

Research article

Songbird response to rest-rotation and season-long cattle grazing in a grassland sagebrush ecosystem

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ABSTRACT

Grazing on natural rangelands, which are areas dominated by native vegetation that are used for livestock grazing, can achieve desired vegetation outcomes, preserve native habitat, and economically benefit multiple stakeholders. It is a powerful tool that can be manipulated to reduce wildlife declines and benefit ecosystems. However, the benefits of conservation grazing systems on many wildlife communities remain relatively unexplored. We compared songbird communities between two grazing systems in eastern Montana: rest-rotation, which is a conservation grazing system, and season-long. We measured differences in abundance of eight songbird species over a two year period using dependent double-observer transect surveys and a multispecies dependent double-observer abundance model. The species were chosen to be representative of the sagebrush grassland community: a sagebrush obligate, Brewer's sparrow (*Spizella breweri*); a facultative grassland species, brown-headed cowbird (*Molothrus ater*); grassland obligate species, chestnut-collared longspur (*Calcarius ornatus*), horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), McCown's longspur (*Rhynchophanes mccownii*), and western meadowlark (*Sturnella neglecta*); and a generalist, vesper sparrow (*Poocetes gramineus*). Our results show that these species exhibit mixed responses to these two grazing systems. The sagebrush obligate (Brewer's sparrow), generalist (vesper sparrow), and two grassland associated species (horned lark and chestnut-collared longspur) were equally abundant on both grazing systems, suggesting grazing system had no effect on their abundance. However, the remainder of the grassland associated species showed a response to grazing: three (brown-headed cowbird, lark bunting, and western meadowlark) were more abundant in season-long than rest-rotation, whereas one (McCown's longspur) was more abundant in rest-rotation. These results suggest that differences in grazing management affect a subset of grassland obligate species and that only one species, McCown's longspur, preferred conservation grazing. Our findings provide useful information for assessing the suitability of grazing as a conservation tool for songbirds.

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1. Introduction

Livestock grazing is one of the most common land uses worldwide (Raven, 2002). In the United States livestock grazing occurs on approximately 40 percent of total land (Holechek et al., 2011) and approximately 70 percent of land in the west (Fleischner, 1994). Incentives to use grazing as a conservation tool are increasing, as grazing can represent a favorable alternative for native wildlife when compared with other land uses such as agricultural crop

production (Lipsey et al., 2015), provide economic and cultural benefits to land owners, and achieve desired vegetation outcomes. In the western United States, federally funded livestock grazing easements, legal agreements between livestock producers and natural resource managers that specify grazing characteristics (e.g., time, intensity) for an area, aimed at benefiting wildlife populations are being implemented on >809,000 ha across 11 states on private lands (NABCI, 2013).

Large-scale implementation of grazing types for conservation may have large impacts on native wildlife. However, the impacts of grazing on wildlife are not well understood (Krausman et al., 2009). Most studies on this topic focus on the abundance of a single species, which provides only a partial measure of livestock grazing impacts, as livestock grazing types are likely to differentially affect

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multiple species that have diverse life history strategies (Bock et al., 1993; Briske et al., 2008; Krausman et al., 2009). In addition, these studies compare grazing systems to areas with no livestock grazing (e.g., Bock and Webb, 1984; Harrison et al., 2010; Nelson et al., 2011), a scenario that is unrealistic for many landscapes in the western US.

We chose songbirds to explore the effects of different livestock grazing systems on wildlife for multiple reasons. They are widespread and accessible for monitoring (Bradford et al., 1998), sensitive to habitat change (Canterbury et al., 2000; Coppedge et al., 2008), respond to livestock grazing (Coppedge et al., 2006), and have declined concurrently with the increase of livestock production (Fuhlendorf and Engle, 2001). Songbirds also play an integral role in ecological communities by interacting with other species as predators, prey, pollinators, and seed dispersers (Murphy and Romanuk, 2012). Many songbirds within sagebrush ecosystems are designated as species of conservation concern by local, regional, or national organizations (Rich et al., 2004; Montana Natural Heritage Program, 2014; IUCN, 2015). Sagebrush ecosystem songbirds exhibit a varying degree of reliance on the grass component of sagebrush ecosystems (Rich et al., 2005). They range from: sagebrush obligates that use sagebrush shrubs for the majority of their life history needs; to facultative grassland species that use both grass and sagebrush shrubs to meet their life history needs; to grassland obligates species that use grass vegetation for the majority of their life history needs.

