2 for species names associated with each code.

Species Code	Number of positive associations	Number of negative associations	Number of random associations
AMGO	2	1	34
BRBB	1	1	10
DEJU	1	1	20
BBMA	0	1	36
YRWA	5	0	24
WISN	4	0	18
BASW	3	0	29
SASP	3	0	10
BEKI	2	0	9
SPSA	2	0	35
TRSW	2	0	15
WEME	2	0	35
COYE	1	0	11
BHCO	1	0	10
DUFL	1	0	11
LISP	1	0	8
OCWA	1	0	8
RTHA	1	0	11
WIWA	1	0	12
AMCR	0	0	39
AMRO	0	0	9
BCCH	0	0	9
BHGR	0	0	6
BTHU	0	0	11
CHSP	0	0	37
HAWO	0	0	6
HOWR	0	0	1
MAWA	0	0	8
MOBL	0	0	6
MOCH	0	0	9
NOFL	0	0	11
PISI	0	0	1
RCKI	0	0	8

RWBB	0	0	6
SOSP	0	0	8
VESP	0	0	9
WAVI	0	0	11
WCSP	0	0	32
YEWA	0	0	6
VGSW	0	0	9