



# Changes in Avian and Plant Communities of Aspen Woodlands over 12 Years after Livestock Removal in the Northwestern Great Basin

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**Abstract:** *Riparian and quaking aspen (Populus tremuloides) woodlands are centers of avian abundance and diversity in the western United States, but they have been affected adversely by land use practices, particularly livestock grazing. In 1990, cattle were removed from a 112,500-ha national wildlife refuge in southeastern Oregon. Thereafter, we monitored changes in vegetation and bird abundance in years 1–3 (phase 1) and 10–12 (phase 2) in 17 riparian and 9 snow-pocket aspen plots. On each 1.5-ha plot, we sampled vegetation in 6 transects. Three times during each breeding season, observers recorded all birds 50 m to each side of the plot's 150-m centerline for 25 minutes. We analyzed data with multivariate analysis of variance and paired t tests with p values adjusted for multiple comparisons. In both periods, riparian and snow-pocket aspen produced extensive regeneration of new shoots ( $\bar{x}$  = 2646 stems/ha and 7079 stems/ha, respectively). By phase 2, a 64% increase in medium-diameter trees in riparian stands indicated successful recruitment into the overstory, but this pattern was not seen in snow-pocket stands, where the density of trees was over 2 times greater. By phase 2 in riparian and snow-pocket stands, native forb cover had increased by 68% and 57%, respectively, mesic shrub cover had increased by 29% and 58%, and sagebrush cover had decreased by 24% and 31%. Total avian abundance increased by 33% and 39% in riparian and snow-pocket aspen, respectively, ground or understory nesters increased by 133% and 67% and overstory nesters increased by 34% and 33%. Similarly, ground or understory foragers increased by 25% and 32%, aerial foragers by 55% and 57%, and overstory foragers by 66% and 43%. We interpreted the substantial regeneration of aspen shoots, increased densities of riparian forbs and shrubs, and increased avian abundances as a multitrophic-level response to the total removal of livestock and as substantial movement toward recovery of biological integrity.*

**Keywords:** aspen, avian abundance, Great Basin, habitat recovery, livestock grazing, riparian woodland, snow-pocket aspen

Cambios en las Comunidades de Aves y Plantas en Bosques de Álamo a lo Largo de 12 Años Después de la Remoción de Ganado en la Gran Cuenca Noroccidental

**Resumen:** *Los bosque ribereños y de Populus tremuloides son centros de abundancia y diversidad de aves en el occidente de Estados Unidos, pero han sido afectados adversamente por prácticas de uso de suelo, particularmente pastoreo de ganado. En 1990 se removió el ganado de un refugio nacional de vida silvestre de 112,500 ha en el sureste de Oregon. Desde entonces, monitoreamos cambios en la vegetación y la abundancia de aves en los años 1–3 (fase 1) y 10–12 (fase 2) en 17 parcelas ribereñas y 9 de álamo. En cada parcela de 1.5 ha muestreamos la vegetación en 6 transectos. Tres veces durante cada época reproductiva,*

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observadores registraron durante 25 minutos a todas las aves 50 m a cada lado de la línea central de cada parcela. Analizamos los datos con análisis multivariado de varianza y pruebas pareadas de *t* con valores de *p* ajustados para comparaciones múltiples. En ambos periodos, los bosques ribereños y de álamo produjeron una regeneración extensiva de rebrotes nuevos ( $\bar{x}$  = 2646 tallos/ba y 7079 tallos/ba, respectivamente). En la fase 1, un incremento de 64% en el diámetro promedio de árboles en los bosques ribereños indicó un reclutamiento exitoso en el dosel, pero este patrón no se observó en los bosques de álamo, donde la densidad de árboles fue más de 2 veces mayor. En la fase 2 en bosques ribereños, la cobertura herbácea nativa había incrementado en 68% y 57%, respectivamente, la cobertura arbustiva métrica había incrementado en 29% y 58%, y la cobertura de artemisa había decrecido en 24% y 31%. La abundancia aviar total incrementó en 33% y 39% en bosques ribereños y de álamo, respectivamente, las especies que anidan en el suelo o en el sotobosque incrementaron en 133% y 67% y las especies que anidan en el dosel incrementaron en 34% y 33%. Similarmente, las aves forrajeras de suelo o sotobosque incrementaron en 25% y 32%, los forrajeadores aéreos en 55% y 57% y los forrajeadores de dosel en 66% y 43%. Interpretamos la regeneración sustancial de rebrotes de álamos, el incremento de las densidades de hierbas y arbustos ribereños y el incremento en las abundancias de aves como una respuesta a nivel multitrófico de la remoción total de ganado y como un avance sustancial hacia la recuperación de la integridad biológica.

**Palabras Clave:** abundancia de aves, álamo, bosque ribereño, Gran Cuenca, pastoreo de ganado, *Populus tremuloides*, recuperación de hábitat

## Introduction

Riparian woodlands composed of deciduous trees and shrubs occupy <1% of the western United States, but they support higher diversity and abundance of birds than other cover types (Dobkin & Wilcox 1986; Knopf et al. 1988; Skagen et al. 1998). Similarly, in the 11 western U.S. states (hereafter the West), aspen (*Populus tremuloides*) woodlands harbor greater avian diversity and abundance than surrounding vegetation (Turchi et al. 1995; Griffis-Kyle & Beier 2003; Hollenbeck & Ripple 2007).