It is important to understand the effects of grazing systems on wildlife in ecosystems dominated by livestock grazing. First, sagebrush (*Artemisia* spp.) ecosystems in the western US ecosystems have undergone extensive loss and fragmentation (Knick et al., 2003; Knick and Connelly, 2011). Second, as stated by Knick et al. (2003) “virtually all sagebrush lands are managed principally for livestock grazing.” As a result, native wildlife species in these ecosystems rely on the vegetation disturbance provided by livestock grazing (Fuhlendorf et al., 2017).

In these sagebrush ecosystems of the western US, the US Department of Agriculture - Natural Resource Conservation Service (NRCS) is currently implementing a conservation grazing system, rest-rotation grazing, to support both wildlife species and domestic livestock (NRCS, 2015). This grazing system involves alternating two-to three-month grazing periods, followed by 15–18 months of rest, such that a given area will not be grazed during the same season (growing or non-growing) repeatedly over multiple years. This is different than one of the more common grazing practices in the western US, season-long grazing systems, which involves the continuous presence of livestock in the same area during a growing season (e.g., May through November) repeatedly over multiple years (Briske et al., 2008; Holechek et al., 1999).

Livestock grazing affects vegetation by altering plant species composition, physical plant structure and the amount of vegetation available in an ecosystem (Olf and Ritchie, 1998; Briske et al., 2008; Lwiwski et al., 2015). This has led some to suggest that livestock function as “ecosystem engineers” (Derner et al., 2009). Livestock grazing affects the structural heterogeneity of grass vegetation (Fuhlendorf and Engle, 2001) that provides a range of conditions for nest concealment and foraging activity for songbirds (Henderson and Davis, 2014).

It is unclear if differences in structural heterogeneity produced by different grazing systems result in differences in songbird abundance. Therefore, we address the question: how does a widely implemented grazing systems in the United States, season-long compare to a more recently proposed conservation grazing system, rest-rotation grazing (Briske et al., 2008; Holechek et al., 1999), influence songbird communities in sagebrush ecosystems? Season-long grazing has been suggested to result in higher grass vegetation

structural heterogeneity than rest-rotation grazing at both local- and broad-scales (Fuhlendorf and Engle, 2001; but see Lwiwski et al., 2015). Neither grazing system is expected to have an effect on the density of sagebrush. Veblen et al. (2015) showed that the density of sagebrush and size of sagebrush shrubs was the same in areas livestock were present and control areas where they were excluded.

We test the hypothesis that songbirds respond to grazing based on their reliance on grass vegetation. We predict that grassland obligate species are more abundant in the season-long grazing system because it is suggested to produce more structural heterogeneity (Fuhlendorf and Engle, 2001). In addition, we predict that the strength of the effect of season-long grazing on the difference in abundance depends on how much species depends on grassland. Thus grassland obligates will show a greater difference in abundance between the two systems than facultative grassland species or generalists. Finally, we predict that sagebrush obligate species will show no difference in abundance between the two grazing systems because they are not closely tied to changes in grass structural heterogeneity and livestock grazing is not known to affect sagebrush shrubs (Veblen et al., 2015).

Our study uses songbirds to explore if a recently implemented conservation grazing system has different impacts on wildlife. We conduct our study in the western US sagebrush ecosystem where livestock grazing is a dominant disturbance. Our study offers the first comparison that we are aware that compares different grazing systems, rather than comparing a grazing system to no grazing. We feel there is strength in examining grazing systems rather than specific vegetation metrics because the grazing system is the likely level at which land managers will implement or monitor grazing activities (Henderson and Davis, 2014). In addition, we include land ownership, public and private, which can have a significant effect on management practices (Sorice et al., 2014).

2. Materials and methods

We conducted this study across 89,000 ha of sagebrush landscape in Golden Valley and Musselshell Counties near Roundup, Montana. We accessed areas in private landownership and public land managed by US Department of Interior Bureau of Land Management (BLM). The area is arid, with average annual precipitation of 0.36 m and the highest amount of precipitation occurring in May (0.07 m). Average temperatures in this region range from -11 °C in January to 30 °C in July (US Climate Data, 2016). Vegetation is dominated by Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) intermixed with western wheatgrass (*Pascopyrum smithii*), needle-and-thread grass (*Stipa comata*), blue grama (*Bouteloua gracilis*) and prairie Junegrass (*Koeleria macrantha*). Additional vegetation includes smaller areas dominated by Ponderosa pine (*Pinus ponderosa*) forests and riparian areas.

