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Bird Responses to Removal of Western Juniper in Sagebrush-Steppe ☆

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ABSTRACT

We investigated bird abundance in response to western juniper *(Juniperus occidentalis)* removal using a short-term chronosequence approach and generated estimates of density and responses to management for the most abundant species. Stands targeted for tree removal were primarily in the middle stages of juniper encroachment (Phase II, 7 851 ha). Trees were removed using hand felling combined with either lop and scatter, single tree burning, or jackpot burning, which were carried out to minimize loss of shrub cover. Brewer's sparrow *(Spizella breweri)* density was greater at treated versus untreated portions of the study area. At sites in the third year following tree removal, Brewer's sparrow density was 23.6 (95% confidence interval [CI]: 19.4–27.8) territories per km^2 higher than locations that had not yet been treated. This equates to a net increase of 1 212 — 1 737 nesting pairs within the project area. Green-tailed towhee increased by 4.6 (95% CI: 3.1–6.1) territories per km^2 for an estimated project-wide increase of 194–381 nesting pairs, and vesper sparrow *(Poocetes gramineus)* increased by 6.5 (95% CI: 4.6–8.4) territories per km^2 corresponding to an estimated increase of 460–559 nesting pairs within the project area. Density of gray flycatcher *(Empidonax wrighti)* was lower in cut areas, and over the entire project area we estimate a net loss of 183–486 nesting pairs as a result of juniper tree removal. This study demonstrates that conifer removal projects designed to retain shrub cover and structure can have benefits to multiple species of ground and shrub nesting birds, including several species of conservation concern.
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Introduction

The sagebrush ecosystem, despite its vast extent in western North America and large amount of public ownership, is considered one of the most imperiled in the United States (Noss et al., 1995). Multiple stressors have contributed to its degradation including fragmentation from agriculture, livestock grazing, energy development, invasive plants, woodland expansion, and altered fire regimes (Knick et al., 2003; Leu et al., 2008; Davies et al., 2011). More than 350 sagebrush-associated plant and animal species have been identified as species of conservation concern (Dobkin and Sauder, 2004; Suring et al., 2005; Wisdom et al., 2005).

Expansion of conifers into productive mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* [Rydb.] B. Boivin) communities has occurred since the middle of the 19th century (Tausch et al., 1981; Miller et al., 2005). Juniper (*Juniperus* spp.) woodlands in the northern Great Basin and Columbia Plateau have increased from 0.3 million ha in 1870 to over 3.5 million ha (Miller et al., 2000), including 2.6 million ha of western juniper (*Juniperus occidentalis* Hook) in Oregon (Azuma et al., 2005).

The ecological dynamics of pinyon and juniper woodlands is thought to have been altered following Euro-American settlement, although numerous questions about the historical disturbance regimes and ecological processes driving vegetation dynamics in this system remain (Romme et al., 2009). Western juniper expansion into sagebrush vegetation communities has been attributed to a reduction in fire frequency as a result of livestock grazing (leading to reduced fine fuel loadings and continuity), as well as direct fire-suppression efforts following World War II (Miller and Rose, 1995, 1999). Presettlement juniper trees were largely restricted to relatively fire-safe areas such as rocky outcrops or low sagebrush (*Artemisia arbuscular* Nutt.) communities that burned only infrequently (Miller and Tausch, 2001). Fluctuations in climate since the mid-1800s, as well as increased fertilization from rising CO_2 levels, have also been implicated. Soule et al. (2004) postulated that the initial pulses of juniper establishment were facilitated by the interaction of favorable climatic conditions and fire exclusion due to livestock grazing, while more recent increases in tree density have been driven primarily by increases in seed production as established trees mature.

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Juniper encroachment into sagebrush shrublands occurs along a successional gradient that relates to community processes and has been described as three phases by Miller et al. (2005). During Phase I, sagebrush and other shrubs are the dominant overstory species with only scattered juniper present. As trees increase in size and density, they eventually become codominant with shrubs (Phase II) and begin to modify community processes resulting in reduced shrub and forb diversity (Miller et al., 2000; Miller et al., 2005). As Phase II stands transition to Phase III (juniper is the dominant species), sagebrush and other shrubs lose vigor and begin dying off. This happens initially under the trees but eventually extends beyond the tree canopies. At 50% juniper canopy cover, Miller et al. (2000) documented sagebrush cover at approximately 20% of its maximum levels. In areas of closed tree canopy, shrub cover can disappear entirely and herbaceous productivity and diversity decline. Not all Phase II stands transition at the same rates to Phase III, and a number of environmental factors likely influence rates and trajectories of stand development.

Resource managers are increasingly concerned about the implications of encroachment for sensitive wildlife species, livestock forage management and production (Bates et al., 2000), and the risk of severe crown fires and associated problems with invasive plants (Miller and Tausch, 2001). Connelly et al. (2004) identified woodland expansion as a threat to greater sage-grouse (*Centrocercus urophasianus;* hereafter, sage-grouse) in their range-wide conservation assessment, and it was determined to be an extinction risk for sage-grouse in the western portion of their range (US Fish and Wildlife Service, 2005). Recent work in Oregon showed that sage-grouse leks do not persist when conifer cover in the surrounding landscape exceeds 4% (Baruch-Mordo et al., 2013), indicating relatively low tolerance for trees on the landscape.