Both aspen and riparian woodlands are greatly affected by land-use practices, and aspen are declining in much of the West because of altered fire regimes, succession to conifers, ungulate herbivory, drought, disease, and insect outbreaks (Romme et al. 1995; Kay & Bartos 2000; Worrall et al. 2008). Livestock grazing, primarily by cattle, has a pervasive influence on riparian areas in the West (Fleischner 1994; Belsky et al. 1999), including approximately 90% of the region's extensive federal lands (Fleischner 2010). Besides direct consumption of vegetation, trampling by cattle can cause soil compaction, reduced bank stability, channel widening, increased groundwater depth, and decreased abundance of stream macroinvertebrates (Belsky et al. 1999; Fleischner 1994, 2010). Through direct and indirect effects, cattle and wild ungulates (especially elk [*Cervus elaphus*]) can dramatically impair aspen's ability to regenerate (Fitzgerald & Bailey 1984; Kay & Bartos 2000; Kaye et al. 2005) in riparian and nonriparian settings.

Avian abundance in aspen and other deciduous riparian habitats in the West is reduced in the presence of cattle (Saab et al. 1995; Tewksbury et al. 2002; Earnst et al. 2005). Ground- and shrub-nesting birds tend to be most affected by cattle, as expected from the greater effect that cattle have on low-growing vegetation (Saab et al. 1995),

but effects throughout the avian community have been documented in cases where cattle have highly altered vegetation (Tewksbury et al. 2002; Krueper et al. 2003).

In the high-desert riparian areas of Hart Mountain National Antelope Refuge (HMNAR) in southeastern Oregon (U.S.A.), cattle were contributing to the poor condition of riparian areas and were removed from the refuge after >120 years of grazing (USFWS 1994). The removal of cattle from this relatively large landscape (112,500 ha) in 1990 and subsequent monitoring of vegetation and avian abundance in years 1–3 and 10–12 after cattle removal, provide a unique opportunity to investigate long-term consequences of cattle removal at a landscape scale (Earnst et al. 2005). During the first 3 years after cattle removal, herbaceous cover and avian abundance, especially that of ground and understory specialists began to increase (Dobkin et al. 1998; Tewksbury et al. 2002). We compared vegetation structure and abundance of breeding birds in riparian and snow-pocket aspen 1–3 (phase 1) and 10–12 (phase 2) years after livestock removal.

## Methods

### Study Area

HMNAR is in the northwestern Great Basin in southeastern Oregon (42°25'N, 119°40'W) and is predominantly sagebrush (*Artemisia* spp.) shrubsteppe. Hart Mountain is a fault block that rises gradually from the east to 2438 m and drops as a steep escarpment to the west. Riparian woodlands and snow-pocket aspen stands provide the only trees except for a few stands of mountain mahogany (*Cercocarpus ledifolius*) and western juniper (*Juniper occidentalis*) (USFWS 1994). Of the 134 linear km of riparian habitat and snow-pocket aspen on

HMNAR, 29% is aspen along perennial streams, 10% aspen in snow pockets (small, relatively high-elevation depressions where snow collects), 11% willow (*Salix* spp.), 12% mixed deciduous, 29% sedge or grass meadow, and 9% sagebrush shrubsteppe (Earnst et al. 2005). Annual precipitation, primarily snow, is generally 20–30 cm on the tableland and 30–46 cm on the mountain (USFWS 1994).

### Study Plots

The 4324-ha study area encompassed most aspen stands on the east side of the escarpment. We excluded 1 drainage with aspen from the study area due to difficult access and 1 drainage in which a prescribed burn was planned. Within the study area, the 17 riparian and 9 snow-pocket plots were well distributed throughout areas with aspen, and 3–10 plots were in each of the 5 drainages ( $\bar{x} = 5.2$ ). Most riparian-aspen plots were in mature stands ( $n = 13$ ). Two were in stands with little regeneration and a large proportion of dead trees, and 2 were in a young, dense, even-aged stand that had burned in a 1972 wildfire. Average elevation of riparian and snow-pocket plots was 1951 m (range 1873–2121 m) and 2145 m (2042–2212 m), respectively.

Plots were 1.5 ha (150 × 100 m) and separated by at least 125 m. The width of the aspen stand was often <100 m, and the remainder of the plot consisted of shrubsteppe vegetation. The center line of the plot, which was marked at 50-m increments with permanent steel fence posts, ran near and parallel to the stream.

### Vegetation Measurements

On each of the 26 plots, 6 100-m vegetation transects were placed perpendicular to and bisected by the 150-m center line. Vegetation transects were 25 m apart, and location of the first was chosen at random within the first 12.5 m of the center line. The same vegetation transect locations were used in each phase. At 10-m intervals along vegetation transects, we measured canopy cover with a spherical densitometer and estimated percent ground covered by herbaceous vegetation, litter, and bare ground within a 0.125-m<sup>2</sup> sampling frame. We measured shrub cover (identified to species) as the percentage of the vegetation-transect line that was intercepted by live shrubs below 2 m (gaps <10 cm were ignored). We pooled riparian shrub species for analyses. We estimated tree density by counting all woody stems within 2 m of each vegetation transect line and recorded species, height, and diameter at breast height (dbh). We classified aspen stems as shoots if they were ≤1.5 m in height and as small- (0.1–6.0 cm dbh), medium- (6.1–18.0 cm dbh), or large- (>18.0 cm dbh) diameter trees if they were >1.5 m in height.

Within each set of vegetation measurements (ground cover, shrub cover, and aspen stem density), we tested for an overall difference between phases with a repeated-measures multivariate analyses (MANOVA). In each MANOVA, we tested for differences between phases within categories (such as shrub cover) with paired *t* tests, and we adjusted for multiple comparisons as in Benjamini and Hochberg (1995). Because plots were fairly evenly distributed throughout aspen on the east slope and plots were placed in aspen vegetation irrespective of drainage, we analyzed the data as a simple one-stage sample. We used only vegetation measurements taken within the wooded zone of each plot. Each 10-m section of the vegetation transect was defined as being within the wooded zone if it contained any tree stems or canopy cover. Both avian and plant data are given as means per wooded hectare.

