



Original Research

Small-Scale Woodland Reduction Practices Have Neutral or Negative Short-Term Effects on Birds and Small Mammals[☆]

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ABSTRACT

Woodland reduction has been under way for decades to improve habitat for certain wildlife species, increase forage for livestock, improve watershed function and reduce soil erosion, and increase plant community heterogeneity. Land managers have implemented a variety of techniques to reduce woodlands. Yet most studies on outcomes are observational and focus on plant communities; fewer studies experimentally compare the relative effects of woodland reduction methods on wildlife. We conducted an experiment to evaluate the effects of three mechanical tree removal methods on habitat use by native birds and abundance of small mammals in the first 2 yr after treatment. Located in the Piceance Basin, Colorado, United States, this study consisted of seven replicated 1-ha stands of pinyon-juniper woodland treated with chaining, roller-chop, hydro-ax, as well as untreated plots ($n = 28$ plots). We found no differences in initial bird habitat use or small mammal abundance among the woodland reduction treatment methods. However, we found evidence that habitat use was significantly lower in all woodland reduction treatment plots than in control plots of dense woodland and open woodland habitats, and that use was positively associated with tree cover. Furthermore, no grassland or shrubland obligate birds used the treatment plots, suggesting that small-scale woodland reduction treatments may not provide attractive habitat for shrubland or grassland birds, at least within 2 yr following treatment. Because some bird species responded negatively to all methods of woodland reduction treatments, and no bird or small mammal species responded positively, the initial effects of small-scale chaining, roller-chop, and hydro-ax treatments on wildlife should not be overlooked.

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Introduction

Pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands have expanded over the past 100–150 yr into many sagebrush and grassland areas (Romme et al., 2009), which has had diverse ecosystem consequences. Increased woodland overstory has been associated with decreased diversity and cover of shrubs and grasses (Tausch et al., 1981; Miller et al., 2000), reduced soil seed bank density (Koniak and Everett, 1982), increased erosion potential, altered water availability and watershed function (Roundy and Vernon, 1999; Kormos et al., 2017), and impacts to habitat for sagebrush obligate wildlife (Falkowski et al., 2017). The practice of clearing or reducing pinyon and juniper woodland stands (henceforth referred to as woodland reduction) is commonly used to control conifer encroachment (Redmond et al., 2014), improve

habitat for wildlife species of conservation concern (Baruch-Mordo et al., 2013; Bergman et al., 2014), increase forage for livestock (Aro, 1971; Belsky, 1996), improve watershed function and reduce soil erosion (Roundy and Vernon, 1999), reduce fuels under fire mitigation plans (Schoennagel and Nelson, 2011), and/or increase plant community heterogeneity (Miller et al., 2014).

The use of woodland reduction is likely to continue as these practices are included in regional or federal management plans for rare or economically important wildlife species (e.g., mule deer *Odocoileus hemionus* Rafinesque, sage grouse *Centrocercus* spp.) (US Bureau of Land Management, 2011; Baruch-Mordo et al., 2013; DOI, 2013; Bergman et al., 2014; Stephens et al., 2016), as well as for fuel reduction under the National Fire Plan (Schoennagel and Nelson, 2011). However, pinyon and juniper woodlands support a high diversity of animal species and provide specialized or critical habitat for some species (Bombaci and Pejchar, 2016). Therefore, conversion of pinyon and juniper woodlands may have important implications for the maintenance of regional biodiversity (Gallo and Pejchar, 2016; Gallo et al., 2016). To sustain diverse native assemblages in areas undergoing pinyon and/or juniper removal, it is important to understand the effects of different woodland reduction practices on diverse wildlife species.

Land managers have implemented a variety of techniques to reduce woodlands and/or to improve sagebrush habitat (e.g., mechanical

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removal, prescribed burning, and thinning [see Jones et al., 2013; Bombaci and Pejchar, 2016]). Although comparisons of wildlife responses between prescribed burning or thinning treatments and mechanical treatments have been made in pinyon-juniper habitat (Kundaali and Reynolds, 1972; Turkowski and Watkins, 1976; Short et al., 1977; Severson, 1986), few studies have experimentally compared the relative effects of different mechanical woodland reduction methods on wildlife (Bombaci and Pejchar, 2016). Thus, we know little about whether animal species respond differentially to various mechanical woodland reduction methods. Furthermore, many previous studies on the effects of mechanical woodland reduction on wildlife have occurred in chaining treatments (dragging a boat anchor chain attached to two bulldozers across a stand, which uproots and kills trees) (O'Meara et al., 1981; Tausch and Tueller, 1995; Ranglack and du Toit, 2015; Bombaci and Pejchar, 2016). Hydro-ax (full mastication of trees using an articulating mower) and roller-chop (crushing of trees with a heavy bladed drum attached to a bulldozer) methods are also being used to reduce woodlands, but few studies have evaluated how wildlife in pinyon-juniper and sagebrush steppe ecosystems have responded to the vegetation and structural changes associated with these practices (Bombaci and Pejchar, 2016). Different mechanical woodland reduction methods generate different soil disturbance patterns that are likely to produce unique patterns of vegetation reestablishment (Stephens et al., 2016). These differences may affect how certain animal species respond to post-treatment conditions. Thus, understanding the comparative effects of various mechanical woodland reduction strategies on nongame species is ecologically interesting and has important conservation implications.

We used a series of small (1-ha) experimental plots to evaluate the initial effects that three different mechanical woodland reduction methods (chaining, hydro-ax, and roller-chop) have on small mammal abundance and bird habitat use. This experiment was originally designed to compare the effect of these different mechanical woodland reduction methods on grass, herb, and shrub regeneration and production. Although these plots were small in scale, we considered this to be a valuable and rare opportunity to use an experimental approach to assess short-term effects of different mechanical tree reduction methods on birds and small mammals.

We hypothesized that bird habitat use in treatment and control plots would vary by functional group (i.e., birds of dense woodland habitat, open woodland habitat, or shrubland-grassland habitat; see methods for functional group classification). Specifically, we predicted lower use of all woodland reduction treatments compared with control plots by birds of dense woodlands, higher use of all treatments compared with control plots by birds of shrublands and grasslands, and that habitat use would not differ among all treatments and control plots for birds of open woodlands. We did not expect bird habitat use to vary among treatment types since we predicted that birds would respond more strongly to the wholesale removal of trees than to the finer-scale differences in vegetation and substrate cover generated by the different treatment methods. Furthermore, we suspected that the experimental plots may be too small to assess differences in bird use among treatment methods.

In contrast to birds, we hypothesized that small mammals would respond differentially to fine-scale differences in vegetation and substrate cover among the treatment types. Hydro-ax treatments often alter forest structure by reducing all trees to a uniform layer of fine mulch, whereas chaining and roller-chop treatments leave larger woody debris within the treatment plots, likely providing better protective cover for small mammals. Previous studies have found a positive relationship between the abundance of several small mammal species and slash (i.e., dead woody debris; Baker and Frischknecht, 1973; Severson, 1986; Kruse, 1999). Therefore, we hypothesized that small mammal abundance would be higher in chaining and roller-chop plots because these treatment types have higher slash cover, abundance would be lower in hydro-ax plots that have lower slash cover, and abundance would be lowest in control plots with almost no slash cover. Lastly, we

hypothesized that the percent cover of different vegetation characteristics, especially shrub, herb, and grass cover, would also influence small mammal abundance. We did not consider a group-level response to treatments for small mammals because we did not expect to observe a large enough diversity of small mammal species to create meaningful functional groups.

Methods

Study Area

This study was conducted in the Piceance Basin, northwest Colorado, United States. Dominant land uses include energy extraction, domestic livestock grazing, and recreational hunting. Topography in the Piceance Basin ranges from high plateaus to deeply incised valleys. The arid steppe climate of the Piceance Basin varies both spatially and temporally due to the diverse topography and vegetation cover in the region (Wymore, 1974). Vegetation communities in the Piceance Basin range from bottomland irrigated pastures and croplands to upland sagebrush and pinyon-juniper woodland, to higher-elevation spruce, fir, and aspen forest (Wymore, 1974; Lendrum et al., 2012). Irrigated lowlands represent < 1% total cover, whereas upland pinyon-juniper and sagebrush communities characterize the dominant cover type (35% and 32%, respectively) (Wymore, 1974).