We surveyed eight songbird species that represent varying degrees of grass use in sagebrush ecosystems ranging from grassland to sagebrush obligates (Table 1): a sagebrush obligate, the Brewer's sparrow (*Spizella breweri*) (Paige and Ritter, 1999); a facultative grassland species, the brown-headed cowbird (*Molothrus ater*); grassland obligate species, the chestnut-collared longspur (*Calcarius ornatus*), horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), McCown's longspur (*Rhynchophanes mccownii*), and western meadowlark (*Sturnella neglecta*) (Vickery et al., 1999); and a generalist, the vesper sparrow (*Poocetes gramineus*) (Jones and Cornely, 2002).

We randomly selected 40 sampling plots in each of the two grazing systems, total of 80 sample plots, that were 500 m \times 500 m (25 ha). Our goal was to obtain a sample of plots that were representative of sagebrush songbird habitat in the study area.

Table 1

Eight sagebrush ecosystem songbird species, their vegetation association, uses for grassland vegetation, and predicted response of rest-rotation compared to season-long grazing systems on public and private land near Roundup, Montana, in 2013 and 2014.

| Common name | Scientific name | Vegetation association | Uses for grassland vegetation | Predicted response to grazing |
|----------------------------|--------------------------------|------------------------------------|--|-------------------------------|
| Brewer's sparrow | <i>Spizella breweri</i> | Sagebrush obligate ^b | Occasional foraging | Neutral |
| Brown-headed cowbird | <i>Molothrus ater</i> | Facultative grassland ^a | Occasional nesting, foraging | Neutral to negative |
| Chestnut-collared longspur | <i>Calcarius ornatus</i> | Grassland obligate ^a | Nesting, foraging | Negative |
| Horned lark | <i>Eremophila alpestris</i> | Grassland obligate ^a | Nesting, foraging | Negative |
| Lark bunting | <i>Calamospiza melanocorys</i> | Grassland obligate ^a | Nesting, foraging | Negative |
| McCown's longspur | <i>Rhynchophanes mccownii</i> | Grassland obligate ^a | Nesting, foraging | Negative |
| Vesper sparrow | <i>Poocetes gramineus</i> | Generalist ^c | Occasional nesting ^d , foraging | Neutral |
| Western meadowlark | <i>Sturnella neglecta</i> | Grassland obligate ^a | Nesting, foraging | Negative |

^a Vickery et al., 1999.

^b Paige and Ritter, 1999.

^c Jones and Cornely, 2002.

^d Will nest under a shrub if present^c.

Therefore, we did not include plots where forest, open water, or other non-vegetative cover made up 30% or more of the ground cover within the plot. To the extent possible, we excluded plots that included county roads. If a plot was excluded, we selected another random plot to sample so that we maintained 40 sampling plots in each grazing system. Season-long grazing plots were located on public lands managed by BLM. Rest-rotation plots were located on private lands enrolled in the Sage Grouse Initiative conservation program that employs rest-rotation grazing to benefit the greater sage-grouse (*Centrocercus urophasianus*) and other wildlife species.

Bird survey data were collected during the peak songbird breeding season in Montana from May through July in both 2013 and 2014. We included three repeat surveys within a year during the breeding season (approximately once a month in May, June, and July) on each sampling plot to ensure that we had a representative sample of abundance during the entire breeding season. We also sampled across two years to make sure we captured any annual variability that might affect the outcome of songbird abundance.

We used dependent double-observer transect (DDOT) survey method (Nichols et al., 2000) to obtain songbird abundance estimates. We used the DDOT method because it provides higher reliability in this sagebrush grassland ecosystem compared to traditional single-observer avian survey methods (Golding and Dreitz, 2016). The DDOT survey method involved two-person team that walked a transect. The primary observer walked in front and a secondary observer walked approximately 3–5 m behind the primary observer. The observers started the survey on the southeast transect corner of each plot and walked the transect surveying 125 m on either side of the transect (Fig. 1). We chose a distance of 125 m because $\geq 95\%$ of songbird detections occur within 125 m of an observer (Ralph et al., 1995). The primary observer communicated each individual bird observed, including species and approximate location, to the secondary observer who recorded the information. The secondary observer also recorded detections that they observed but the primary observer did not observe. If an auditory detection occurred, an observer was required to get visual confirmation of the bird. The two observers switched roles after each survey. Surveys were conducted between approximately 0600 and 1100 MDT. Surveys were not conducted during inclement weather or when winds were greater than 15 mph.