For descriptive purposes, we report percent change between phases ( $[(\text{phase 2} - \text{phase 1}) / \text{phase 1}] \times 100\%$ ) in the text and phase 1 and phase 2 means in the figures. We used mean differences (the mean across plots of each plot's phase 2 minus phase 1 difference) and the standard error of the difference in statistical comparisons (Supporting Information).

We obtained precipitation data from a weather station at HMNAR headquarters. We pooled these data for October through June (when 86% of annual precipitation falls) annually (1941–2002) and used them as an index of moisture available to plants in a growing season (Dobkin et al. 1998).

### Avian Surveys

We conducted modified fixed-width transect surveys during which observers walked slowly through the center of each plot for 25 minutes and recorded all birds detected by sight or sound within 50 m of the transect (Dobkin & Rich 1998). Surveys were conducted between 0.5 and 3.5 h after sunrise. In phase 1, each plot was surveyed 6 times, once on each of 2 consecutive days in each of 3 survey rounds. In phase 2, each plot was surveyed once in each of 3 survey rounds. Surveys were conducted during phenologically similar periods each year, 7 May–9 July in phase 1 (87% prior to 27 June) and 8 May–27 June in phase 2. In each year, a plot was surveyed by 2 or 3 different observers, and each was responsible for approximately the same total number of surveys and plots. The order in which plots were surveyed within a day alternated between consecutive visits.

For each of the 26 plots, we averaged mean number of individuals detected per visit within a year and among years within each phase (i.e., 1991–1993 and 2000–2002). We then calculated the mean difference in individuals per visit between phases for each plot and each species and conducted a paired *t* test (with plot as the sampling unit) to determine whether the difference

for each species was significantly different from zero. As a means of restricting analyses to those species with a sample size sufficient to provide a reasonable power to detect a difference, we used only species that occurred on at least 5 plots and had an average of  $\geq 0.013$  individuals/ha in either phase (32 species in riparian aspen, 23 in snow-pocket aspen). In addition, we analyzed only passerines, doves, and woodpeckers that nest or forage primarily in woody-riparian and snow-pocket areas on HMNAR. Avian nomenclature follows the most recent revision to the American Ornithologists' Union checklist (Chesser et al. 2011).

We assigned species to nesting guilds (ground and understory cup nesters, overstory cup nesters, and cavity nesters) and foraging guilds (ground and understory, overstory, aerial, and bark foragers) (Ehrlich et al. 1988) (Supporting Information). Change in number of individuals in each nesting and foraging guild per hectare (i.e., phase 2-phase 1) was calculated by pooling individuals for all species within each guild and treating the plot as the primary sampling unit. We used repeated measures multivariate tests (SAS Institute 2004) to test for an overall difference between phases (first among guilds and then species). If the difference was significant, we used a paired *t* test to test for a difference between phases for each guild and each species. We adjusted resulting *p* values for multiple comparisons with Benjamini and Hochberg's (1995) false discover rate to ensure that  $\leq 5\%$  of rejected hypotheses were rejected falsely. We made this adjustment because it is more powerful than holding the family-wise error rate at  $p = 0.05$  and because the error rate is acceptable when an overall significant difference has been established and when one seeks to describe which species comprise the difference (Westfall et al. 1999).

## Results

Riparian and snow-pocket aspen differed in stand structure, but both exhibited substantial regeneration (i.e., production of new shoots) ( $\bar{x} = 2646$  stems/ha for riparian and 7079 stems/ha for snow-pocket aspen, phase 1 and 2 average) (Supporting Information). In both phases, aspen in snow-pocket plots were considerably denser than in riparian plots, primarily because they had 3.5 times more shoots and 2.3 times as many small-diameter trees per ha than riparian aspen (Supporting Information). Tree size was strongly skewed toward small trees in snow-pocket aspen, with shoots ( $< 1.5$  m in height) and small stems ( $< 6$  cm dbh) comprising 93% of all stems in snow-pocket plots and 77% of all stems in riparian plots. Snow-pocket plots tended to have more forb cover and less grass and sedge cover, but similar cover of riparian shrubs, sagebrush, and aspen canopy relative to riparian plots (Supporting Information). In both stand types,