Woodland overstory in our study area was composed primarily of pinyon pine (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* Torr.), and understory shrubs were mainly serviceberry (*Amelanchier* Medik.), bitterbrush (*Purshia tridentata* Pursh), snowberry (*Symphoricarpos rotundifolius* A. Gray), mountain mahogany (*Cercocarpus montanus* Raf.), and big sagebrush (*Artemisia* spp.). We did not identify sagebrush to subspecies, but the region includes a mix of big sagebrush (*Artemisia tridentata* Nutt.), mountain big sagebrush (*Artemisia tridentata* Nutt. subsp. *vaseyana* Rydb.), and Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle and Young). The dominant understory forbs, grasses, and grasslike plants included phlox (*Phlox* L. spp.), Lewis flax (*Linum lewisii* Pursh), tansyaster (*Machaeranthera* Nees. spp.), plains pricklypear cactus (*Opuntia polyacantha* Haw.), sedges (*Carex* L. spp.), wildrye (*Elymus* L. spp.), Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), bluegrass (*Poa* L. spp.), and western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve) (Stephens et al., 2016). Although cheatgrass (*Bromus tectorum* L.) was sparse in the area before treatments were applied, it increased on treatment plots 2 years after tree removal (Stephens et al., 2016). Historical climate records from the Western Regional Climate Center (station #055048 1981–2010 thirty-year average) indicate that total annual precipitation in the study area averaged 430 mm, and average monthly temperatures ranged from a low of -18°C in January to a high of 29°C in July.

Study Design and Site Selection

Tree reduction treatments were applied by Colorado Parks and Wildlife in a randomized complete block design in two locations in the Piceance Basin (a northern site at $39^{\circ}55'26.89''\text{N}$, $108^{\circ}12'38.82''\text{W}$ and a southern site about 4.5 km away at $39^{\circ}54'23.19''\text{N}$, $108^{\circ}15'39.05''\text{W}$). Our sites were embedded in a large continuous stand of pinyon-juniper, away from any boundaries between advancing conifer and sagebrush habitats (Stephens et al., 2016). We estimated that stands at these locations were approximately 100 yr old, but we did not measure stand age empirically, and some trees may be several hundred yr old (Stephens et al., 2016). The northern site was estimated to be in a late phase II successional stage of woodland development, and the southern site was estimated to be in a late phase III stage (Stephens et al., 2016). Treatment plots were established on slopes ranging from 5% to 20%. The plots ranged in elevation from 2000 to 2165 m. The study design included four polygons in a northern site and three

polygons in a southern site. Each polygon was divided into four plots of approximately equal size (1.0 ha), and a mechanical woodland reduction treatment (i.e., chaining, hydro-ax, roller-chop), or an untreated control, was randomly assigned to each plot. This design resulted in 28 plots and 7 replicates of each treatment, including the control treatment. Treatments were applied starting in fall 2011, and all treatments were completed by January 2012 (Anderson, 2013). We conducted small mammal and vegetation surveys from late May through July in 2012 and 2013 and conducted bird surveys in June 2013.

Bird Surveys

Birds were surveyed by conducting 5-min point counts (Buckland et al., 2001) at 28 stations placed near the center of each plot ($n = 7$ per treatment). All birds seen or heard completely within the plot (excluding a 10-m buffer at the plot edge) were recorded. Both territorial breeding songs and call notes were counted. Flyovers were not included. Except for the control plots, the small plot size provided a view of the entire plot, which allowed us to confirm the location of each bird within the plot of interest. Surveyors were thoroughly trained in distance estimation of bird detections, allowing accurate distance estimation for each auditory and visual detection that occurred, including those in the control plots, where many birds were detected by auditory cues alone. Each site was surveyed 12 times in June 2013. Surveys were conducted from 0600 to 0900. Survey-specific data (observer, time of survey, wind, and cloud cover) and site-specific data (treatment type and whether it was the northern or southern site) were also collected. Surveys were not conducted during periods of rain, fog, or high winds (> 15 km/h).

We categorized birds in our dataset into functional groups using the habitat classification categories for each species indicated in *The Birds of North America Online* database from (<http://bna.birds.cornell.edu/bna/>; accessed 10 January 2014, Appendix A). The birds of dense woodlands group included birds that use woodland and/or forest habitats, and the birds of open woodlands group included birds that use woodland edge habitats, woodland savannah habitats, and open woodland-shrubland matrices. We did not detect any shrubland or grassland obligate species during surveys; thus our analysis only included birds that use dense and open woodland habitats.

Mammal Surveys

Small mammals were live-trapped during June–July 2012 and July 2013 on grids in all 28 plots following guidelines established by the American Society of Mammalogists (Sikes and Gannon, 2011). We placed 50 baited (i.e., rolled oats, bird seed, and peanut butter) Sherman (H.B. Sherman Traps, Inc., Tallahassee, FL) live traps in each plot in a grid of 5 rows of 10 traps. Each trap and row was spaced 10 m apart. We trapped animals between 1800 and 1030 over 4 consecutive nights, for 200 trap-nights per trapping period. Captured animals were identified to species, marked with two uniquely numbered ear tags (National Band and Tag Company, Newport, KY), and released at the capture location.

We used fluorescent tracking methods (Lemen and Freeman, 1985) in July–August 2013 to obtain movement data for small mammal species. Animals were trapped at the start of their activity period, coated in uniquely colored nontoxic fluorescent pigment powders (DayGlo Color Corp., Cleveland, OH), and released. Fluorescent trails were detected the following night with an ultraviolet flashlight. Individual tracks were recorded using a Global Positioning System. To avoid the possibility of influencing natural animal movement patterns, fluorescent tracking was conducted separately from the trapping effort described earlier.

Vegetation Surveys

To assess the association between vegetation or substrate characteristics and bird habitat use or small mammal abundance, we collected data on understory plants and ground cover at 10 random subplots

(July–August 2012) and 16 random subplots (July–August 2013) within each of the 28 plots. We sampled percent cover of bare soil, rock, litter, wood or slash, mulch, tree, shrub, grass, and herb cover in 1-m² sample frames (0.5 m × 2 m) at four different height classes (0–40 cm, 40.1–80 cm, 80.1–137 cm, and 137 cm+) using the ocular cover method to the nearest quarter percent (Korb et al., 2003). We collected overstory data in 2012 in three random 10 × 20 m subplots within each of the 28 plots. We tallied all shrub and tree species and used the ocular cover method to estimate percent cover of both live and dead vegetation at six different height classes (0–0.5 m, 0.6–1 m, 1.1–2 m, 2.1–5 m, 5.1–10 m, > 10 m).

Data Analysis

We used 1-way analysis of variance with the Tukey Honest Significant Difference pairwise comparison method to test for significant differences in the percent cover of vegetation and substrate characteristics among treatments for both 2012 and 2013 data.

Bird Analysis

To test for differences in bird habitat use among treatment plots, we used single-season occupancy models (MacKenzie et al., 2006) to estimate the probability that a treatment plot is used by a given species (“habitat use”). Some birds may move between plots, creating a potential failure to meet the assumption that sites are independent. Therefore, we infer our results as habitat use and not true occupancy, as recommended by MacKenzie et al. (2006). Models were developed using a multiple-species modeling framework that shares information on the detection process across species with similar detectability to model data more parsimoniously (Allredge et al., 2007; see Appendix B for information on how birds were categorized into detection groups). Models included predictor variables that we expected to explain variation in the probability of use and detection based on a priori hypotheses. Specifically, we modeled habitat use probabilities as a function of treatment type (i.e., chaining, hydro-ax, roller-chop, or control), as a function of a control variable that considered habitat use as the same across all mechanical treatment methods (i.e., mechanical treatment or control) or as a function of site (i.e., northern or southern site). We modeled habitat use as a function of any of these covariates individually, or as additive or interactive effects with functional group (birds of dense woodlands or birds of open woodlands) or species. We modeled detection probability as a function of treatment type, the control variable, site, observer, wind, cloud, or time of day, either individually or as additive effects with detection group (see Appendix B) or species. Models that did not converge were excluded from the analysis.

We analyzed models using the RMark package (Laake, 2013) in R (R Core Team, 2016). Model selection and ranking were based on Akaike’s Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002). An overdispersion parameter was calculated from the MacKenzie and Bailey (2004) bootstrap goodness of fit test using 10,000 simulations, which was also used to assess model fit for the most parameterized model that our data could support. When applicable, we adjusted AICc values using our overdispersion parameter and calculated the difference in QAICc (quasi-likelihood AICc) values between the most parsimonious model and other models in the model set (Δ QAICc) and calculated model QAICc weights (w) (Burnham and Anderson, 2002; Anderson, 2008). We interpreted estimates of habitat use for each treatment type from the highest-ranking model and compared results with any other plausible best-fitting models (Δ QAICc values ≤ 2 , Burnham and Anderson, 2002). We considered habitat use to be significantly different between any two treatment types if the 84% confidence intervals did not overlap. Comparing 84% confidence intervals closely mimics traditional pairwise statistical tests with an α level of 0.05 for both symmetric (Payton et al., 2003) and asymmetric (MacGregor-Fors and Payton, 2013) confidence intervals.

We used a separate occupancy analysis to estimate bird habitat use as a function of vegetation and substrate cover, irrespective of treatment type. We used the same AIC model selection procedure described earlier to rank models with different vegetation and substrate predictor variables that we expected to explain variation in detection and habitat use by birds. We modeled habitat use probabilities as a function of the percent cover of trees, shrubs, grasses and herbs, slash, mulch, or bare soil. Shrub cover was correlated with tree cover, so we did not include shrub cover in our model set. We modeled habitat use as a function of any of these habitat covariates individually or as an additive effect with functional group or species. We modeled detection probability as a function of tree cover, site, observer, wind, cloud, or time of day, either individually or as an additive effect with detection group (see Appendix B) or species. Models that did not converge were excluded from the analysis. We interpreted regression coefficient relationships between vegetation or substrate cover and probability of use estimates from the highest-ranking model and compared results to any other plausible best-fitting models ($\Delta AICc$ values ≤ 2 , Burnham and Anderson, 2002), if applicable. We considered any vegetation or substrate covariate whose 84% confidence intervals around the regression coefficient did not overlap zero to be a significant variable.