Songbird abundance may be affected by a variety of factors operating independent of variability in grass vegetation caused by livestock grazing systems. In arid rangeland environments, researchers have found that abiotic factors play a strong role in governing the abundance and distribution of species (Wiens and Rotenberry, 1980; Vander Haegen et al., 2000). To account for abiotic factors, we used an index of biomass potential produced by

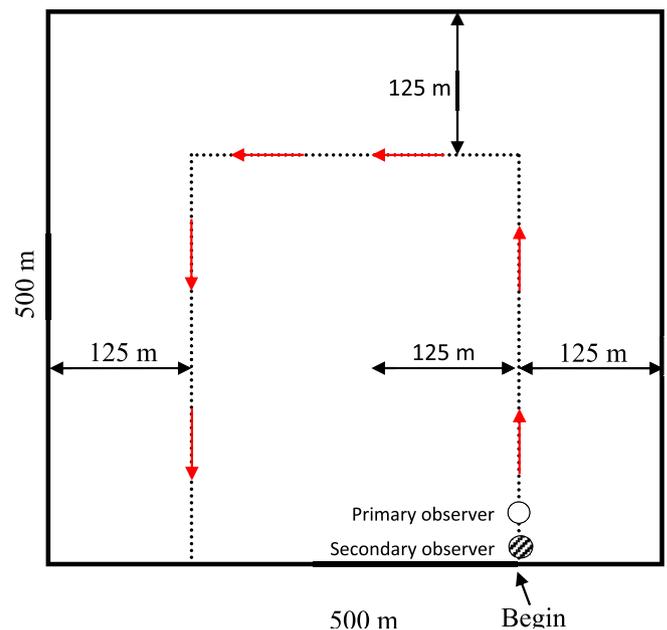


Fig. 1. An illustration of the dependent double-observer transect method. The primary (open circle) and secondary observer (dashed circle) walk single-file along the transect (dotted line) within a 500 m × 500 m sampling plot. Observers survey up to 125 m on either side of the transect. All surveys start at the lower right corner of the transect. Red arrows indicate direction of travel. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

NRCS (2011). The index relates abiotic factors, including soil, climate, and topography, to the expected amount of non-tree biomass that can grow annually. We determined that biomass potential, measured in pounds per acre of potential biomass, was lower on average in season-long grazing (1038.45 [95% confidence interval: 1036.89–1040.01]) than on rest-rotation grazing (1182.53 [95% confidence interval: 1180.76–1184.30]) grazing systems in our study area. We used this measure to account for additional sources of heterogeneity within grazing systems. To account for additional spatial and temporal variation in abundance, we included parameters for sampling plot and year. Many species respond to management actions differently because of different life history requirements (Lindenmayer et al., 2002). Therefore, we assumed the effects of grazing and these additional factors on abundance vary by species, as described below.

We used a modified multispecies abundance model, the multi-species dependent-double observer abundance model (MDAM; Golding et al., 2017), to track changes in abundance of multiple

sagebrush songbird species. We modeled abundance of species i at plot j in year y (N_{ijy}) as function of a Poisson random variable with mean species abundance per plot in each year (λ_{ijy}).

$$N_{ijy} \sim \text{Poisson}(\lambda_{ijy}) \quad (1)$$

We modeled the mean species abundance per plot in each year (λ_{ijy}) as a function of a species-specific intercept (β_{0i}), plus a species-specific fixed-effect of grazing system, (β_{1i}), a species-specific fixed effect for biomass potential (β_{2i}) to account for underlying sources of variation in the landscapes between the two grazing systems, a species-specific fixed effect for year that varied by species (β_{3i}) to account for difference in abundance between the 2013 and 2014 sampling periods, plus a random effect for plot (α_j) to account for site-level variation not otherwise captured by the aforementioned covariates.

$$\log(\lambda_{ijy}) = \beta_{0i} + \beta_{1i} \times \text{grazingtype}_i + \beta_{2i} \times \text{biomasspotential}_i + \beta_{3i} \times \text{year}_i + \alpha_j \quad (2)$$

We used vague normal distributions, Normal (0, 1000), for the priors of the coefficients of the linear predictor of mean species abundance (λ_{ijy}). For the random plot effect (α_j), we used a prior uniform distribution ranging from 0 to 100.

The DDOT survey method produces observations with three possible outcomes: 1) the primary observer detects an individual, which is described by the detection probability of the primary observer (p_1); 2) the secondary observer detects an individual the primary observer misses, which is the product of the probability that the primary observer does not see the individual ($1 - p_1$) and the detection probability of the secondary observer (p_2); and 3) both the primary and secondary observer do not detect an individual, which is the product of the probability that the primary and observer do not see the individual $(1 - p_1)(1 - p_2)$.