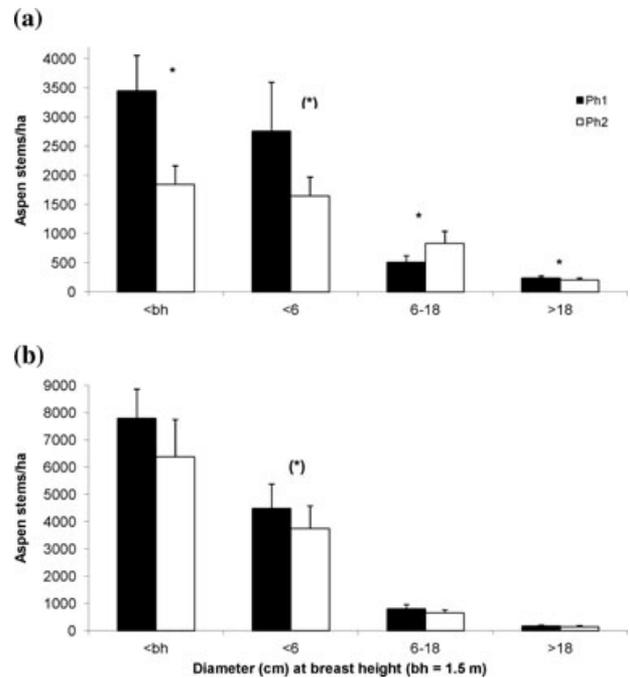


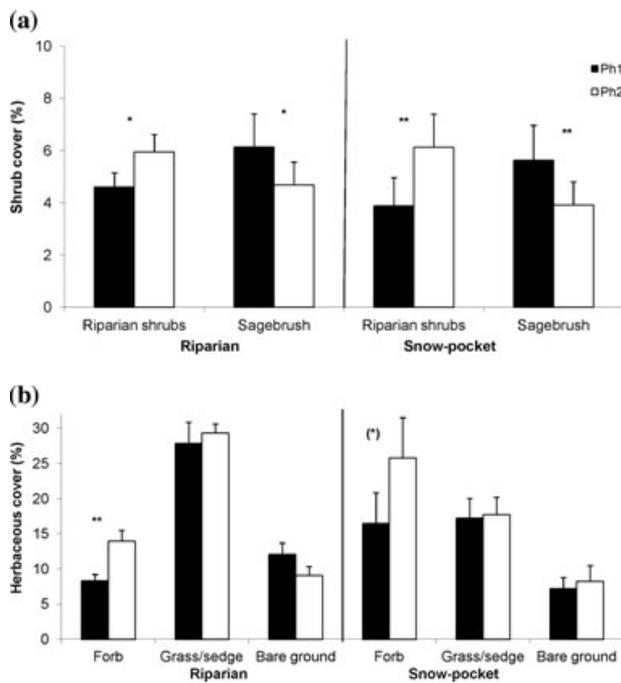
Figure 1. Density of live aspen stems in 4 size classes ( $< bh$ , 1.5 m in height; other classes are  $> 1.5$  m in height and unit of measure is diameter at breast height in centimeters) in (a) riparian aspen plots ( $n = 17$ ;  $F_{48,3} = 6.1$ ,  $p = 0.001$ ) and (b) snow-pocket aspen plots ( $n = 9$ ;  $F_{24,3} = 1.1$ ,  $p = 0.36$ ) in years 1-3 (Ph1) and years 10-12 (Ph2) after cattle removal (multivariate repeated measures analysis and paired *t* tests with adjustment for multiple comparisons: (\*)  $p < 0.10$ ; \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ).

herbaceous and shrub communities were composed of native species.

Riparian plots had more than twice as many total individual birds per hectare as snow-pocket plots (27.2 [SE 2.0] versus 13.0 [1.6], respectively;  $t = 5.5$ ,  $p < 0.0001$ , 33 species pooled), and the difference was evident across all nesting and foraging guilds. Most species (27 of 32) were more common in riparian than snow-pocket aspen plots (on the basis of phase 2 means) (Supporting Information). The identity of 8 of the 10 most abundant species was the same in riparian and snow-pocket plots.

## Change in Vegetation Structure and Composition

Riparian stands exhibited substantial changes in stand structure between phase 1 and phase 2, including decreases in the density of shoots (47% change from phase 1 to phase 2,  $p = 0.02$ ), small diameter trees (40%,  $p = 0.06$ ), and large diameter trees (16%,  $p = 0.02$ ), and a 64% increase in medium diameter trees ( $p = 0.02$ ) (Fig. 1a). The density of snags  $> 18$  cm in diameter (33.3 versus 33.8 stems/ha, phases 1 and 2, respectively;  $t = 0.04$ ,



**Figure 2.** Percent cover of (a) shrubs in riparian ( $n = 17$ ,  $F_{16,1} = 24.2$ ,  $p = 0.0002$ ) and snow-pocket aspen plots ( $n = 9$ ,  $F_{8,1} = 25.5$ ,  $p = 0.001$ ) and (b) herbaceous vegetation in riparian ( $F_{32,2} = 4.1$ ,  $p = 0.03$ ) and snow-pocket aspen plots ( $F_{16,2} = 2.3$ ,  $p = 0.01$ ) in years 1–3 (Ph1) and years 10–12 (Ph2) after cattle removal (multivariate repeated measures analysis and paired  $t$  tests with adjustment for multiple comparisons: (\*) $p < 0.10$ ; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ).

$p = 0.97$ ) and canopy cover (54% versus 53%,  $t = 0.71$ ,  $p = 0.49$ ) did not change.

In snow-pocket stands the relative distribution of trees among size classes was unchanged from phase 1 to phase 2; however, there were consistent but nonsignificant decreases in the density of live stems in all classes (shoots, 18% decrease,  $p = 0.25$ ; small diameter, 17%,  $p = 0.24$ ; medium diameter, 19%,  $p = 0.24$ ; large diameter, 14%,  $p = 0.25$ ) (Fig. 1b). The density of snags >18 cm in diameter increased significantly (11.1 versus 29.7 stems/ha,  $t = 3.79$ ,  $p = 0.004$ ), and canopy cover declined significantly (55% versus 49%,  $t = 2.71$ ,  $p = 0.02$ ).

In riparian and snow-pocket plots, riparian shrub cover increased significantly (29% [ $p = 0.03$ ] and 58% [ $p = 0.008$ ], respectively) and sagebrush cover decreased significantly (24% [ $p = 0.03$ ] and 31% [ $p = 0.009$ ] respectively) (Fig. 2a). Cover of forbs increased substantially in riparian and snow-pocket plots (68% [ $p = 0.006$ ] and 57% [ $p = 0.08$ ], respectively) (Fig. 2b), and bare ground decreased nonsignificantly in riparian aspen (25% [ $p = 0.12$ ]) (Fig. 2b). The combined category of grasses and sedges provided substantial cover in riparian and snow-

pocket aspen plots (29% and 18%, respectively) and did not change significantly between phases (5% [ $p = 0.62$ ] and 3% [ $p = 0.89$ ], respectively).