Small Mammal Analyses

We used Huggins closed capture models (Huggins, 1989, 1991) and a variance components analysis (White and Burnham, 1999) to derive estimates of mean abundance (no./200 trap-nights, averaged across the seven plots of the same treatment type and the two sites) for deer mice (*Peromyscus maniculatus* Wagner) and least chipmunks (*Tamias minimus* Bachman) in each treatment type in both 2012 and 2013. We also used these models to estimate the probability that an animal will be initially captured and the probability of recapture, conditional on an animal having been captured at least once before. First, we used Program MARK (White and Burnham, 1999) to identify the most general model of deer mouse and least chipmunk detection and recapture probabilities that our data would support. These models were constructed based on our a priori hypotheses that detection probability could be a function of treatment type, time (day of survey), plot, or site (northern or southern site) and that animals may show a behavioral response, with a greater or lower recapture probability. Models included these variables independently or as additive combinations of treatment type, time, and site or of plot, time, and site, with and without a behavioral response. Models that did not converge were excluded from the analysis. Second, we used the most supported detection model to analyze variance in derived estimates of deer mouse and least chipmunk abundance using a variance components analysis in Program Mark (White et al., 2001; Burnham and White, 2002). The variance components analysis allowed us to separate the sampling variance from the biological process variance associated with each hypothesized effect on abundance (treatment type, site, and percent cover of various vegetation and substrate characteristics). This allowed us to further calculate the percent of process variance in abundance explained by each effect (White et al., 2001; Burnham and White, 2002).

We used the fluorescent tracking data to calculate the probability of availability (White and Shenk, 2001) (i.e., the probability that deer mice and least chipmunks will stay within a sampled plot). We subtracted this value from one to provide a measure of the probability of animal movement off the sampled plots. We also calculated the proportion of times an individual was caught on more than one treatment plot to provide another measure of animal movement among plots.

Results

Post-Treatment Vegetation

The mean percent cover of several vegetation and substrate characteristics varied among treatments in both 2012 and 2013 (Table 1). In

2012, the percent cover of trees was significantly higher in the control plots than in any of the mechanical treatment plots, the percent cover of slash was significantly higher in the chaining and roller-chop treatment plots than on the control or hydro-ax plots, and mulch cover was significantly higher in the hydro-ax treatment plots (see Table 1). In 2013, these patterns remained the same for tree, slash, and mulch cover, but shrub cover was also higher on control plots than all other treatment types. Furthermore, grass and herb cover was greater in 2013 than 2012 across all treatment types but did not significantly differ among treatment types. Litter cover also significantly differed between hydro-ax and control plots in 2013 (see Table 1).

Bird Habitat Use

We detected a total of 39 bird species in the woodland reduction treatment and control plots. Our analysis focused on 22 species; the other 17 species were detected too infrequently to provide sufficient data for reliable parameter estimation (see Appendix A).

The highest-ranking model from the woodland reduction treatment analysis indicated habitat use was a function of the control variable (habitat use differed between mechanical treatments and controls only) and the species effect (habitat use differed among all species). This was the only competitive model ($\Delta AICc$ values ≤ 2 , Burnham and Anderson, 2002) (Table 2). Models with a treatment effect (habitat use differed among all treatment methods) had little support (see Table 2).

Birds of dense and open woodlands had higher habitat use in control plots than in all types of mechanical woodland reduction plots (Table 3). However, the difference in habitat use between the control plots and treatment plots was generally larger for birds in the dense woodland functional group than in the open woodland functional group. Furthermore, habitat use probabilities indicated birds of dense woodlands rarely used the woodland reduction treatment plots, whereas most birds of open woodlands occasionally used these plots. Bird habitat use did not differ among the various woodland reduction treatment types (i.e., chaining, hydro-ax, or roller-chop) for either functional group (see Table 3). Finally, the bootstrap goodness of fit test indicated overdispersion in the data ($\hat{c} = 1.37$) for the most general model that our data could support; thus, we used an overdispersion factor, \hat{c} , to

Table 1

Mean (standard of error) percent cover of vegetation and substrate characteristics measured in control and treatments plots in the first (2012) and second (2013) yr after mechanical woodland reduction treatments were applied.

% Cover	Control	Chain	Hydro-ax	Roller-chop
2012				
Bare soil	28.9 (5.0)	23.6 (4.7)	18.1 (3.5)	25.3 (3.9)
Litter	49.4 (4.9)	43.4 (3.3)	44.0 (4.5)	40.4 (4.0)
Slash	1.6 (0.5) ^{CH,RC}	32.5 (5.1) ^{CO,HA}	9.9 (1.1) ^{CH,RC}	26.9 (4.1) ^{CO,HA}
Mulch	0.8 (0.2) ^{HA}	2.1 (0.8) ^{HA}	21.9 (6.8) ^{all}	1.6 (0.3) ^{HA}
Trees	46.5 (7.0) ^{all}	0.0 ^{CO}	0.0 ^{CO}	0.0 ^{CO}
Shrubs	15.5 (4.8)	5.8 (3.1)	4.3 (2.5)	8.08 (3.5)
Grasses & herbs	0.3 (0.1)	0.2 (0.1)	0.1 (0.04)	0.2 (0.1)
2013				
Bare soil	17.2 (2.7)	22.0 (5.5)	15.5 (4.4)	26.3 (3.2)
Litter	66.5 (2.1) ^{HA}	56.1 (6.2)	37.0 (8.0) ^{CO}	46.9 (3.6)
Slash	3.8 (0.9) ^{CH,RC}	20.7 (5.8) ^{CO,HA}	5.1 (0.8) ^{CH,RC}	18.0 (2.1) ^{CO,HA}
Mulch	0.1 (0.1) ^{HA}	0.0 ^{HA}	36.3 (10.6) ^{all}	0.1 (0.1) ^{HA}
Trees	53.5 (6.3) ^{all}	0.0 ^{CO}	0.0 ^{CO}	0.0 ^{CO}
Shrubs	18.9 (7.2) ^{all}	2.2 (0.6) ^{CO}	2.2 (0.8) ^{CO}	2.3 (0.6) ^{CO}
Grasses & herbs	1.5 (0.2)	2.6 (0.2)	5.1 (2.3)	3.5 (0.5)

CH indicates chain; RC, roller-chop; CO, control; HA, hydro-ax.

Superscripts indicate significant differences in mean percent cover (analysis of variance with Tukey honestly significant difference pairwise adjustment) between two or more treatment types.

Table 2

Akaike Information Criterion (AIC) model selection results for bird woodland reduction treatment occupancy models and habitat association occupancy models. Modeled effects related to bird habitat use (ψ) and detection (p) probabilities include parameter variability by: all habitat treatments (Treatment), controls vs. treatments (Control), habitat-based guilds (Functional group), species (Species), detection-based guilds (Detection group), time of day when the survey was conducted (Time), and % cover of trees (Trees).

Model	K ¹	QAIC _c	Δ QAIC _c	QAIC _c weight	Deviance
<i>Bird woodland reduction occupancy models</i> ²					
ψ (Control + Species) p(Time + Detection group)	27	1952.56	0.00	0.70	1895.98
ψ (Control · Functional group) p(Control + Detection group)	8	1955.70	3.14	0.15	1307.50
ψ (Control · Functional group) p(Treatment + Detection group)	10	1957.82	5.26	0.05	1305.50
ψ (Control · Functional group) p(Species)	26	1957.83	5.28	0.05	1271.49
ψ (Treatment · Functional group) p(Control + Detection group)	12	1959.13	6.57	0.03	1302.66
<i>Bird habitat association occupancy models</i>					
ψ (Trees + Functional group) p(Trees + Species)	27	2664.18	0.00	0.71	2607.61
ψ (Trees + Species) p(Trees + Detection group)	27	2666.22	2.04	0.26	2609.65
ψ (Trees) p(Trees + Species)	25	2671.12	6.94	0.02	2618.91

Models with Δ AICc values ≤ 7 are shown; models with Δ AICc values > 7 have little support (Burnham and Anderson, 2002). Models with Δ QAICc values ≤ 2 are all plausible best-fitting models for the observed data.

¹ K = no. of parameters.

² Bird woodland reduction treatment models were adjusted by an overdispersion parameter ($\hat{c} = 1.37$), producing QAICc values. No overdispersion adjustment was needed for bird habitat association models ($\hat{c} = 0.92$).

inflate standard errors and used QAICc for model selection (MacKenzie and Bailey, 2004).