We modeled the total number of each species i at a given plot j in year y at within-year survey replicate k observed by both observers, $nobs_{ijk}$, as a binomial random variable that is a function of latent abundance, N_{ijy} , and the probability that either observer observed species i at plot j in year y at within-year replicate k , $pcap_{ijk}$.

$$pcap_{ijk} = 1 - \left((1 - p_{1ijk}) \times (1 - (p_{2ijk} \times (1 - p_{1ijk}))) \right) \quad (3)$$

$$nobs_{ijk} \sim \text{Binomial}(N_{ijy}, pcap_{ijk}) \quad (4)$$

We modeled the observed abundance, y_{ijk} , of species i at plot j in year y at within-year survey replicate k by each observer as a multinomial random variable that is a function of the number observed by both observers, $nobs_{ijk}$, and three multinomial cell probabilities π_{ijk} that represent the DDOT survey outcomes described above.

$$y_{ijk} \sim \text{Multinomial}(nobs_{ijk}, \pi_{ijk}) \quad (5)$$

We accounted for multiple sources of variation in detection, including differences in detection based on individual and species. We used vague normal distributions, Normal (0, 10,000), for the prior distributions of detectability for each observer and species that informed multinomial cell probabilities.

3. Results

Two-person teams completed a total of 478 DDOT surveys in 2013 and 2014. Each year, teams conducted 120 surveys per grazing

system, with the exception of rest-rotation grazing in 2013, when there were 118 surveys completed due to access constraints on a single plot. These surveys resulted in 11,267 observations in 2013 and 12,175 observations in 2014 of the eight songbird species. In both 2013 and 2014, total observations were higher in rest-rotation (6080 and 6,878, respectively) than season-long grazing (5187 and 5,297, respectively), although this pattern differed by species. In 2013 and 2014, more Brewer's sparrows, brown-headed cowbirds, lark buntings, vesper sparrows, and western meadowlarks were observed in season-long grazing than in rest-rotation grazing. In contrast, in 2013 and 2014 more horned larks and McCown's longspurs were observed in rest-rotation than season-long grazing. More chestnut-collared longspurs were observed in rest-rotation grazing in 2013, but this was reversed in 2014.

We did not detect an effect for year (i.e., the CRI overlapped with 0) for most species (Table 2), thus, we present results based on the 2013 sampling year. Compared to season-long grazing, there was no or minimal effect (presented on a log scale) of rest-rotation grazing on abundance for half of the species examined: Brewer's sparrow, chestnut-collared longspur, horned lark, and vesper sparrow (Table 2). Rest-rotation grazing had a negative effect on the abundance of three species: brown-headed cowbird, lark bunting, and western meadowlark. The effect of rest-rotation grazing was positive only for McCown's longspur.

The effect of biomass potential on abundance was positive for six of the eight species examined: brown-headed cowbird, chestnut-collared longspur, horned lark, lark bunting, McCown's longspur, and western meadowlark (Table 2). The effect was negative for Brewer's sparrow. For vesper sparrow, there was no or minimal effect of biomass potential (Table 2).

Songbird abundance differed between the two grazing systems (Figs. 2 and 3) when accounting for the effect of biomass potential and year. Abundance estimates presented are the average predicted number of individuals of a species per 25 ha sampling plot. We considered abundance to be different between the two grazing systems if the CRIs for the predicted abundance did not overlap (i.e., it was 100% likely that the abundances were different). Abundance was different between the two grazing systems for four of eight species: brown-headed cowbird, lark bunting, McCown's longspur and western meadowlark (Table 3). Three species were on average more abundant per 25 ha in season-long grazing than rest-rotation grazing: brown-headed cowbird, lark bunting, and western meadowlark. McCown's longspur was more abundant per 25 ha in rest-rotation grazing than season-long grazing systems. The remaining four species showed no difference (i.e., CRIs overlapped) in abundance between grazing systems: Brewer's sparrow, chestnut-collared longspur, horned lark, and vesper sparrow.

The relative role of grazing system and biomass potential on abundance varied by species (Fig. 4). Overall, grazing system appeared to have a larger effect on abundance than biomass potential for brown-headed cowbird, lark bunting, McCown's longspur, and western meadowlark. Biomass potential appeared to have a larger effect on abundance than grazing system for Brewer's sparrow, chestnut-collared longspur, and horned lark. For vesper sparrows, both grazing system and biomass potential appeared to have a minimal effect on abundance.