### Change in Bird Abundance

By 10–12 years after cattle removal, pooled avian abundance had increased by 33% in riparian aspen (from 20.4 to 27.2 individuals/ha,  $p = 0.001$ ) and by 39% in snow-pocket aspen (from 9.3 to 13.0 individuals/ha,  $p = 0.004$ ). Most species in both riparian aspen (69%, 22/32) and snow-pocket aspen (70%, 16/23) increased (Table 1). In riparian aspen, abundances of 10 species increased significantly and 2 decreased significantly after adjusting for multiple comparisons. In snow-pocket aspen, abundances of 4 species appeared to increase significantly and 1 to decrease significantly, but no differences remained significant after adjusting for multiple comparisons (Table 1).

Among nesting guilds, significant increases in avian abundance occurred in both riparian and snow-pocket aspen. Ground and understory nesters increased by 133% and 67%, and overstory nesters increased by 34% and 33% in riparian and snow-pocket aspen, respectively (Fig. 3a). Abundance in most foraging guilds also increased significantly: ground and understory foragers increased by 25% and 32%, aerial foragers by 55% and 57%, and overstory foragers by 66% and 43% in riparian and snow-pocket aspen, respectively (Fig. 3b). Neither the bark-gleaning foraging guild nor the cavity-nesting guild increased significantly in either plot type.

Most species that increased significantly in abundance between phases became more abundant in plots where they had been present in phase 1 (9 of 10 species) and were present on more plots than in phase 1 (5 of 10 species; Table 1). Likewise, the 2 species that decreased significantly in abundance between phases decreased in abundance in plots where they had been present in phase 1 and were present on fewer plots than in phase 1 (Table 1). Cavity-nesting species also were present in fewer plots in phase 2 than in phase 1 (5 of 8 cavity nesters in riparian aspen and 5 of 7 in snow-pocket aspen).

Total precipitation (1 October through 30 June) was greater, but not significantly, in phase 1 than in phase 2 (32.25 cm [SE 6.17] versus 19.48 cm [2.31],  $t = 1.94$ ,  $p = 0.12$ ). The tendency for higher rainfall in phase 1 was the opposite of that expected if the increase in bird abundance were related to increased precipitation. The total number of individuals per hectare (species pooled, averaged across plots) did not increase as precipitation increased, either within or between phases (Fig. 4a). Total precipitation increased nonsignificantly from 1941 to 2002 ( $p = 0.08$ , Fig. 4b).

For most species, increases in avian abundance at HMNAR did not reflect regional Breeding Bird Survey (BBS) trends in the Great Basin Bird Conservation Region

Table 1. Mean change in avian abundance from years 1–3 to years 10–12 after cattle removal on riparian and snow-pocket aspen plots ( $n = 17$  and 9, respectively).

Abundance status <sup>a</sup> and common name	Scientific name	Riparian aspen		Snow-pocket aspen	
		change in individuals/bd <sup>b</sup>	change in presence <sup>c</sup>	change in individuals/bd <sup>b</sup>	change in presence <sup>c</sup>
<b>Increasing</b>					
Yellow Warbler	<i>Setophaga petechia</i>	1.64 <sup>***</sup>	1	0.45 <sup>[****]</sup>	2
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	1.37 <sup>**</sup>	1	0.37	0
Warbling Vireo	<i>Vireo gilvus</i>	0.80 <sup>***</sup>	3	0.35	0
Tree Swallow	<i>Tachycineta bicolor</i>	0.79	2	0.28 <sup>[*]</sup>	2
Dusky Flycatcher	<i>Empidonax oberholseri</i>	0.70 <sup>**</sup>	0	0.76	0
<i>Empidonax</i> spp. <sup>d</sup>	<i>Empidonax</i> spp.	0.31 <sup>***</sup>	7	0.24 <sup>[*]</sup>	1
Yellow-rumped Warbler	<i>Setophaga coronata</i>	0.28 <sup>[*]</sup>	2	0.01	-2
Song Sparrow <sup>e</sup>	<i>Melospiza melodia</i>	0.27 <sup>*</sup>	5		
Western Tanager	<i>Piranga ludoviciana</i>	0.26 <sup>*</sup>	1	0.09	4
Cassin's Finch	<i>Carpodacus cassinii</i>	0.24	1	-0.04	-2
Mourning Dove <sup>e</sup>	<i>Zenaidura macroura</i>	0.24 <sup>*</sup>	4		
Spotted Towhee <sup>e</sup>	<i>Pipilo maculatus</i>	0.23 <sup>*</sup>	8		
House Finch <sup>e</sup>	<i>Carpodacus mexicanus</i>	0.20 <sup>*</sup>	7		
Dark-eyed Junco	<i>Junco hyemalis</i>	0.19 <sup>[*]</sup>	6	0.37 <sup>[**]</sup>	3
American Robin	<i>Turdus migratorius</i>	0.17	0	0.10	0
MacGillivray's Warbler <sup>e</sup>	<i>Geothlypis tolmiei</i>	0.16 <sup>[*]</sup>	5		
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	0.12	-1	0.05	-3
Lazuli Bunting <sup>e</sup>	<i>Passerina amoena</i>	0.12	2		
Western Wood-Pewee	<i>Contopus sordidulus</i>	0.09	-1	0.05	0
Orange-crowned Warbler	<i>Oreothlypis celata</i>	0.08	-1	0.11	0
Hairy Woodpecker	<i>Picoides villosus</i>	0.07	-4	-0.01	-4
Fox Sparrow	<i>Passerella iliaca</i>	0.02	-2	-0.05	-1
<b>Decreasing</b>					
European Starling <sup>e</sup>	<i>Sturnus vulgaris</i>	-0.70 <sup>*</sup>	-1		
Bullock's Oriole	<i>Icterus bullockii</i>	-0.35 <sup>**</sup>	-9	-0.06 <sup>[*]</sup>	-6
House Wren	<i>Troglodytes aedon</i>	-0.28	-1	0.18	-1
Northern Flicker	<i>Colaptes auratus</i>	-0.10	0	0.10	-1
Swainson's Thrush <sup>e</sup>	<i>Catbarus ustulatus</i>	-0.07	-5		
Hummingbird spp. <sup>e,f</sup>	<i>Selasphorus/Stellula</i>	-0.03	-1		
Mountain Bluebird	<i>Sialia currucoides</i>	-0.03	2	0.19	0
Brown-headed Cowbird	<i>Molothrus ater</i>	-0.01	0	-0.04	-2
Downy Woodpecker	<i>Picoides pubescens</i>	-0.01	-4	-0.04	-3
Sapsuckers <sup>g</sup>	<i>Sphyrapicus nuchalis, S. ruber</i>	-0.001	-1	-0.03	-4