The highest-ranking model from the habitat association analysis modeled habitat use as a function of tree cover and functional group (see Table 2). This was the only competitive model (Δ AICc values ≤ 2 ; Burnham and Anderson, 2002), and models that included an effect of slash, mulch, bare soil, or grass and herb cover had virtually no support (Δ AICc values ≤ 7 ; Burnham and Anderson, 2002). Thus, we only interpret regression coefficient (β) relationships with tree cover.

We found that higher percent tree cover was associated with higher habitat use across both bird functional groups (Open woodland: $\beta = 2.77$ 84% CI 1.98–3.56; Dense woodland: $\beta = 3.81$ 84% CI 3.38–4.24). Finally, the bootstrap goodness of fit test indicated good model fit ($p = 0.80$) and no overdispersion in the data ($\hat{c} = 0.92$) for the most parameterized model that our data could support (MacKenzie and Bailey, 2004).

Small Mammal Abundance and Availability

We captured five small mammal species in the woodland reduction treatment and control plots (deer mice, least chipmunks, Uinta chipmunks *Tamias umbrinus* J. A. Allen, golden-mantled ground squirrels *Spermophilus lateralis* Say, and bushy-tailed woodrats *Neotoma cinerea* Ord). Our analysis focused on species with sufficient data to estimate parameters (deer mice and least chipmunks); the other three species were captured too infrequently to provide sufficient data for reliable parameter estimation.

The most supported model for deer mouse detection probability indicated that detection was a function of treatment type and a recapture effect in 2012 (AICc weight = 0.31, Deviance = 1076.88), and that detection was a function of plot and time in 2013 (AICc weight = 0.99, Deviance = 5350.45). Mean deer mouse abundance (averaged across the 7

Table 3

Probability of habitat use estimates (+84% confidence interval) for birds of dense woodlands and birds of open woodlands detected in experimental woodland reduction treatment and control plots ($n = 7$ plots/treatment or control, 28 total) in 2013, the Piceance Basin, northwest Colorado.

Species	ψ (95% CI)			
	Control	Chaining	Hydro-ax	Roller-chop
<i>Birds of dense woodlands</i>				
Plumbeous vireo	0.83 (0.56–1.00) ¹	0.00 (0.00–0.02)	0.00 (0.00–0.02)	0.00 (0.00–0.02)
Mountain chickadee	0.99 (0.94–1.00) ¹	0.06 (0.00–0.14)	0.06 (0.00–0.14)	0.06 (0.00–0.14)
Blue-gray gnatcatcher	0.67 (0.37–0.97) ¹	0.00 (0.00–0.01)	0.00 (0.00–0.01)	0.00 (0.00–0.01)
Black-throated gray warbler	1.00 (0.99–1.00) ¹	0.35 (0.20–0.50)	0.35 (0.20–0.50)	0.35 (0.20–0.50)
Dark-eyed junco	1.00 (0.98–1.00) ¹	0.21 (0.01–0.40)	0.21 (0.01–0.40)	0.21 (0.01–0.40)
Red crossbill	0.30 (0.05–0.54) ¹	0.00 (0.00–0.01)	0.00 (0.00–0.01)	0.00 (0.00–0.01)
Evening grosbeak	0.83 (0.56–1.00) ¹	0.00 (0.00–0.02)	0.00 (0.00–0.02)	0.00 (0.00–0.02)
<i>Birds of open woodlands</i>				
Mourning dove	1.00 (0.99–1.00) ¹	0.73 (0.56–0.91)	0.73 (0.56–0.91)	0.73 (0.56–0.91)
Black-chinned hummingbird	1.00 (0.99–1.00) ¹	0.73 (0.39–1.00)	0.73 (0.39–1.00)	0.73 (0.39–1.00)
Broad-tailed hummingbird	1.00 (0.99–1.00) ¹	0.28 (0.13–0.43)	0.28 (0.13–0.43)	0.28 (0.13–0.43)
Hairy woodpecker	1.00 (0.99–1.00) ¹	0.31 (0.07–0.55)	0.31 (0.07–0.55)	0.31 (0.07–0.55)
Northern flicker	1.00 (0.98–1.00) ¹	0.21 (0.01–0.40)	0.21 (0.01–0.40)	0.21 (0.01–0.40)
Ash-throated flycatcher	0.76 (0.51–1.00) ¹	0.00 (0.00–0.01)	0.00 (0.00–0.01)	0.00 (0.00–0.01)
Empidonax flycatchers	1.00 (0.98–1.00) ¹	0.17 (0.04–0.29)	0.17 (0.04–0.29)	0.17 (0.04–0.29)
Woodhouse's scrub-jay	1.00 (0.98–1.00) ¹	0.21 (0.01–0.40)	0.21 (0.01–0.40)	0.21 (0.01–0.40)
Violet-green swallow	1.00 (0.99–1.00) ¹	0.75 (0.60–0.89)	0.75 (0.60–0.89)	0.75 (0.60–0.89)
Juniper titmouse	0.62 (0.11–1.00) ¹	0.00 (0.00–0.01)	0.00 (0.00–0.01)	0.00 (0.00–0.01)
White-breasted nuthatch	0.98 (0.90–1.00) ¹	0.04 (0.00–0.11)	0.04 (0.00–0.11)	0.04 (0.00–0.11)
Mountain bluebird	1.00 (0.99–1.00) ¹	0.39 (0.22–0.56)	0.39 (0.22–0.56)	0.39 (0.22–0.56)
Spotted towhee	0.74 (0.50–0.99) ¹	0.00 (0.00–0.01)	0.00 (0.00–0.01)	0.00 (0.00–0.01)
Chipping sparrow	1.00 (0.99–1.00) ¹	0.50 (0.34–0.66)	0.50 (0.34–0.66)	0.50 (0.34–0.66)
Cassin's finch	1.00 (0.99–1.00) ¹	0.45 (0.29–0.60)	0.45 (0.29–0.60)	0.45 (0.29–0.60)

Estimates are from the only competitive model (Δ AICc values ≤ 2) in the model set, ψ (Control + Species) p(Time of Day + Detection group), model weight = 70.2%.

¹ Indicates that habitat use significantly differs from other treatment types based on nonoverlapping 84% confidence intervals.

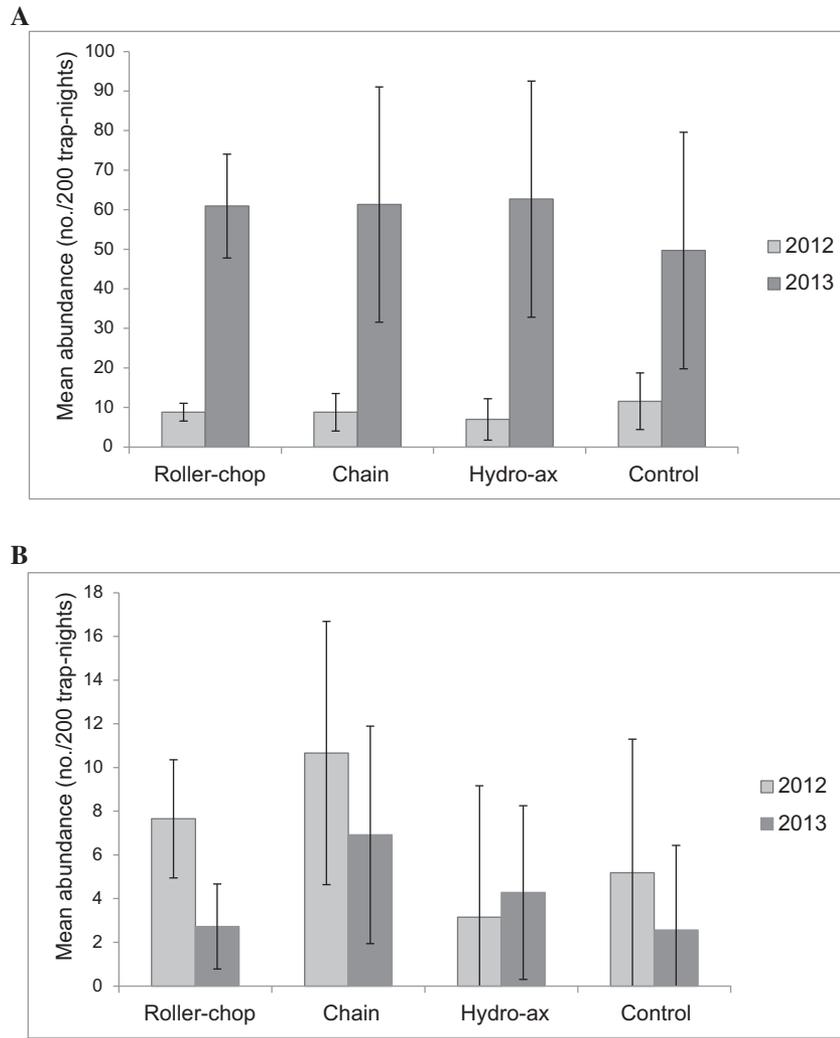


Figure 1. Deer mouse and least chipmunk abundance by treatment. **A**, Deer mouse and **B**, least chipmunk mean abundance estimates (\pm 84% confidence interval) per plot for each woodland reduction treatment type ($n = 7$ plots/treatment or control, 28 total) during 2012 and 2013 in the Piceance Basin, northwest Colorado. Estimates were calculated using Huggins closed-capture models and a variance components analysis to obtain derived mean estimates of abundance for each treatment.

plots of the same treatment type and the two sites over 4 consecutive trapping d) did not differ significantly among treatment types in either 2012 or 2013 (Fig. 1). Likewise, treatment type did not explain any

variance in deer mouse abundance estimates in 2012 or 2013 (Table 4). Site and shrub cover effects explained a small amount of variance in 2012 (7.900% and 12.110%, respectively), and these same

Table 4
Percent of process variance in deer mouse abundance explained by treatment type, site, or percent cover of vegetation and substrate covariates on 28 experimental woodland reduction treatment and control plots in the Piceance Basin, Colorado, in 2012 and 2013.