4. Discussion

Overall facultative and grassland obligate species were either more abundant on season-long grazing or equally abundant on the two grazing systems. As expected, the sagebrush obligate, Brewer's sparrow, showed no difference in abundance between the two grazing systems. One species did not support our predictions. McCown's longspur was more abundant on rest-rotation grazing.

Table 2

Effects of covariates on average predicted abundance (N) and ninety-five percent credible intervals per 25 ha for eight avian species. The effects are on a log scale. Predictions are derived from the multispecies dependent double-observer abundance model using data collected in rest-rotation and season-long grazing near Roundup, Montana in 2013 and 2014.

| Species | Grazing ^a | Biomass potential ^b | Year ^c |
|----------------------------|-----------------------|--------------------------------|-----------------------|
| Brewer's sparrow | 0.122 (−0.109–0.355) | −0.192 (−0.308–0.075) | −0.200 (−0.310–0.091) |
| Brown-headed cowbird | −0.713 (−1.000–0.429) | 0.371 (0.224–0.519) | 0.211 (−0.052–0.489) |
| Chestnut-collared longspur | 0.121 (−0.146–0.39) | 1.219 (1.064–1.377) | −0.446 (−0.656–0.238) |
| Horned lark | 0.177 (−0.052–0.408) | 0.344 (0.226–0.462) | 0.244 (0.149–0.339) |
| Lark bunting | −0.961 (−1.215–0.707) | 0.441 (0.314–0.568) | −1.660 (−2.030–1.316) |
| McCown's longspur | 0.914 (0.685–1.143) | 0.704 (0.587–0.821) | 0.082 (0.011–0.154) |
| Vesper sparrow | 0.072 (−0.159–0.303) | −0.002 (−0.117–0.113) | 0.064 (−0.042–0.171) |
| Western meadowlark | −0.582 (−0.820–0.346) | 0.181 (0.061–0.302) | 0.402 (0.277–0.529) |

^a The effect of rest-rotation relative to season-long grazing.

^b The effect of a one unit increase in biomass potential relative to average biomass potential.

^c The effect of 2014 relative to 2013.

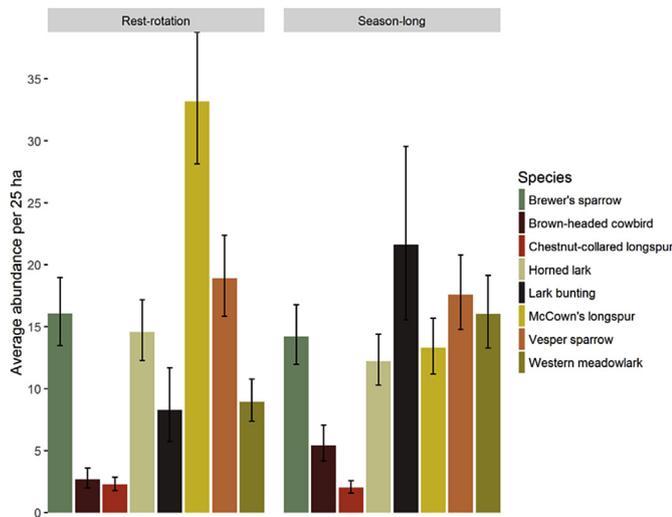


Fig. 2. The estimated abundance of species per 25 ha for eight sagebrush songbird species in rest-rotation and season-long grazing systems. Estimates are derived from data collected in a sagebrush ecosystem near Roundup, Montana, during 2013 using the multispecies dependent double-observer abundance model.

Biomass potential had a positive effect on six out of the eight species and the relative role compared to grazing varied by species. These results are consistent with other studies that suggest abiotic factors interact with grazing to play an important role in determining abundance (Lipsey and Naugle, 2016; Wiens and Rotenberry, 1980) and that grazing has varying impact on different songbirds species (Pipher et al., 2016).

Some grassland obligate species, lark bunting and western meadowlark, were more abundant on season-long grazing. Both of these species nest and forage on the ground; a wide variety of grass vegetation structure supports their ability to both conceal nests and efficiently forage. The facultative grassland species, the brown-headed cowbird, responded in a similar manner and was more abundant on the season-long grazing. This species parasitizes nests of other songbirds. Although the brown-headed cowbird has considerable flexibility in its nesting choices (Forsman and Martin, 2009), the species evolved with grassland systems in North America and is closely tied to the nesting habits of grassland obligate and facultative songbirds.