Little has been published on the responses of other species of birds to juniper removal (Knick et al., 2014), although the assumption is often made in land management planning documents that shrub-associated species benefit. Previous research examining patterns of bird distribution and abundance along successional gradients of woodland expansion and development have found that shrub and ground nesting birds tend to decrease with increased woodland density (Knick et al., 2005; Reninkensmeyer et al., 2007).

Several shrub and ground nesting species of birds are of conservation concern or have documented long-term (1966−2012) population declines in Oregon and in other portions of their range (Sauer et al., 2014). In Oregon, for example, green-tailed towhees have an annual rate of change of −2.2% (−3.5% to −0.9%), Brewer's sparrows have an annual rate of −2.0% (−3.0% to −0.8%), and vesper sparrows have an annual rate of −2.3% (−3.7% to −1.0%). Due in large part to documented declines, both green-tailed towhee and Brewer's sparrow are considered birds of conservation concern in the Great Basin Bird Conservation Region and Fish and Wildlife Service regions 1 and 8 (US Fish and Wildlife Service, 2008, 2011).

Removal of juniper from sagebrush vegetation communities is occurring in Oregon at an accelerating rate. Public land management agencies that historically managed juniper primarily as a means to increase forage production are now designing juniper removal projects with the creation or improvement of sage-grouse habitat as a primary goal (Bureau of Land Management, 2014). The Sage Grouse Initiative (SGI) is a collaborative partnership among federal and state agencies, conservation organizations, and private landowners that was launched in 2010. The initiative's goals are to increase ecological understanding, identify critical management needs, and reduce threats to sage-grouse through habitat management. With financial assistance from the Natural Resources Conservation Service (NRCS) through the SGI, the scale of juniper removal on private lands in Oregon has increased >1 400% since 2010 (NRCS, 2015). Many additional hectares have been treated by federal land management agencies, although statistics have not yet been compiled on a statewide basis.

Our primary objective was to assess changes in passerine abundance in response to juniper removal in sagebrush-steppe. We predicted that shrub and ground nesting birds, specifically sagebrush associates like Brewer's sparrow, vesper sparrow, and green-tailed towhee, would increase in abundance as a function of tree removal and that species associated with woodlands and those that nest in trees would decrease in abundance.

Methods

Study Area

The South Warner juniper removal project area (hereafter study area) is located 25 km east of the town of Lakeview in Lake County, Oregon. It extends from just north of the tristate boundary of California, Nevada, and Oregon northward to Highway 140. This 27 875-ha area is a high-elevation plateau that is dissected by several deep drainages containing riparian vegetation. Most of the study area (78%) is publicly owned and administered by the federal Bureau of Land Management (BLM) with the remainder being privately owned ranchlands. Elevations range from 1 370 m to 1 945 m, with most lands above 1 675 m. Dominant vegetation communities include low sagebrush and mountain big sagebrush, often with a bitterbrush (*Purshia tridentata* [Pursh] DC.) component. Additional shrubs that occur in the uplands include gray rabbitbrush (*Ericameria nauseosa* [Pursh] G.L. Nelson & G.I. Baird), green rabbitbrush (*Chrysothamnus viscidiflorus* Nutt.), several species of horsebrush (*Tetradymia* spp.), and mountain snowberry (*Symphoricarpos oreophilus* A. Gray). Localized areas of silver sagebrush (*Artemisia cana* Pursh) occur in soils with poor drainage at the top of the plateau (Bureau of Land Management, 2011). Western juniper stands vary in age, composition, and density and occur within all of the shrub communities. The most common grasses include Sandberg's bluegrass (*Poa secunda* J. Presl), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), Idaho fescue (*Festuca idahoensis* Elmer), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love). Cheatgrass (*Bromus tectorum* L.) occurs throughout the project area and with a few exceptions is found in relatively low density. The western and southwestern borders of the study area include transition zones between sagebrush-juniper−dominated plant communities and mixed conifer forests characterized by ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) and white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.).

Management Treatments

The BLM developed juniper management treatment prescriptions (hereafter treatments) on a stand-by-stand basis following guidance in Miller et al. (2007). Complementary and integrated management actions on adjacent private lands were generally similar in scope and execution, although some landowners began using heavy machinery to remove trees in 2014. Vegetation units were digitized using 1-m resolution imagery from the National Agricultural Imagery Program. Staff from BLM then inventoried vegetation communities and juniper stand structure for individual units. The BLM is slated to remove up to 9 967 ha (1 527 ha of Phase I; 7 851 ha of Phase II, 552 ha of Phase III) of postsettlement juniper while leaving untreated another 7 434 ha (Bureau of Land Management, 2011). Treatments began in 2012 and are anticipated to take up to 10 yr to complete.

A stated goal when selecting techniques for juniper removal was maintenance of sagebrush cover required by sagebrush-obligate birds, especially sage-grouse. Four methods that all entail hand cutting trees were used: 1) cut and leave felled trees, 2) cut and lop branches such that cut vegetation does not exceed 1.25 m in height, 3) cut and single-tree burn, and 4) cut and burn piles of lopped branches. Burning of single trees, including small piles of single trees (jackpot burns) and piles of lopped branches, typically occurs in the fall 2 yr after trees are cut. These methods maintain existing shrub communities and allow selective removal of invasive young trees and retention of old-growth juniper (Fig. 1).