Effect	Process variance	95% LCL	95% UCL	Percent of variance explained
2012				
Treatment type	6.601	2.743	17.240	0.000
Site	5.438	2.142	15.145	7.900
Grasses & herbs	6.284	2.667	16.616	0.000
Slash	6.281	2.671	16.577	0.000
Mulch	6.157	2.611	16.354	0.000
Trees	6.284	2.674	16.484	0.000
Shrubs	5.189	2.285	13.077	12.100
2013				
Treatment type	579.017	247.079	1804.643	0.000
Site	497.510	227.502	1448.541	2.510
Grasses & herbs	440.613	188.199	1368.033	13.650
Slash	542.376	246.822	1556.401	0.000
Mulch	541.987	246.373	1559.992	0.000
Trees	540.595	243.692	1569.204	0.000
Shrubs	497.351	231.468	1431.626	2.540

LCL indicates lower confidence level; UCL, upper confidence level.

Process variance from the mean model was 5.904 (95% confidence interval [CI]: 2.521 – 15.411) in 2012 and 510.292 (95% CI: 235.026 – 1438.618) in 2013.

Table 5

Percent of process variance in least chipmunk abundance explained by treatment type, site, or percent cover of vegetation and substrate covariates on 28 experimental woodland reduction treatment and control plots in the Piceance Basin, Colorado, in 2012 and 2013.

Effect	Process variance	95% LCL	95% UCL	Percent of variance explained
<i>2012</i>				
Treatment	25.811	14.910	52.471	17.370
Site	24.695	14.534	48.621	20.940
Grasses & herbs	32.540	19.278	63.760	0.000
Slash	30.821	18.245	60.429	1.300
Mulch	28.339	16.745	55.638	9.270
Trees	31.247	18.519	61.213	0.000
Shrubs	30.434	17.984	59.746	2.570
<i>2013</i>				
Treatment	2.797	−2.923	7.675	0.000
Site	2.740	−2.766	7.359	0.000
Grasses & herbs	2.740	−2.765	8.716	0.000
Slash	2.740	−2.923	7.394	0.000
Mulch	2.740	−2.748	8.570	0.000
Trees	2.740	−2.923	7.405	0.000
Shrubs	2.740	−2.923	6.747	0.000

Process variance from the mean model was 31.236 (95% confidence interval [CI]: 18.648 – 60.364) in 2012 and 2.740 (95% CI: −2.751 – 6.766) in 2013.

effects explained an even smaller amount of variance in 2013 (2.510% and 2.540%, respectively; see Table 4). Grass and herb cover also explained 13.650% of variance in deer mouse abundance estimates in 2013. However, neither slash, mulch, nor tree cover explained any variance in deer mouse abundance estimates in either year (see Table 4).

The probability of availability was high for deer mice ($\bar{p} = 0.99$ 95% CI 0.98 – 1.00), and thus the inverse probability of an individual moving off of sampled plots was low. Estimates of the proportion of times an individual deer mouse was caught on more than one treatment plot were also low (0.01).

The most general model for least chipmunk detection probability indicated that detection was a function of time in 2012, and that detection was a function of site and time in 2013. Mean least chipmunk abundance did not differ among treatment types in either 2012 or 2013 (see Fig. 1). Treatment type explained 17.370% of variance in least chipmunk abundance estimates in 2012 but did not explain any variance in 2013 (Table 5). Site, mulch, and shrub cover effects also explained some of the variance in abundance estimates in 2012 (20.940%, 9.270%, and 2.570%, respectively). None of the effects considered explained any variance in least chipmunk abundance in 2013 (see Table 5). The probability of availability was high for least chipmunks ($\bar{p} = 0.98$ 95% CI 0.95 – 1.00), the inverse probability of an individual moving off of sampled plots was low, and the proportion of times an individual least chipmunk was caught on more than one treatment plot was low (0.05).

Discussion

The practice of reducing woodlands in small proximate patches is a common habitat management tool in the Piceance basin and other regions (Howard et al., 1987; Sedgwick and Ryder, 1987; Albert et al., 1995; Kruse, 1999; Reemts and Cimprich, 2014). Clearing woodlands in patchy mosaics is thought to benefit species like mule deer by simultaneously providing increased forage and access to nearby protective woodland cover (Short et al., 1977; Howard et al., 1987). It is important to understand the effects of woodland reduction on nontargeted wildlife, especially as this approach becomes more widely used to improve habitat for mule deer and other species.

Our findings provide new insight into bird and small mammal habitat use in small patches of mechanically reduced woodland. We found no differences in bird habitat use or small mammal abundance among chaining, hydro-ax, or roller-chop treatments. Yet we found that habitat use was significantly lower in all woodland reduction treatment plots than in control plots for birds of open woodland and dense woodland habitats. Furthermore, we did not find the hypothesized positive effect of woodland reduction on grassland and shrubland species because

we did not detect shrubland or grassland obligate birds in any plots. For small mammals, this finding is likely a true nonresponse and we discuss next why small mammal abundance may not vary among the different mechanical woodland reduction treatments on the basis of the results from our variance components analysis.

The lack of significant differences in bird habitat use among the three woodland reduction methods may relate to a lack of variation in important habitat characteristics for birds in our study. We found that bird habitat use was positively associated with tree cover, which only differed among the treatment and control plots. Thus, the treatment types were homogeneous with respect to the habitat component most influential for birds. However, we acknowledge that the small spatial scale and configuration of treatments may limit our ability to detect differences in use among treatment types for birds. Because our experiment was originally designed to study plant responses to woodland reduction, the treatment plots are small and close together. Given that birds are mobile and have greater dispersal distances than plants, this study's experimental design is probably most effective at estimating bird habitat use of a heterogeneous mix of treatments and comparing that with the use of untreated woodlands. Thus, hereafter we restrict our discussion of inferences and management implications for birds to comparisons between control and treatment plots, rather than variation in use among treatment methods.

Our findings suggest that small woodland reduction treatments, at least initially, do not attract shrubland and grassland birds. Similar to our findings, most other studies have not found a positive response of shrubland and grassland birds to woodland reduction (Bombaci and Pejchar, 2016; but see Crow and van Riper, 2010 and Severson et al., 2017). The lack of a significant response by shrubland and grassland birds in our study and most others may be due to the short time since treatment over which most bird responses have been measured. Positive responses by shrubland and grassland birds to woodland reduction may not occur until 2 or more decades after treatments are completed (O'Meara et al., 1981; Arkle et al., 2014), when the early and mid-successional plant communities have reestablished. McAdoo et al. (1989) found that grassland and shrubland bird species diversity was highest in grasslands where mid-successional invasion of sagebrush took place, because these habitats supported both shrubland and grassland birds. Other studies that have evaluated bird responses to successional gradients have found that birds associated with open habitat, such as shrub nesting, ground nesting, and ground foraging birds, had higher abundances in early and intermediate successional stages along grassland-shrubland-woodland gradients (Rosenstock and Van Riper, 2001; Reinkensmeyer et al., 2007). The lack of a positive response from shrubland and grassland birds to treatments may also be related

to the availability of suitable shrubland and grassland habitat at the broader regional scale. It was beyond the scope of this study to assess habitat quality in nearby shrublands and woodlands, but we acknowledge that shrubland and grassland birds may avoid these small treatment patches if nearby areas of high-quality habitat are available and unoccupied by competitors.

We found that even small woodland reduction patches had almost no use by most birds of dense woodlands, and although birds of open woodlands occasionally used woodland reduction patches, habitat use was significantly lower in treatment plots than control plots for this functional group. Potential loss of habitat for birds in these functional groups should therefore be considered even when management plans call for small areas to be cleared. Other investigators have found reduced numbers of many bird species in woodland reduction plots of varying sizes treated with chaining, thinning, and burning compared with untreated control plots (Kruse et al., 1979; O'Meara et al., 1981; Sedgwick and Ryder, 1987; Albert et al., 1995). Yet most of these studies did not test for significant differences in bird abundance between treatments and controls (Kruse et al., 1979; O'Meara et al., 1981; Albert et al., 1995). Among studies that did test for significant differences, only woodland birds were frequently impacted by woodland reduction (Bombaci and Pejchar, 2016), which is consistent with our findings.