<sup>a</sup> For ease of presentation, increasing or decreasing status assigned on basis of riparian plots.

<sup>b</sup> Significance on the basis of paired  $t$  tests with adjustment for multiple comparisons:  $p < 0.05$ ;  $** p < 0.01$ ;  $*** p < 0.001$ ;  $[\ ]$ , differences significant before adjustment but not after.

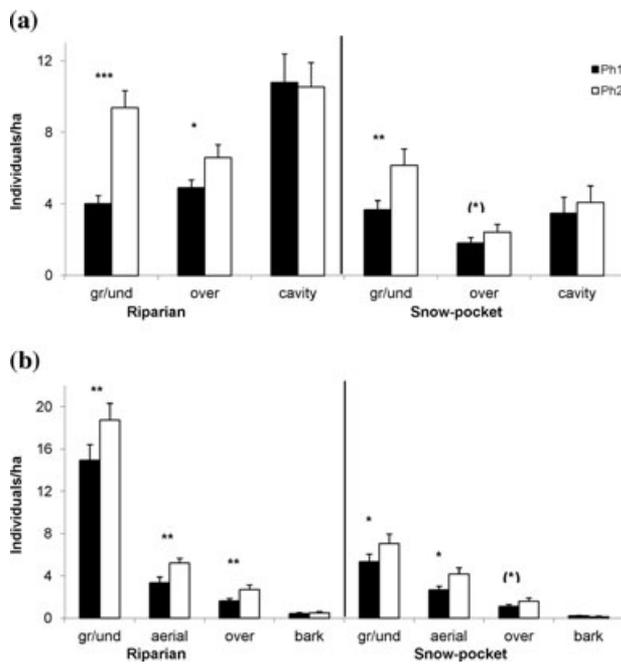
<sup>c</sup> Change in presence is the change in number of plots in which the species was present.

<sup>d</sup> Species include Hammond's (E. hammondi), Cordilleran (E. occidentalis), Pacific-slope (E. difficilis), Willow Flycatchers (E. traillii), and unidentified Empidonax flycatchers. Dusky Flycatchers were analyzed separately.

<sup>e</sup> Species was too rare for meaningful analyses in snow-pocket stands. Criteria for inclusion were an average of  $\geq 0.013$  individuals/ba and occurring on  $\geq 5$  plots in either period.

<sup>f</sup> Hummingbird species includes Broad-tailed (Selasphorus platycercus), Rufous (S. rufus), and Calliope Hummingbirds (Stellula calliope), and unidentified hummingbirds.

<sup>g</sup> Sapsucker species includes Red-naped Sapsucker (S. ruber), hybrids, and those recorded as unidentified.



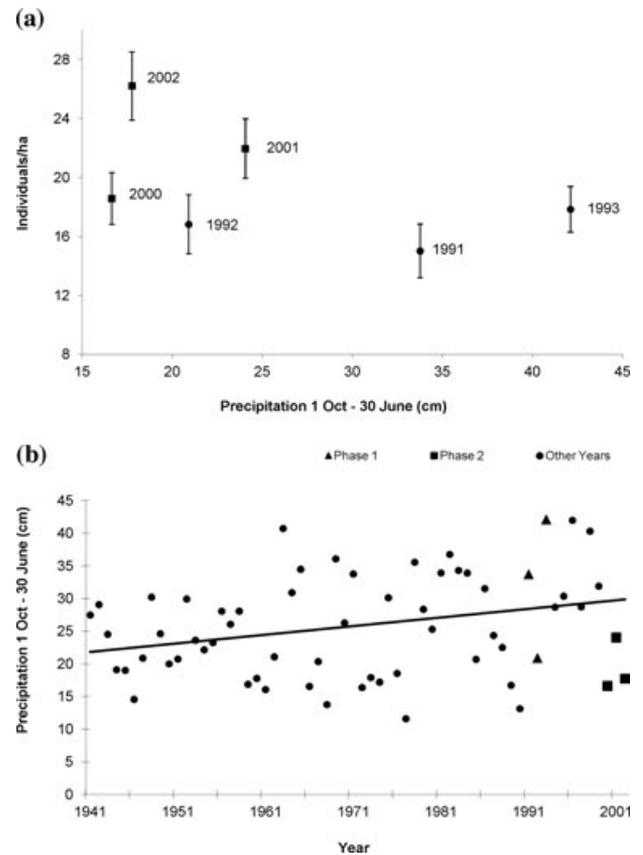
**Figure 3.** Avian abundance in years 1–3 (Ph1) and years 10–12 (Ph2) after cattle removal for (a) nesting guilds in riparian ( $n = 17$ ,  $F_{32,2} = 15.9$ ,  $p < 0.0001$ ) and snow-pocket aspen ( $n = 9$ ,  $F_{16,2} = 6.2$ ,  $p = 0.01$ ) plots and (b) foraging guilds in riparian ( $F_{48,3} = 10.7$ ,  $p < 0.0001$ ) and snow-pocket aspen ( $F_{24,3} = 9.0$ ,  $p = 0.0004$ ) plots (multivariate repeated measures analysis and paired  $t$  tests with adjustment for multiple comparisons: (\*) $p < 0.10$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).