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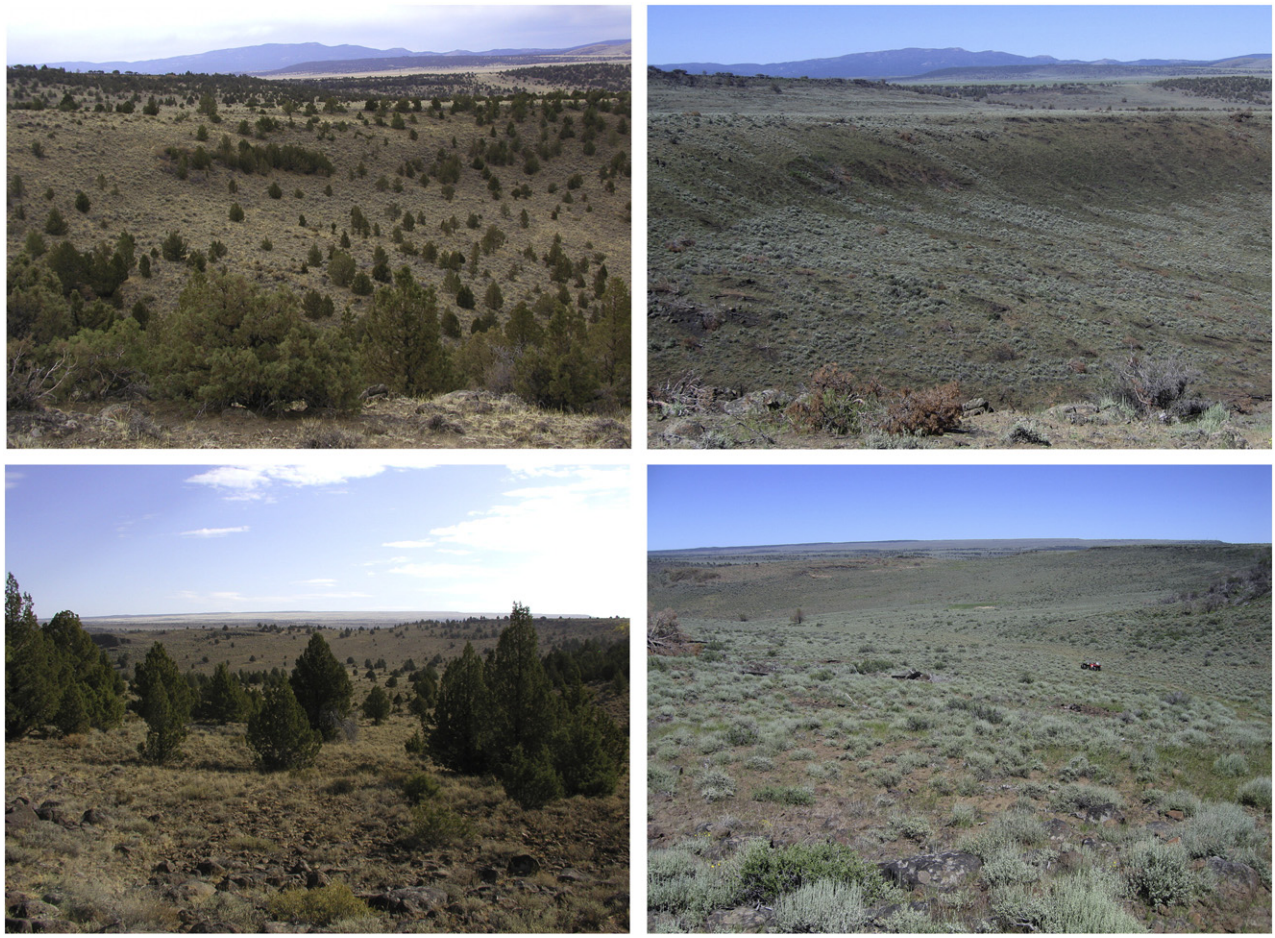


Figure 1. Two portions of the South Warner Project Area before treatment in 2008 (left) and after (right, 2015) hand felling of Phase II juniper trees (photo credit Todd Forbes, Bureau of Land Management).

Study Design

To quantify temporal elements of bird responses to conifer removal we applied a chronosequence approach that substituted space for time. Bird densities were estimated at sagebrush sites where conifer had not yet been removed and along a chronosequence of cut sites during 1-, 2-, and 3-yr postremoval.

We systematically placed 597 sampling points on a 400 m grid across the public lands portion of the study area (Fig. 2). We excluded 54 points that lacked control sites because BLM had already cut all Phase I juniper stands before our study began. We also excluded from the survey those points that fell within vegetation units mapped as having a shrub layer composed exclusively of low sagebrush. Low sagebrush points were centrally located atop a plateau that was relatively free of postsettlement trees. Lastly, after visiting sampling points in the field, we excluded those that fell within ponderosa pine and fir forest communities along the edges of the study area. Thus we sampled birds and vegetation at a total of 404 points that fell within vegetation units mapped as Phase II ($n = 377$) or Phase III ($n = 27$) juniper. Sample points were treated before bird surveys began (II = 178; III = 15) or were slated for treatment in upcoming years (II = 199; III = 12).