We think that the small scale and close proximity of our study plots was less limiting for small mammal inference than for birds because both least chipmunks and deer mice rarely moved off of the plot of their original capture, according to our high probability of availability estimates (deer mice $\bar{p} = 0.99$ and least chipmunk $\bar{p} = 0.98$) and low estimates of the proportion of times an individual of a species was caught on more than one sampled plot (deer mice = 0.01 and least chipmunk = 0.05). Thus, our data suggest that small mammals in our study rarely moved among treatments and any lack of differences detected are likely not related to animal movement. Furthermore, although we baited traps, which may draw animals into trapping grids and bias estimates of abundance, our low estimates of the proportion of times an individual was caught on more than one sampled plot indicated that animals were rarely being drawn into grids from nearby plots. We also do not expect the attraction to bait to vary among the different woodland reduction treatments, and thus any unintended effects of baiting should not have influenced our treatment comparisons.

Contrary to our predictions, we found no significant differences in initial abundance estimates among the three treatment methods for deer mice or least chipmunks (see Fig. 1), and minimal variance was explained by treatment type for either species across both years (see Tables 4 and 5). We believe this finding may be due to the general lack of differences in vegetation and substrate characteristics among the three treatment types. Aside from the expected higher slash cover found in the roller-chop and chaining treatment plots and higher mulch cover found in hydro-ax plots, few other characteristics varied among the three treatment types in 2012 or 2013. Given that deer mice and least chipmunks in our study did not appear to respond to one of the major differences observed among the three treatments (i.e., slash cover), it is not surprising that we did not find differences in small mammal abundance among the different treatment types. Previous studies have found both positive (Baker and Frischknecht, 1973; Severson, 1986; Albert et al., 1995; Kruse, 1999) and negative (Severson, 1986; Kruse, 1999) responses to slash cover by small mammals, suggesting that the relationship between small mammal abundance and slash cover is context dependent. We also hypothesized that small mammals would respond to expected differences in grass and herb cover among treatments. Although our variance components analysis indicated that some variance in deer mouse abundance in 2013 was explained by grass and herb cover, this cover type did not differ among any treatment type in either year (see Table 1) and did not exceed 1% cover in 2012 or 5% cover in 2013. Thus, there may have not been a sufficient amount, or enough variation, in grass and herb cover among treatment types to make a difference for deer mice or least chipmunks.

Although these lines of reasoning explain why small mammal abundance did not vary among the three treatment types, they do not explain why abundance was also similar between treatment and control plots, which differed in tree, shrub, and litter cover in one or both years. The lack of response found in our study may be related to the generalist nature of the species studied. Both deer mice and least chipmunks are opportunistic generalist feeders (Jameson, 1952; Johnson, 1961; Verts and Carraway, 2001) and occur in a wide range of habitats and habitat edges (Whitaker, 1996; Verts and Carraway, 2001; Armstrong et al., 2011). We expect that small mammals that strongly prefer woodland, shrubland, or grassland habitats would show stronger responses to woodland reduction treatments. For example, some studies have found negative short-term responses by the woodland-adapted pinyon mouse (*Peromyscus truei* Shufeldt) to thinning (Kruse, 1999) and burning treatments (Smith and Urness, 1984). However, although pinyon mice captures declined in the year following treatments in a previous study, captures resumed pretreatment levels a year later (Kruse, 1999). Thus, the lack of variation in responses among treatments or between treatment and control plots could also reflect more generalized trends among small mammal responses to woodland reduction. Indeed, a recent synthesis found that > 80% of study results did not indicate significant differences in small mammal abundance between treatment and control plots from multiple investigations of small mammal responses to a variety of mechanical woodland reduction treatments (Bombaci and Pejchar, 2016).

Abundance estimates of deer mice were about six times higher in 2013 than in 2012 across all treatment types, and least chipmunk abundance estimates in 2013 were about half of the values in 2012 for most treatment types (see Fig. 1). Because some variance in deer mouse abundance was explained by grass and herb cover in 2013, the increase in deer mouse abundance across all treatment types may be partially related to higher grasses and herbs in all plots in 2013. Other studies have shown dramatic increases in deer mouse abundance after woodland reduction treatments are applied (Turkowski and Reynolds, 1970; Baker and Frischknecht, 1973; O'Meara et al., 1981; Sedgwick and Ryder, 1987; Albert et al., 1995; Kruse, 1999), and some authors have discussed how these increases could relate to greater grass and herb cover on cleared areas, but we found no studies that directly quantified relationships between small mammal abundance and vegetation or substrate cover found in treatment plots. Our results suggest that although a relationship exists between deer mouse abundance and grass and herb cover, it may only partially explain the initial attraction of deer mice to woodland reduction treatment plots found in some studies. Interestingly, this increase in deer mouse abundance may be partially responsible for the decrease in least chipmunk abundance in 2013. Deer mice and least chipmunks partition food resources in spring to avoid competition (Verts and Carraway, 2001), so the increase of deer mice in 2013 may have driven many least chipmunks out of the area.

Management Implications

This study presents an experimental comparison of bird habitat use and small mammal abundance among pinyon-juniper woodlands treated with chaining, hydro-ax, and roller-chop treatments. We found that woodland reduction at a small scale was associated with lower habitat use for birds of both dense and open woodland habitats, irrespective of treatment type. Thus, we recommend that land managers identify and monitor woodland-dependent bird species when implementing woodland reduction projects, especially those species that rarely used treatment plots in our study (see Table 3).

We also found that two habitat generalist small mammals did not respond strongly to treatment type or variation in slash or vegetation cover. Thus, the type of mechanical woodland reduction employed may have little consequence for generalist small mammals when implemented at small scales. However, effects on habitat specialist small mammals have yet to be evaluated across multiple mechanical

treatment types. Because we found that some species initially responded negatively to woodland reduction, and no species responded positively, the effects of woodland reduction on wildlife should not be overlooked in forest and range management, even when implemented at small scales.

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Appendix A. Bird Species and Functional Group Classification

Bird species and functional group classification for birds encountered in the mechanical woodland reduction treatment plots, Piceance Basin, Colorado, June 2013. Functional groups for birds that were not included in the analysis due to sparse data are indicated with NA.

Common name	Scientific name	Functional group
Cooper's hawk ¹	<i>Accipiter cooperii</i>	NA
Mourning dove	<i>Zenaida macroura</i>	Open woodland
Common nighthawk ¹	<i>Chordeiles minor</i>	NA
Black-chinned hummingbird	<i>Archilochus alexandri</i>	Open woodland
Broad-tailed hummingbird	<i>Selasphorus platycercus</i>	Open woodland
Williamson's sapsucker ¹	<i>Sphyrapicus thyroideus</i>	NA
Downy woodpecker ¹	<i>Picoides pubescens</i>	NA
Hairy woodpecker	<i>Picoides villosus</i>	Open woodland
Northern flicker	<i>Colaptes auratus</i>	Open woodland
Western wood-peewee ¹	<i>Contopus sordidulus</i>	NA
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>	Open woodland
Gray flycatcher ²	<i>Empidonax wrightii</i>	Open woodland
Dusky flycatcher ²	<i>Empidonax oberholseri</i>	Open woodland
Plumbeous vireo	<i>Vireo plumbeus</i>	Dense woodland
Woodhouse's scrub-jay	<i>Aphelocoma woodhouseii</i>	Open woodland
Clark's nutcracker ¹	<i>Nucifraga columbiana</i>	NA
Common raven ¹	<i>Corvus corax</i>	NA
Violet-green swallow	<i>Tachycineta thalassina</i>	Open woodland
Mountain chickadee	<i>Poecile gambeli</i>	Dense woodland
Juniper titmouse	<i>Baeolophus griseus</i>	Open woodland
Bush-tit ¹	<i>Psaltriparus minimus</i>	NA
White-breasted nuthatch	<i>Sitta carolinensis</i>	Open woodland
House wren ¹	<i>Troglodytes aedon</i>	NA
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	Dense woodland
Western bluebird ¹	<i>Sialia mexicana</i>	NA
Mountain bluebird	<i>Sialia currucoides</i>	Open woodland
Hermit thrush ¹	<i>Catharus guttatus</i>	NA
American robin ¹	<i>Turdus migratorius</i>	NA
Yellow-rumped warbler ¹	<i>Setophaga coronata</i>	NA
Black-throated gray warbler	<i>Setophaga nigrescens</i>	Dense woodland
Western tanager ¹	<i>Piranga ludoviciana</i>	NA
Green-tailed towhee ¹	<i>Pipilo chlorurus</i>	NA
Spotted towhee	<i>Pipilo maculatus</i>	Open woodland
Chipping sparrow	<i>Spizella passerine</i>	Open woodland
Dark-eyed junco	<i>Junco hyemalis</i>	Dense woodland
Brown-headed cowbird ¹	<i>Molothrus ater</i>	NA
Cassin's finch	<i>Haemorhous cassinii</i>	Open woodland
Red crossbill	<i>Loxia curvirostra</i>	Dense woodland
Evening grosbeak	<i>Coccothraustes vespertinus</i>	Dense woodland

¹ Species not included in occupancy models due to sparse data.