The two grassland obligate species, chestnut-collared longspur and horned lark, and a generalist, vesper sparrow, showed no clear difference in abundance between rest-rotation and season-long grazing. This may represent the incredible variability grassland obligate songbirds exhibit in their vegetation preferences that vary

by where the species is within its broader range and what vegetation is present in the surrounding areas (Vickery et al., 1999). Therefore, it is probable that there is no “one size fits all” amount of structural heterogeneity that is appropriate for all grassland obligate and facultative songbirds. This variation may also explain why the strength of the influences of season-long grazing did not follow our prediction that grassland obligate species would respond more strongly than facultative grassland species.

The response of McCown's longspur was counter to our predictions. McCown's longspur was more than twice as abundant per 25 ha in rest-rotation grazing than season-long grazing. Over two years of the study, McCown's longspurs were only observed on slightly less than half of the plots within season-long grazing (41%), whereas they were seen on ~ 75% of the rest-rotation plots. McCown's longspurs are known to breed in loose colonies (Sedgwick, 2004), suggesting that there is a social, or conspecific attraction, component to their location on a landscape. We consistently observed large colonies of nesting McCown's longspurs with few other songbird species present. In addition, McCown's longspurs prefer very short grass vegetation (Knopf, 1996; Sedgwick, 2004) and this requirement may be more dominant than the need for structural heterogeneity. In addition, the social aspect of their nesting may strengthen the observed relationship between the abundance and vegetation association of the species (i.e., more individuals may nest in areas where individuals are already present (Sedgwick, 2004)).

The effect of biomass potential was positive for six of the eight species examined: brown-headed cowbird, chestnut-collared longspur, horned lark, lark bunting, McCown's longspur, and western meadowlark. This is consistent with previous findings that species in sagebrush environments may be heavily influenced by abiotic conditions (Wiens and Rotenberry, 1987). Only Brewer's sparrow showed a negative response to biomass potential and likely the result of Brewer's sparrow dependences on sagebrush shrubs that grow in poor, unproductive soil. For vesper sparrow the lack of an effect of range quality is consistent with the description of this species as a generalist (Jones and Cornely, 2002).

While there is clearly a great deal of variability that is not explained by either grazing system or biomass potential, these species show measurable responses to both. However, both the nature of the response and the importance of these two factors on site-level abundance varies widely across bird species (Fig. 4). Abundance of some, such as Brewers sparrow and chestnut-collared longspur are more strongly driven by productivity and grazing system appears relatively unimportant. Abundance of others, such western meadowlark, are more strongly affected by grazing systems with biomass potential having little importance (Fig. 4). However, both the relative strengths of these two factors