Bird Surveys

We conducted point count surveys between 17 May and 1 July in 2013 ($n = 174$) and 2014 ($n = 230$) following standard protocols (Ralph et al., 1993). This period corresponds with the peak of the nesting season at this elevation and maximum detectability and song-rates of target species. Points were grouped into routes that could be completed in one morning, and routes were randomly assigned to each year. Points were surveyed twice, each time by a different observer, with at least 12 days between visits. Within each year, the order in which routes were surveyed during the first visit was random in order to avoid any potential bias with respect to timing within the breeding season and bird activity. Six different observers completed 808 surveys of 404 points over the course of the study. We began surveys approximately 20 minutes after local sunrise and completed them within 3.5 h. The order in which a route was surveyed was reversed for the second visit to minimize the influence of time of day on bird activity (Shields, 1977; Verner and Ritter, 1986). We did not conduct surveys during precipitation or sustained high winds (>15 kph). Observers recorded all birds seen or heard in a 125-m radius of the point during a 5-min period; distance to birds was recorded using a digital rangefinder (Leica LRF900), and we noted type of detection (song, call, or visual) and whether a bird initially detected visually or by a call subsequently sang. If a bird was not located visually, a distance was measured to the patch of vegetation from which the call or song was perceived.

Vegetation Sampling

At each sampling point we measured shrub cover along two 50-m transects. Few bird detections are typically made close to the survey point in radial counts due to the fact that the area surveyed increases with distance from the observer (Buckland et al., 2001). Transects thus began 40 m from the point to correspond with the area where

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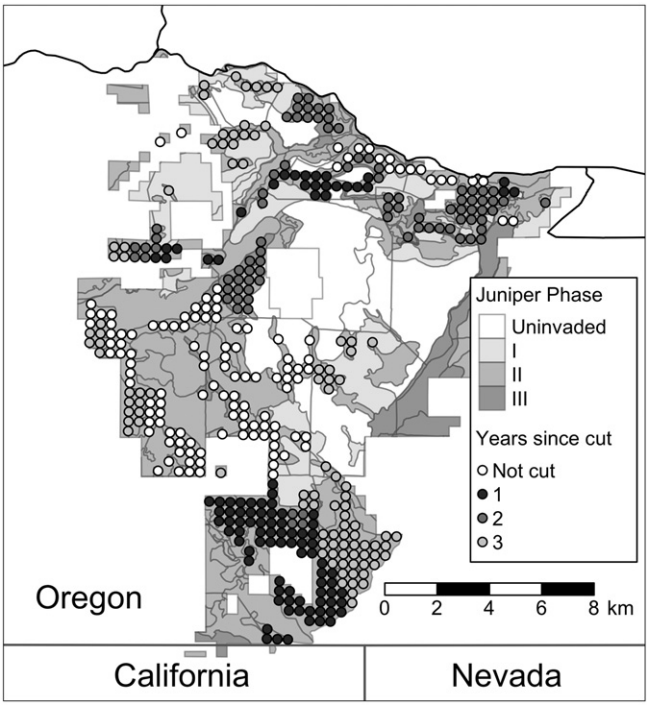


Figure 2. South Warner Project Area showing juniper expansion phase, bird survey locations, and number of breeding seasons post cut that bird surveys were conducted.

most bird detections are made and were oriented along two randomly selected cardinal directions. We recorded species, height, and intercept of each shrub along the transect (Canfield, 1941). We measured canopy rather than foliar cover and excluded gaps ≥20 cm within otherwise continuous shrub canopies. Vegetation was sampled between 25 May and 3 July in the same year that bird surveys were conducted. We estimated juniper tree density from tree point data developed using spatial wavelet analysis (Falkowski and Evans, 2012) based on 1-m digital aerial photography acquired in 2009—2010; http://nrcs-sgi.s3-website-us-east-1.amazonaws.com/). We calculated tree density within a 125 m radius of sampling points both before and after tree removal. Post—tree removal density was estimated by intersecting tree point data with treatment boundaries using ARCGIS 10.1 (Environmental Systems Research Institute, 2011) and adding field-based counts of trees that were left following cuts.

Statistical Analysis

Sampling locations were assigned to one of four treatment categories: not yet treated, first breeding season post-treatment, second breeding season post-treatment, and third breeding season post-treatment (Table 1). We used program DISTANCE version 6 (Thomas et al., 2010) to generate estimates of density and limited our analysis to those species that occurred on at least 25% of the sampling points to ensure adequate data to develop robust estimates. Data from both of the surveys at each point were used, and a multiplier of 0.5 was incorporated into models in program DISTANCE. Only singing males were included, and we therefore make the assumption that singing males are in a territory that is being defended and that pairing rates of territorial males are similar between cut and uncut survey areas.