² Data from *Empidonax* flycatchers were pooled and modeled as *Empidonax* spp. due to uncertainty in field identification of individual *Empidonax* species.

Appendix B. Detection Group Variable Categorization

Characteristics used to categorize birds species into low, medium, and high detection categories for the detection group variable used in the occupancy analysis. Categorical values were converted to the numerical scores shown in parentheses. Scores were then standardized and summed to create a detection index. The detection index was then divided into lower third (low), middle third (med), and upper third (high) detection categories. Minimum body length and foraging habit data were obtained from *The Birds of North America Online* database from the Cornell Lab of Ornithology and the American Ornithologist's Union (available at: <http://bna.birds.cornell.edu/bna/>; accessed 10 January 2014). Vocalization pitch, vocalization length, and flocking data were derived from our own observations of species behavior at the field site.

Species	Min. body length (cm)	Foraging habit	Vocalization pitch	Vocalization length	Flocking	Detection category
Dark-eyed junco	14	Ground forager (1)	Low (1)	Short (1)	Occasional (2)	Low
Black-chinned hummingbird	9	Aerial forager (3)	Low (1)	Short (1)	Solitary (1)	Low
Woodhouse's scrub-jay	28	Ground forager (1)	Med (2)	Short (1)	Solitary (1)	Low
Blue-gray gnatcatcher	10	Foliage gleaner (2)	Low (1)	Med (2)	Occasional (2)	Low
Plumbeous vireo	12	Foliage gleaner (2)	Med (2)	Med (2)	Solitary (1)	Low
<i>Empidonax</i> spp.	14	Aerial forager (3)	Med (2)	Short (1)	Solitary (1)	Low
Juniper titmouse	15	Foliage gleaner (2)	Med (2)	Med (2)	Solitary (1)	Low
Broad-tailed hummingbird	8	Aerial forager (3)	Med (2)	Med (2)	Solitary (1)	Med
Hairy woodpecker	18	Bark forager (2)	High (3)	Short (1)	Solitary (1)	Med
Northern flicker	28	Ground forager (1)	High (3)	Short (1)	Solitary (1)	Med
Mountain chickadee	11	Foliage gleaner (2)	Low (1)	Med (2)	Flocking (3)	Med
White-breasted nuthatch	13	Bark forager (2)	Med (2)	Med (2)	Occasional (2)	Med
Mourning dove	23	Ground forager (1)	Low (1)	Med (2)	Flocking (3)	Med
Mountain bluebird	16	Aerial forager (3)	Low (1)	Short (1)	Flocking (3)	Med
Black-throated gray warbler	11	Foliage gleaner (2)	Med (2)	Long (3)	Occasional (2)	High
Chipping sparrow	12	Ground forager (1)	High (3)	Long (3)	Occasional (2)	High
Violet-green swallow	12	Aerial forager (3)	Low (1)	Med (2)	Flocking (3)	High
Evening grosbeak	16	Ground forager (1)	High (3)	Med (2)	Flocking (3)	High
Cassin's finch	16	Ground forager (1)	Med (2)	Long (3)	Flocking (3)	High
Spotted towhee	17	Ground forager (1)	High (3)	Long (3)	Occasional (2)	High
Ash-throated flycatcher	19	Aerial forager (3)	Med (2)	Med (2)	Occasional (2)	High
Red crossbill	13	Foliage gleaner (2)	High (3)	Med (2)	Flocking (3)	High

assistance. Wildlife observation and handling procedures were approved by the Colorado State University Institutional Animal Care and Use Committee under Protocol 12-3277A. Earlier drafts of the manuscript were improved by several anonymous reviewers.

References

- Albert, S.K., Luna, N., Chopito, A.L., 1995. Deer, small mammal, and songbird use of thinned pinon-juniper plots: preliminary results. In: Shaw, D.W., Aldon, E.F., LoSapio, C. (Eds.), *Desired future conditions for pinyon-juniper ecosystems*. Gen. Tech. Rep. RM-GTR-258. Fort Collins, Colorado. USDA Forest Service, Flagstaff, AZ, USA, pp. 54–64.
- Allredge, M.W., Pollock, K.H., Simons, T.R., Shriner, S.A., 2007. Multiple-species analysis of point count data: a more parsimonious modelling framework. *Journal of Applied Ecology* 44, 281–290.
- Anderson, C.R., 2013. Population performance of Piceance basin mule deer in response to natural gas land extraction and mitigation efforts to address human activity and habitat degradation (Wildlife Research Report). Colorado Parks and Wildlife, Denver, CO, USA 21 p.
- Anderson, D.R., 2008. *Model based inference in the life sciences: a primer on evidence*. Springer, New York, NY, USA.
- Arkle, R.S., Pilliod, D.S., Hanser, S.E., Brooks, M.L., Chambers, J.C., Grace, J.B., Knutson, K.C., Pyke, D.A., Welty, J.L., Wirth, T.A., 2014. Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. *Ecosphere* 5, 1–32.
- Armstrong, D.M., Fitzgerald, J.P., Meaney, C.A., Fitzgerald, J.P., 2011. *Mammals of Colorado*. second ed. Denver Museum of Nature & Science/University Press of Colorado, Boulder, CO, USA.
- Aro, R.S., 1971. Evaluation of pinyon-juniper conversion to grassland. *Journal of Range Management* 24, 188–197.
- Baker, M.F., Frischknecht, N.C., 1973. Small mammals increase on recently cleared and seeded juniper rangeland. *Journal of Range Management* 26, 101–103.
- Baruch-Mordo, S., Evans, J.S., Severson, J.P., Naugle, D.E., Maestas, J.D., Kiesecker, J.M., Falkowski, M.J., Hagen, C.A., Reese, K.P., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. *Biological Conservation* 167, 233–241.
- Belsky, A.J., 1996. Viewpoint: Western juniper expansion: is it a threat to arid northwestern ecosystems? *Journal of Range Management* 49, 53–59.
- Bergman, E.J., Bishop, C.J., Freddy, D.J., White, G.C., Doherty, P.F., 2014. Habitat management influences overwinter survival of mule deer fawns in Colorado. *Journal of Wildlife Management* 78, 462–445.
- Bombaci, S., Pejchar, L., 2016. Consequences of pinyon and juniper woodland reduction for wildlife in North America. *Forest Ecology and Management* 365, 34–50.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, New York, NY, USA 448 p.
- Burnham, K.P., Anderson, D.R., 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. second ed. Springer, New York, NY, USA.
- Burnham, K.P., White, G.C., 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245–264. <http://dx.doi.org/10.1080/02664760120108755>.
- Crow, C., van Riper III, C., 2010. Avian community responses to mechanical thinning of a pinyon-juniper woodland: specialist sensitivity to tree reduction. *Natural Areas Journal* 30, 191–201.
- DOI, 2013. *Endangered and Threatened Wildlife and Plants; Endangered Status for Gunnison Sage-Grouse Part II (Federal Register No. 78 FR 2486)*, 50 CFR Part 17. Department of the Interior, Washington, DC, USA.
- Falkowski, M.J., Evans, J.S., Naugle, D.E., Hagen, C.A., Carleton, S.A., Maestas, J.D., Khalyani, A.H., Poznanovic, A.J., Lawrence, A.J., 2017. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. *Rangeland Ecology & Management* 70, 15–24.
- Gallo, T., Pejchar, L., 2016. Woodland reduction and long-term change in breeding bird communities: long-term effects of tree removal on birds. *The Journal of Wildlife Management* <http://dx.doi.org/10.1002/jwmg.21188>.
- Gallo, T., Stinson, L.T., Pejchar, L., 2016. Pinyon-juniper removal has long-term effects on mammals. *Forest Ecology and Management* 377, 93–100.
- Howard, V.W., Cheap, K.M., Hier, R.H., Thompson, T.G., Dimas, J.A., 1987. Effects of cabling pinyon-juniper on mule deer and lagomorph use. *Wildlife Society Bulletin* 15, 242–247.
- Huggins, R.M., 1989. On the statistical analysis of capture experiments. *Biometrika* 76, 133.
- Huggins, R.M., 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47, 725.
- Jameson, E.W., 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boyleyi*, in the northern Sierra Nevada, California. *Journal of Mammalogy* 33, 50.
- Johnson, D.R., 1961. The food habits of rodents on rangelands of southern Idaho. *Ecology* 42, 407–410.
- Jones, A., Catlin, J., Vasquez, E., 2013. Mechanical treatment of pinyon-juniper and sagebrush systems in the intermountain west: a review of the literature. *Wild Utah Project*, Salt Lake City, UT, USA.
- Koniak, S., Everett, R.L., 1982. Seed reserves in soils of successional stages on pinyon woodlands. *American Midland Naturalist* 102, 295–303.
- Korb, J.E., Covington, W.W., Fule, P.Z., 2003. Sampling techniques influence understory plant trajectories after restoration: an example from ponderosa pine restoration. *Restoration Ecology* 11, 504–515.
- Kormos, P.R., Marks, D., xD., Pierson, F.B., Williams, C.J., Hardegree, S.P., Havens, S., Hedrick, A., Bates, J.D., Svejcar, T.J., 2017. Ecosystem water availability in juniper versus sagebrush snow-dominated rangelands. *Rangeland Ecology & Management* 70, 116–128.
- Kruse, W.H., Balda, R.P., Simono, M.J., MacRander, A.M., Johnson, C.D., 1979. Community-development in two adjacent pinyon-juniper eradication areas 25 years after treatment. *Journal of Environmental Management* 8, 237–247.