for 1991–2002 (Sauer et al. 2008). Of the 10 species with abundances that increased significantly in riparian plots, 3 increased significantly in the Great Basin (Mourning Dove [*Zenaida macroura*], Song Sparrow [*Melospiza melodia*], and Warbling Vireo [*Vireo gilvus*]), and 2 decreased significantly (Dusky Flycatcher [*Empidonax oberholseri*] and other *Empidonax*) (Supporting Information).

## Discussion

Ours is the first study to quantify the response of avian and plant communities in aspen woodlands to the removal of livestock across ecologically informative spatial and temporal scales in the semi-arid Intermountain West and to illustrate the response at multiple, interrelated organizational levels. The increase in avian abundance across the 12 years following cessation of >100 years of livestock grazing was large and widespread throughout foraging and nesting guilds.

Increases in forb and shrub cover from phase 1 to phase 2 and the high density of aspen shoots and small trees



**Figure 4.** Total precipitation relative to (a) mean (SE) avian abundance (all species pooled) per plot visit each year and for (b) the 62 years preceding and during this study (1941–2002) (phase 1, 1–3 years after cattle removal; phase 2, 10–12 year after cattle removal). Mean total precipitation was 25.5 cm, and the slope of the long-term trend was 0.10 (SE 0.05) ( $t = 1.8$ ,  $p = 0.08$ ).

in both phases created a structurally robust understory of native species. The recovering understory vegetation is the most parsimonious explanation for the strong increases that we documented in guilds of species that nest or forage in the understory (Saab et al. 1995; Tewksbury et al. 2002). Understory vegetation is adversely affected by livestock grazing (Belsky & Blumenthal 1997) and is an often overlooked component of habitat structural diversity that contributes substantially to avian diversity and abundance in aspen and riparian woodlands (Hobson & Bayne 2000; Scott et al. 2003; Dickson et al. 2009).

Overstory nesters and overstory and aerial foragers also increased significantly in our study. Other studies have documented effects of grazing throughout the avian community, especially when vegetation was altered extensively (Tewksbury et al. 2002; Krueper et al. 2003). Such widespread changes in avian communities may be expected if invertebrate abundance is affected by altered vegetation (Pettersson et al. 1995; McIver &

McInnis 2007) and if insectivorous avian communities mirror changes in their prey (Croonquist & Brooks 1991; Seagle & Sturtevant 2005).

Exceptions to the trend of increasing abundance were bark gleaners and cavity nesters, neither group increased significantly in either plot type. This result is consistent with the loss of 14%–16% of large-diameter trees in riparian (significant) and snow-pocket (nonsignificant) plots. Cavity nesters prefer aspen rather than other trees for nesting in boreal woodlands (Martin et al. 2004), and at HMNAR they preferentially nested in the largest aspen, both living and dead (Dobkin et al. 1995). Among cavity nesters in our study, only the European Starling (*Sturnus vulgaris*) decreased significantly. In addition, 6 of 8 cavity nesters in riparian aspen exhibited nonsignificant declines, including sapsuckers and the Northern Flicker (*Colaptes auratus*), which are the 2 primary excavators and keystone species in this cavity-nesting community (Dobkin et al. 1995; Martin & Eadie 1999).

Most aspen stands on HMNAR before livestock exclusion had either 1- or 2-layered aspen canopies (USFWS 1994), which reflected the episodic nature of successful recruitment of shoots into the canopy over many previous decades. This structural pattern is not uncommon in aspen woodlands in the West (Mueggler 1989; Suzuki et al. 1999; Wall et al. 2001) and is often attributed to extensive herbivory, either by wild ungulates or livestock (Kay & Bartos 2000; Ripple & Larsen 2000; Kaye et al. 2005), although insects, disease, or drought may also contribute to this episodic pattern (Kurz et al. 2007).

We interpret the very high density of aspen shoot regeneration on most plots during phase 1 as an immediate response to release from grazing, but we discuss alternate explanations below. Similar large pulses in shoot density are well documented after other types of disturbance such as cutting or burning (Bartos & Mueggler 1981; Crouch 1983; Prévost & Pothier 2003). We documented a large decrease in shoot density from phase 1 to phase 2, which is consistent with density-dependent mortality expected among shoots at high density during recovery from a major disturbance (Bartos & Mueggler 1981; Crouch 1983), including ungulate browsing (Baker et al. 1997).