We used the Multiple Covariate Distance Sampling (MCDS) engine with a hazard rate key function and a simple polynomial adjustment term (Marques et al., 2007). The hazard rate key function fits a model with a left shoulder corresponding to 100% detectability, which is appropriate for singing males given their high detectability when near the observer. We followed analysis guidelines suggested by Marques et al. (2007) and Thomas et al. (2010). We first conducted an exploratory analysis for each species using both exact distances and short interval groupings to assess goodness of fit visually using quantile-quantile plots and histograms. Data were then grouped into intervals that improved fit and further evaluated both visually and using the χ^2 goodness-of-fit test (Buckland et al., 2001). Because birds may avoid the area close to the observer, we grouped sightings within 20 m into a single interval. Finally, we estimated four models for each species: no covariates, a binary covariate indicating whether trees had been removed or not, a covariate for observer, and a model with both observer and whether a site had been cut as covariates. Densities are presented as the number of territories per km^2, and estimates of project-wide impacts to local population size are calculated on the basis of only the areas sampled (i.e., the proportion of the total treatment area on public lands that was included in analyses; 6 251 ha).

Table 1
Distribution of sampling points by survey year and number of breeding seasons since cutting occurred

Number of breeding seasons since cutting occurred	Survey Yr		Total
	2013	2014	
Not cut	113	80	193
1	36	30	66
2	25	49	74
3	0	71	71
Total	174	230	404

Results

Vegetation and Environment

Environmental and vegetation community variables that we measured (or attributed using GIS) at survey points were largely similar among the cut and uncut points and by number of breeding seasons post-treatment (Table 2). The precutting density of juniper trees surrounding sampling points that were surveyed in their first breeding season following treatment was slightly lower than the not-yet-cut points. Likewise, points surveyed in the second and third breeding seasons post treatment were approximately 50 m lower in elevation, on average, than the points that had not yet been cut (and CIs did not overlap), resulting in a relatively small but significant difference in elevation between the cut and uncut points. Although CIs overlap, there appears to be a slight trend for small increases in the cover of shrubs >40 cm in height for the years following cutting with cover increasing from a mean of 10.02% in the uncut sample to 11.14% in the first growing season following tree removal, 13.39% in the second season, and 14.09% in the third season. Total shrub cover (including big sagebrush, low sagebrush, bitterbrush, horsebrush, rabbitbrush, and snowberry) averaged just over 20% and was similar among all treatment categories (see Table 2). For points that were cut, an average of 94.9% (95% CI: 93.6–96.2) of the area within the 125 m radius was within a treatment boundary and tree density following treatments averaged 0.82 trees per ha (0.42–1.22).

Birds

We detected a total of 58 species of birds within 125 m of the survey points. Most species were detected at few survey locations and are therefore not well suited to statistical analysis. The six most widespread and abundant species (Table 3) represented 2 733 (68%) of the 3 990 bird detections.

For three of the five species investigated, the best model, as determined by Akaike information criterion, included a covariate for observer, while the other two included the covariate for whether a site had been cut (Table 4). Detection probability (P) for singing birds was not statistically different based on treatment history except for

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Table 2
Mean values (95% confidence intervals) of habitat variables. Cut points are divided on the basis of the number of breeding seasons following treatment

Variable	Uncut ($n = 193$)	Cut ($n = 211$)	No. of yr post cut		
			1 ($n = 66$)	2 ($n = 74$)	3 ($n = 71$)
Elevation (m)	1 768 (1 758-1 778)	1 735 (1 726-1 744)	1 775 (1 763-1 789)	1 716 (1 697-1 736)	1 717 (1 707-1 728)
Slope (%)	13.06 (11.18-14.95)	14.51 (12.76-16.25)	13.1 (9.93-16.27)	16.4 (13.19-19.60)	13.86 (11.07-16.64)
Trees/ha[1] precut	45.05 (41.69-48.41)	41.22 (38.25-44.19)	35.75 (30.90-40.61)	41.08 (36.26-45.91)	46.44 (40.80-52.08)
ARTR[2] (%)	3.21 (2.35-4.07)	4.45 (3.60-5.30)	3.27 (2.16-4.38)	5.34 (3.67-7.02)	4.61 (3.06-6.15)
ARAR[3] (%)	10.52 (9.29-11.75)	8.77 (7.61-9.94)	10.03 (7.82-12.25)	9.27 (7.40-11.14)	7.08 (5.05-9.11)
PUTR[4] (%)	4.59 (3.57-5.62)	5.34 (4.46-6.22)	5.09 (3.67-6.50)	4.35 (2.86-5.84)	6.6 (4.92-8.28)
Shrubs >40 cm[5]	10.02 (8.48-11.57)	12.92 (11.45-14.40)	11.14 (8.68-13.60)	13.39 (10.71-16.08)	14.09 (11.53-16.65)
Total shrub (%)	20.23 (18.67-21.78)	20.72 (19.20-22.24)	20.86 (18.16-23.55)	21.06 (18.42-23.71)	20.25 (17.56-22.93)

[1] Density of trees before any cutting occurred.
[2] *Artemisia tridentata.*
[3] *Artemisia arbuscular.*
[4] *Purshia tridentata.*
[5] Shrub cover (all species) for shrubs >40 cm in height.

rock wren. For singing males, *P* for Brewer's sparrow was 0.66 (95% CI: 0.61–0.71) at uncut points and 0.59 (95% CI: 0.56–0.63) at cut points. Green-tailed towhee detection probability was 0.7 (95% CI: 0.64–0.76) at uncut and 0.75 (95% CI: 0.71–0.80) at cut points. Vesper sparrow detection probability was 0.72 (95% CI: 0.64–0.80) at uncut and 0.67 (95% CI: 0.63–0.73). Gray flycatcher detection probability was 0.48 (95% CI: 0.42–0.56) and 0.50 (95% CI: 0.39–0.64), respectively. Rock wren detection probability was 0.81 (95% CI: 0.74–0.89) and 0.95 (95% CI: 0.91–0.99), respectively.