- Kruse, W.H., 1999. Commercial fuelwood harvesting effects on small mammal habitats in central Arizona. In: Monsen, S.B., Stevens, R. (Eds.), Proceedings: ecology and management of pinyon-juniper communities within the interior West. Proceedings RMRS-P-9. USDA Forest Service, Ogden, UT, USA, pp. 215–218.
- Kundaali, J.N., Reynolds, H.G., 1972. Desert cottontail use of natural and modified pinyon-juniper woodland. *Journal of Range Management* 25, 116–118.
- Laake, J.L., 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01. Alaska Fish Science Center, NOAA, National Marine Fisheries Service, Seattle, WA, USA 25 p.
- Lemen, C.A., Freeman, P.W., 1985. Tracking mammals with fluorescent pigments: a new technique. *Journal of Mammalogy* 66, 134–136.
- Lendrum, P.E., Anderson, C.R., Long, R.A., Kie, J.G., Bowyer, R.T., 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. *Ecosphere* 3, 1–19.
- MacGregor-Fors, I., Payton, M.E., 2013. Contrasting diversity values: statistical inferences based on overlapping confidence intervals. *PLoS ONE* 8, e56794.
- MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics* 9, 300–318.
- MacKenzie, D.I., Nichols, J.D., Andrew Royle, J., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species. Academic Press, Burlington, MA, USA 324 p.
- McAdoo, J.K., Longland, W.S., Evans, R.A., 1989. Nongame bird community responses to sagebrush invasion of crested wheatgrass seedings. *Journal of Wildlife Management* 53, 494–502.
- Miller, R.F., Svejcar, T., Rose, J.A., 2000. Impacts of western juniper on plant community composition and structure. *Journal of Range Management* 53, 574–585.
- Miller, R.F., Ratchford, J., Roundy, B.A., Tausch, R.J., Hulet, A., Chambers, J., 2014. Response of conifer-encroached shrublands in the Great Basin to prescribed fire and mechanical treatments. *Rangeland Ecology & Management* 67, 468–481.
- O'Meara, T.E., Haufler, J.B., Stelter, L.H., Nagy, J.G., 1981. Wildlife responses to chaining of pinyon-juniper woodlands. *Journal of Wildlife Management* 45, 381–389.
- Payton, M.E., Greenstone, M.H., Schenker, N., 2003. Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? *Journal of Insect Science* 3, 34.
- Ranglack, D.H., du Toit, J.T., 2015. Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland. *Ecological Indicators* 56, 145–151.
- R Core Team, 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria Available at: <http://www.R-project.org/>.
- Redmond, M.D., Golden, E.S., Cobb, N.S., Barger, N.N., 2014. Vegetation management across Colorado plateau BLM lands: 1950–2003. *Rangeland Ecology & Management* 67, 636–640.
- Reemts, C.M., Cimprich, D.A., 2014. Restoring early-successional shrubland habitat for black-capped vireos using mechanical mastication. *Natural Areas Journal* 34, 400–407.
- Reinkensmeyer, D.P., Miller, R.F., Anthony, R.G., Marr, V.E., 2007. Avian community structure along a mountain big sagebrush successional gradient. *Journal of Wildlife Management* 71, 1057–1066.
- Romme, W.H., Allen, C.D., Bailey, J.D., Baker, W.L., Bestelmeyer, B.T., Brown, P.M., Eisenhart, K.S., Floyd, M.L., Huffman, D.W., Jacobs, B.F., Miller, R.F., Muldavin, E.H., Swetnam, T.W., Tausch, R.J., Weisberg, P.J., 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. *Rangeland Ecology & Management* 62, 203–222.
- Rosenstock, S.S., Van Riper III, C., 2001. Breeding bird responses to juniper woodland expansion. *Journal of Range Management* 54, 226–232.
- Roundy, B.A., Vernon, J.L., 1999. Watershed values and conditions associated with pinyon-juniper communities. In: Monsen, S.B., Stevens, R. (Eds.), Proceedings: ecology and management of pinyon-juniper communities within the interior West. Proceedings RMRS-P-9. USDA Forest Service, Ogden, UT, USA, pp. 173–187.
- Schoennagel, T., Nelson, C.R., 2011. Restoration relevance of recent National Fire Plan treatments in forests of the western United States. *Frontiers in Ecology and the Environment* 9, 271–277.
- Sedgwick, J.A., Ryder, R.A., 1987. Effects of chaining pinyon-juniper on nongame wildlife. In: Everett, R.L. (Ed.), Proceedings: Pinyon-Juniper Conference. General Technical Report INT-GTR-215. USDA Forest Service, Ogden, UT, USA, pp. 541–551.
- Severson, K.E., 1986. Small mammals in modified pinyon-juniper woodlands, New Mexico. *Journal of Range Management* 39, 31–34.
- Severson, J.P., Hagen, C.A., Maestas, J.D., Naugle, D.E., Forbes, J.T., Reese, K.P., 2017. Short-term response of sage-grouse nesting to conifer removal in the northern Great Basin. *Rangeland Ecology & Management* 70:50–58. <http://dx.doi.org/10.1016/j.rama.2016.07.011>.
- Short, H.L., Evans, W., Boeker, E.L., 1977. The use of natural and modified pinyon pine-juniper woodlands by deer and elk. *Journal of Wildlife Management* 41, 543–559.
- Sikes, R.S., Gannon, W.L., 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92, 235–253.
- Smith, C.B., Urness, P.J., 1984. Small mammal abundance on native and improved foothill ranges, Utah. *Journal of Range Management* 37, 353–357.
- Stephens, G.J., Johnston, D.B., Jonas, J.L., Paschke, M.W., 2016. Understorey responses to mechanical treatment of pinyon-juniper in northwestern Colorado. *Rangeland Ecology & Management* 69, 351–359.
- Tausch, R.J., West, N.E., Nabi, A.A., 1981. Tree age and dominance patterns in Great-Basin pinyon-juniper woodlands. *Journal of Range Management* 34, 259–264.
- Tausch, R.J., Tueller, P.T., 1995. Relationships among plant species composition and mule deer winter range use on eastern Nevada piñon-juniper chaining. In: Shaw, D.W., Aldon, E.F., LoSapio, C. (Eds.), Desired future conditions for pinyon-juniper ecosystems. General Technical Report, RM-GTR-258, Fort Collins, Colorado. USDA Forest Service, Flagstaff, AZ, USA, pp. 65–73.
- Turkowski, F.H., Reynolds, H.G., 1970. Response of some rodent populations to pinyon-juniper reductions on the Kaibab Plateau, Arizona. *The Southwestern Naturalist* 15, 23–27.
- Turkowski, F.J., Watkins, R.K., 1976. White-throated woodrat (*Neotoma albigula*) habitat relations in modified pinyon-juniper woodland of southwestern New Mexico. *Journal of Mammalogy* 57, 586–591.
- US Bureau of Land Management, 2011. Notice of intent to prepare environmental impact statements and supplemental environmental impact statements to incorporate greater sage-grouse conservation measures into land use plans and land management plans. Notice of Intent, Federal Register, p. 76, pp. 77008–77011.
- Verts, B.J., Carraway, L.N., 2001. *Tamias minimus*. Mammalian Species 653, 1–10.
- Whitaker, J.O., 1996. National Audubon Society field guide to North American mammals. second ed. Random House, New York, NY, USA 992 p.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–S139.
- White, G.C., Burnham, K.P., Anderson, D.R., 2001. Advanced features of program MARK. In: Field, R., Warren, R.J., Okarma, H., Sievert, P.R. (Eds.), Proceedings of the Second International Wildlife Management Congress. 28 June–2 July 1999. The Wildlife Society, Gödöllő, Hungary, pp. 368–377.
- White, G.C., Shenk, T.M., 2001. Population estimation with radio-marked animals. In: Millsbaugh, J.J., Marzluff, J.M. (Eds.), Radio tracking and animal populations. Academic Press, San Diego, CA, USA, pp. 329–350.
- Wymore, I.F., 1974. Estimated average annual water balance for Piceance and Yellow Creek watershed. Technical Report Series 2. Colorado Water Lands Research Institute, Fort Collins, CO, USA.