The canopies of riparian aspen stands became more layered during the 12 years following cattle removal, as evidenced by the 64% increase in medium-sized trees. The relatively low number of medium-sized trees in phase 1 indicates that conditions were not conducive to shoot regeneration and survival of stems to >6 cm diameter for several decades before phase 1. Likewise, the net loss of large-diameter trees indicates recruitment of medium-into large-diameter trees was inadequate to compensate for natural mortality in the latter, further indicating a paucity of medium-sized trees in prior decades. Elsewhere, the lack of a multilayered aspen canopy and gradual loss of large-diameter trees has been attributed to pro-

longed herbivory that limited the growth and survival of suckers in previous decades (Kay & Bartos 2000; Martin 2007; Hollenbeck & Ripple 2008).

Unlike riparian aspen stands, snow-pocket stands exhibited a slight thinning of all size classes rather than a change in relative stem size composition. Snow-pocket stands, relative to riparian stands, exhibited less self-thinning of shoots and small trees and did not exhibit an increase in medium-sized trees. The latter result suggests slower growth of small stems or lower survival of small stems into medium stems. Snow-pocket stands, which are denser, often on hillsides, and usually do not contain surface water, may have been used less by cattle (e.g., Roath & Krueger 1982) or may have a different optimal, or ecologically stable, stand structure and thus a different recovery trajectory (Laycock 1991; Strand et al. 2009). The statistically nonsignificant loss of large-diameter stems in snow-pocket stands was proportionately similar to that in riparian stands and appears characteristic of natural senescence after decades of limited regeneration (e.g., Martin 2007).

Browsing by wild ungulates, especially by elk in winter, negatively affects aspen regeneration and stand structure (Baker et al. 1997; Suzuki et al. 1999; Kaye et al. 2005). However, elk occurred only incidentally on HMNAR, and neither elk nor the relatively small mule deer (*Odocoileus hemionus*) population (800–1000 individuals) remain in the area during winter (Oregon Department of Fish and Wildlife, unpublished data), when most ungulate browsing of aspen occurs (e.g., Suzuki et al. 1999). Furthermore, mule deer abundance was fairly stable preceding and during phase 1 (1985–1994) and declined somewhat between phases, and thus does not appear to explain changes in the density of aspen shoots, which was high in phase 1 and decreased between phases.

Little evidence links annual variation in precipitation and aspen regeneration (Ripple & Larson 2000; Hessel & Graumlich 2002; Martin 2007). Although phase 1 had higher precipitation and regeneration, the lack of multilayered aspen canopies in phase 1 stands does not appear consistent with multiple precipitation-induced peaks in regeneration that would be expected from long-term precipitation patterns (Fig. 4b) (Baker et al. 1997). Extreme and prolonged drought can contribute to stem mortality of larger size classes, especially as seen in sudden aspen dieback (Hogg et al. 2008; Worrall et al. 2008). However, our stands did not exhibit visual signs of insect or disease outbreaks or drought stress (S.L.E. and D.S.D., personal observation) or rapid crown dieback and cohort loss, which are characteristic of sudden aspen dieback (Worrall et al. 2008). Self-thinning is characteristic of some self-sustaining stands and need not indicate stress (Smith & Smith 2005). Furthermore, conditions during phase 2 were not those of an extreme or prolonged drought; precipitation increased over the long term and was above average before phase 2. Cattle removal remains the most

likely primary driver of the changes we documented, although aspen stand dynamics result from a complex interaction of processes (Romme et al. 1995) and interpretation will benefit from further dendrochronological and longitudinal studies.

Across the 12 years of livestock exclusion, aspen woodlands on HMNAR showed substantial movement toward recovery of biological integrity (as defined by Angermeier & Karr 1994). Relative to elsewhere in the Intermountain West of the United States, most of our stands exhibited high densities of regeneration in both phases (Mueggler 1989; Strand et al. 2009) and substantial recruitment of stems into the overstory (Suzuki et al. 1999; Wall et al. 2001; Rogers et al. 2010). The increased native forb and riparian shrub cover, with a concomitant decrease in sagebrush cover, indicate increased groundwater availability and improved riparian condition (Dobkin et al. 1998; Wright & Chambers 2002). The increased avian abundance and relatively high nesting success (Heltzel & Earnst 2006) illustrate a positive multitrophic-level response to livestock removal. Our study area serves as a landscape-level livestock enclosure (Bock et al. 1993) and can potentially provide comparison to ecologically similar sites in the vast semiarid, grazed ecosystems of western North America.

Federal land-management agencies operate under a mandate to manage for ecological values on lands grazed by livestock (e.g., BLM 2001), but these agencies are faced with the dilemma that livestock exclusion is generally the most effective means of improving degraded riparian areas (Elmore & Kauffman 1994). Nonetheless, given that livestock are present on ~90% (Fleischer 2010) of the 1.5 million km<sup>2</sup> of federally owned land in the West, reducing the negative effects of livestock on federal lands could potentially help restore large expanses of western ecosystems. Similarly, there is growing evidence that the presence of large predators, especially wolves (*Canis lupus*), affect wild ungulate abundance and behavior and initiate a trophic cascade that improves regeneration, health, and persistence of aspen and other deciduous vegetation (Ripple & Larsen 2000), an effect that could be spatially and temporally extensive in the West (Beschta & Ripple 2009). In addition to immediate benefits, diminishing the effects of domestic and wild ungulate populations is likely to improve the resilience of aspen and other woody riparian ecosystems as climate-mediated stressors such as wildfires and drought-induced mortality change in frequency.

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## Supporting Information

Data on avian abundance in phases and the difference in abundance between phases (Appendix S1) and cover and aspen stem density in phases and difference between phases (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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