Brewer's sparrow density increased in a linear fashion based on the number of breeding seasons that had elapsed since trees were removed (Fig. 3). Density was 21.5 (95% CI: 19.8–23.2) territories/km^2 in areas that had not yet been cut, 31.2 (95% CI: 27.5–35.5) the first year following cutting, 34.1 (95% CI: 30.4–38.2) the second year following cutting, and 454.1 (95% CI: 40.3–50.4) territories/km^2 in areas surveyed during the third breeding season following tree removal. The estimated increase at 3 yr post-treatment (with approximate 95% CIs) was 23.6 (95% CI: 19.4–27.8) territories per km^2. Within the public lands portion of the project area that we surveyed, that equates to a net gain of 1 475 (95% CI: 1 212–1 737) territories.

Green-tailed towhee density was also higher at sites that had been cut than those that had not, although it did not increase successively with each additional breeding season following tree removal (see Fig. 3). Density was estimated as 12.36 (95% CI: 11.32–13.39) territories per km^2 at points that had not yet been cut, 16.42 (95% CI: 14.53–18.56) the first year following tree removal, 15.74 (95% CI: 14.06–17.63) the second year, and 18.70 (95% CI: 16.7–20.9) in the third year. Since postcutting estimates did not differ significantly from one another, we estimated the overall increase based simply on precutting and postcutting densities. The estimated change in density is 4.6 (95% CI: 3.1–6.1) territories per km^2, corresponding to an overall predicted gain of 287 (95% CI: 194–381) territories within the project area.

Vesper sparrow densities were also higher in areas 1 − 3 yr post–tree removal than at sites that had not been cut (see Fig. 3). Estimated density was 11.21 (95% CI: 10.07–12.47) territories per km^2 at points that had not yet been cut, 19.14 (95% CI: 16.82–21.78) the first year following tree removal, 14.58 (95% CI: 12.48–17.03) the second year, and 19.75 (95% CI: 16.8–23.2) in the third year. We estimated net change on the basis of the composite estimate for areas 1–3 breeding seasons postcut as 6.54 (95% CI: 4.63–8.44) territories per km^2 for an overall gain of 409 (95% CI: 289–527) territories within the project area.

Gray flycatcher density was highest in the uncut areas, midrange at sites one breeding season following tree removal, and lowest at sites 2 − 3 yr following tree removal (see Fig. 3). Density was estimated as 11.32 (95% CI: 9.75–13.14) territories per km^2 at points that had not

Table 3
Bird species that were detected on >10% of 404 survey points and proportion of points where a species was detected on cut (1–3 breeding seasons post cut) and uncut areas

Species	Not cut ($n = 193$)	Cut ($n = 211$)
Brewer's sparrow *(Spizella breweri)*	59.6	80.6
Green-tailed towhee *(Pipilo chlorurus)*	51.8	64.9
Vesper sparrow *(Pooecetes gramineus)*	49.7	64.9
Rock wren *(Salpinctes obsoletus)*	36.8	41.2
Gray flycatcher *(Empidonax wrightii)*	50.3	19.0
Mountain bluebird *(Sialia currucoides)*	35.7	20.4
Brewer's blackbird *(Euphagus cyanocephalus)*	14.0	19.9
Chipping sparrow *(Spizella passerina)*	24.9	8.5
Oregon junco *(Junco hyemalis)*	22.3	7.6
Western scrub-jay *(Aphelocoma californica)*	13.5	14.2
Spotted towhee *(Pipilo maculatus)*	5.7	19.4
Brown-headed cowbird *(Molothus ater)*	15.0	7.1

Table 4
Covariates used in candidate models, number of parameters in each model, Akaike information criterion (AIC), and ΔAIC

Species	Covariate(s)	No. parameters	AIC	ΔAIC
Brewer's sparrow	Observer	7	2 750.21	0.00
	Observer, cut	8	2 751.50	1.30
	None	2	2 768.72	18.51
	Cut	3	2 771.14	20.93
Vesper sparrow	Observer	7	1 249.61	0.00
	Observer, cut	8	1 251.47	1.86
	None	2	1 281.04	31.43
	Cut	3	1 281.56	31.95
Green-tailed towhee	Cut	2	1 693.81	0.00
	None	3	1 695.96	2.15
	Observer, cut	8	1 696.85	3.04
	Observer	7	1 699.15	5.33
Gray flycatcher	Observer	7	496.85	0.00
	None	2	497.85	1.00
	Observer, cut	8	499.05	2.20
	Cut	3	499.99	3.14
Rock wren	Cut	3	649.05	0.00
	None	2	651.18	2.13
	Observer	7	658.86	9.81
	Observer, cut	8	658.98	9.93

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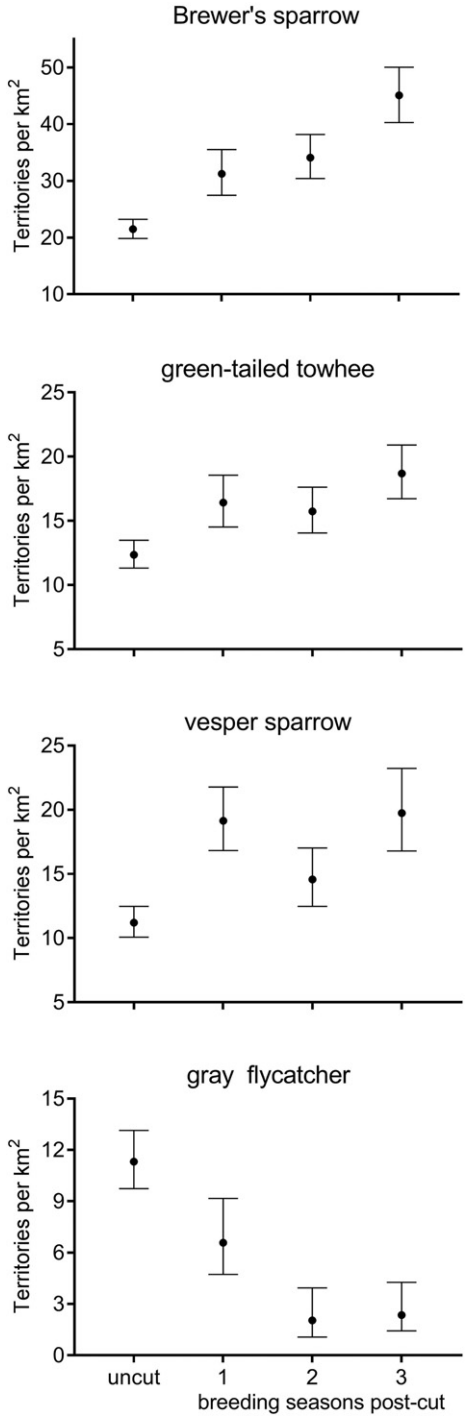


Figure 3. Bird density estimates for portions of the project area that had not yet been cut and those surveyed during the first, second, or third breeding season following tree removal. Error bars are 95% confidence intervals.

yet been cut, 6.58 (95% CI: 4.73–9.17) the first year following tree removal, 2.04 (95% CI: 1.06–3.94) the second year, and 2.35 (95% CI: 1.29–4.27) in the third year. The estimated difference between uncut areas and areas two to three breeding seasons following tree removal was 5.35 (95% CI: 2.92–7.78) territories per km^2, for a net loss of 334 (95% CI: 183–486) territories within the project area.

Rock wren density varied among estimates by as little as two territories per km^2 and did not exhibit a pattern indicating a response to treatment. Density was estimated as 6.05 (95% CI: 5.52–6.63) territories per km^2 at points that had not yet been cut, 4.87 (95% CI: 4.44–5.36) the first year following tree removal, 5.80 (95% CI: 5.34–6.29) the second year, and 4.98 (95% CI: 4.55–5.46) in the third year.

Discussion

We found hand cutting of juniper conducted primarily to benefit sage-grouse resulted in considerable benefits to several nontarget species, as evidenced by large increases in the abundance of a sagebrush obligate songbird species (Brewer's sparrow), a near obligate (green-tailed towhee), and a ground nesting species closely tied to sagebrush plant communities in this region (vesper sparrow). Importantly, the songbirds exhibiting positive responses to treatments are species of high conservation concern that have experienced long-term (1966—2012) population declines in the region (US Fish and Wildlife Service, 2008, 2011; Sauer et al., 2014). Our results are consistent with previous work showing increases in breeding abundance of shrubland and grassland passerines of concern with mechanical pinion-juniper removal in the Southwest (Crow and VanRiper, 2010) and treatment of woody plant encroachment in grasslands of the Chihuahuan Desert (Coffman et al., 2014).

Because we documented only slight differences in the shrub structure between areas that had been cut and those that had not, it appears likely that these species are actively avoiding trees at our study area. Our results are consistent with previous work showing avoidance of trees by grassland birds (Thompson et al., 2014; Lautenbach et al., 2017-this issue). It has been hypothesized that the mechanism behind such avoidance is based on predation or nest parasitism risk, where woody vegetation supports more or different predators or alters their behavior through the provision of perches or protected travel routes (see Thompson et al., 2014 for discussion of potential mechanisms in grassland systems).

Not all species responded similarly to treatments as we expected on the basis of known variation in species composition and abundance along gradients of juniper woodland succession (Knick et al., 2005; Noson et al., 2006; Reninkensmeyer et al., 2007). We documented reduced densities of gray flycatcher territories in areas that had been cut 1–3 yr prior. This species commonly occupies the shrub-woodland ecotone and nests in both taller sagebrush and juniper (Sterling, 1999). Gray flycatcher populations have exhibited long-term population increases in the region (Sauer et al., 2014), a trend that corresponds with increases in favorable habitat conditions due to woodland expansion into sagebrush steppe. Other shrub-nesting birds, including lark sparrow *(Chondestes grammacus),* spotted towhee *(Pipilo maculatus),* and sage thrasher *(Oreoscoptus montanus)* appeared to occur more widely or in greater abundance post treatment, but we lacked sufficient count data to model the responses. Likewise, woodland-associated species including dark-eyed junco *(Junco hyemalis),* chipping sparrow *(Spizella passerina),* and mountain chickadee *(Poecile gambeli)* appeared to occur in lower abundances at treated sites, but high variance in counts and low rates of occurrence also precluded meaningful statistical analyses.

While changes in abundance among species correctly imply that treatments result in biodiversity trade-offs, it is important to acknowledge that a shrub-steppe habitat deficit has been accruing for more than a century as juniper woodlands have slowly replaced sagebrush habitats (Miller et al., 2011). The species that exhibited higher densities at sites that had been cut were species that have shown population declines in the region, whereas gray flycatcher, which occurred at reduced abundance where junipers had been removed, has a long-term positive trend in the region.

Some key assumptions should be considered when interpreting our results. First, we used a chronosequence approach to substitute space for time which biotic and abiotic conditions are similar over the time span of the successional stage being investigated. Because the similarity in conditions is often not evaluated, chronosequence study designs have been criticized as a means of understanding patterns of succession

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(Johnson and Miyanishi, 2008). In this study the chronosequence of tree removal effects spans only two breeding seasons, and all survey points, whether cut before the year they were surveyed or slated for future removal of trees, had fairly similar distributions of juniper densities (before treatment).

Secondly, we did not take into account changes in the landscape configuration and extent of cut areas between 2013 and 2014, which may have contributed to differences in density estimates to the extent that density may be influenced by landscape-scale habitat characteristics. Finally, we used songbird abundance as a metric to infer population performance, which carries with it some caveats. Abundance can be a misleading indicator (Van Horne, 1983), especially in heavily altered areas. However, a synthesis of studies worldwide revealed that reproductive success is most often linked to abundance in ecosystems with limited human development (Bock and Jones, 2004), which lends some validation to our use of abundance as barometer of relative habitat quality.

We documented greater increases in Brewer's sparrow and, to a lesser degree, green-tailed towhee abundance in yr 2 and 3 post-treatment, relative to the initial year following tree removal, providing some support for a lag effect in response. Knick et al. (2014) found that sagebrush-associated birds generally did not respond to juniper treatment in the first 3 — 5 yr, which they attributed to time lags in individual (site fidelity) and population response to vegetation change. However, songbirds generally respond quickly to vegetation change (Gardali et al., 2006; Gardali and Holmes, 2011) and we observed some immediate positive response in abundance, which is consistent with other evaluations of mechanical juniper thinning (Crow and VanRiper, 2010). Differences in study results may be related to treatment techniques evaluated and their effect on post-treatment vegetation structure, as well as landscape composition and connectivity to intact sagebrush communities. Knick et al. (2014) included broadcast burning in their evaluation, which reduced sagebrush cover available for nesting and also left conifer trees as a prevalent structural feature on the landscape (6–24% cover). In our study area, selective hand cutting rendered large expanses of intact shrubland nearly devoid of trees (see Fig. 1) and residual tree cover following treatment was generally limited to small numbers of mostly mature, postsettlement aged trees on rocky sites (<1% cover on the landscape).

Management Implications

Positive responses of sagebrush associate passerines, combined with positive sage-grouse response to treatments in the same study area recorded by others (Severson et al., 2017-this issue), provide the first evidence that carefully designed conifer treatments may yield meaningful biological outcomes for sagebrush-associated birds. Knick et al. (2014) inferred that conifer removal was unlikely to increase available habitat for any species in the sagebrush bird community after evaluating songbird response to pinion-juniper woodland treatments that were not necessarily designed to benefit sagebrush obligates. However, in our direct evaluation of contemporary sage-grouse habitat improvement efforts, conifer removal designed with the explicit objective of maximum shrub retention resulted in increased territory density for certain birds of conservation concern. Broadcast burning is a cost-effective and appropriate tool for restoring ecological processes and achieving long-term resource objectives (Davies et al., 2014; Boyd et al., 2017-this issue) but should not be expected to yield immediate benefits for shrub-dependent birds. Hand cutting of encroaching conifers is an important restoration tool that is increasingly being implemented at large scales through spatially targeted efforts to benefit sage-grouse (and other obligates). We suggest that careful removal of encroaching trees can complement other types of whole watershed restoration efforts designed to produce multiple resource benefits in the long term.

Sage-grouse are often used as an umbrella species for sagebrush habitat conservation because of the breadth of niche overlap with other species at multiple scales (Rowland et al., 2006; Hanser and Knick, 2011). Our study provides additional evidence that benefits from sage-grouse restoration efforts extend to other birds of conservation concern co-occurring in the same landscapes. Quantifying restoration success for landscape-scale species with low reproductive rates, such as sage-grouse, has proven elusive due to extended time lags, environmental noise associated with natural population cycles, and the scale of management action needed to produce a biological response. However, songbirds are relatively easy to monitor during the nesting season and generally respond quickly to environmental change (Gardali et al., 2006, Gardali and Holmes, 2011). As a result, songbirds may serve as early biological indicators of sagebrush habitat restoration effectiveness long before sage-grouse responses are observed and may be useful for informing adaptive management decisions.

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