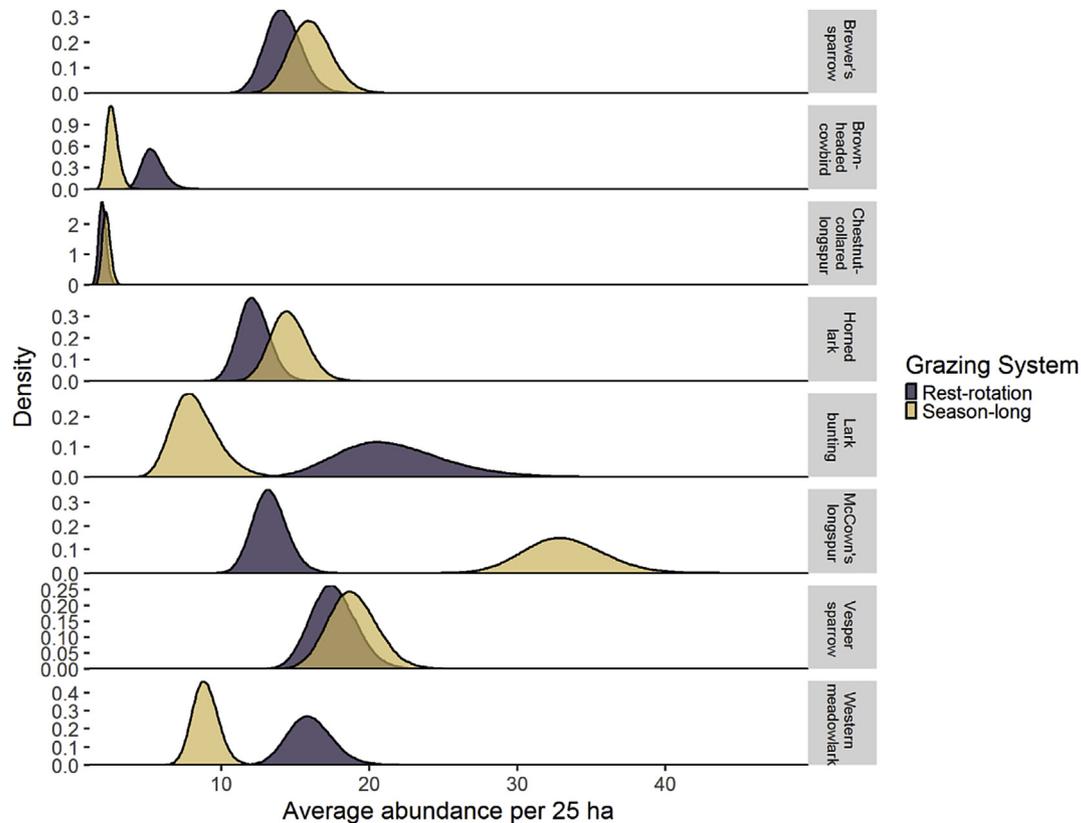


Fig. 3. The posterior distributions of the estimated abundance per 25 ha for eight sagebrush songbird species in rest-rotation and season-long grazing systems. Predictions are derived from data collected in a sagebrush ecosystem near Roundup, Montana, during 2013 using the multispecies dependent double-observer abundance model.

Table 3
The average predicted abundance (N) and ninety-five percent credible intervals (CRI) per 25 ha for eight avian species in rest-rotation and season-long grazing systems. Predictions are derived from the multispecies dependent double-observer abundance model from data collected near Roundup, Montana in 2013 and 2014.

| Species | 2013 | | | | 2014 | | | |
|----------------------------|---------------|-------------|-------------|-------------|---------------|-------------|-------------|-------------|
| | Rest-rotation | | Season-long | | Rest-rotation | | Season-long | |
| | N | CRI | N | CRI | N | CRI | N | CRI |
| Brewer's sparrow | 16.05 | 13.47–18.98 | 14.21 | 11.95–16.77 | 13.20 | 10.44–16.45 | 11.68 | 9.29–14.49 |
| Brown-headed cowbird | 2.66 | 1.97–3.58 | 5.41 | 4.13–7.07 | 3.36 | 2.01–5.50 | 6.82 | 4.19–10.89 |
| Chestnut-collared longspur | 2.26 | 1.77–2.84 | 2.00 | 1.55–2.55 | 1.46 | 0.99–2.10 | 1.29 | 0.87–1.85 |
| Horned lark | 14.58 | 12.28–17.16 | 12.21 | 10.29–14.38 | 18.66 | 14.95–23.00 | 15.62 | 12.54–19.24 |
| Lark bunting | 8.28 | 5.73–11.70 | 21.62 | 15.57–29.54 | 1.61 | 0.88–2.74 | 4.21 | 2.36–6.98 |
| McCown's longspur | 33.18 | 28.15–38.78 | 13.30 | 11.19–15.69 | 36.06 | 29.73–43.33 | 14.45 | 11.81–17.54 |
| Vesper sparrow | 18.91 | 15.85–22.38 | 17.60 | 14.79–20.80 | 20.21 | 16.01–25.23 | 18.81 | 14.92–23.47 |
| Western meadowlark | 8.95 | 7.37–10.77 | 16.02 | 13.29–19.16 | 13.41 | 10.20–17.39 | 24.01 | 18.32–31.00 |

and the direction of the response differ across species. While the general trend for most species is to increase abundance as productivity increases, Brewer's sparrow are more common in low productivity sites, likely because sagebrush are less common in high productivity sites. Most species that show a grazing response occur at higher abundances in areas with traditional grazing methods, but McCown's longspur occurs at greater abundances in sites managed using rest-rotation systems. It is, therefore not possible to state, independent of specific species responses, that one system of grazing is better than the other, or even that higher productivity areas have higher bird abundance.

There are some important limitations of this study. First, this study was conducted over two years, limiting its inference about the long-term effects of the two grazing systems. The long term effects of vegetation changes and songbird associations are

complex in sagebrush ecosystems. For example, [Rotenberry and Wiens \(2009\)](#) found that vegetation associations of songbirds in a sagebrush ecosystem from a six year study were not predictive of habitat associations in the same study area 14 years later. Secondly, although we attempted to capture a range of avian responses with the eight species we selected, eight species may not capture all of the variety within the sagebrush songbird community. Grazing primarily affects grass vegetation and not shrubs ([Veblen et al., 2015](#)). We chose a group of species that represented the range of life histories of the sagebrush songbird community and a proportionally higher number of species that were most likely to be affected by grazing. Finally, although we attempted to account for underlying differences in abiotic factors which may be reflected in current land ownership, we acknowledge that there may be confounding effects of land ownership on the vegetation and songbird

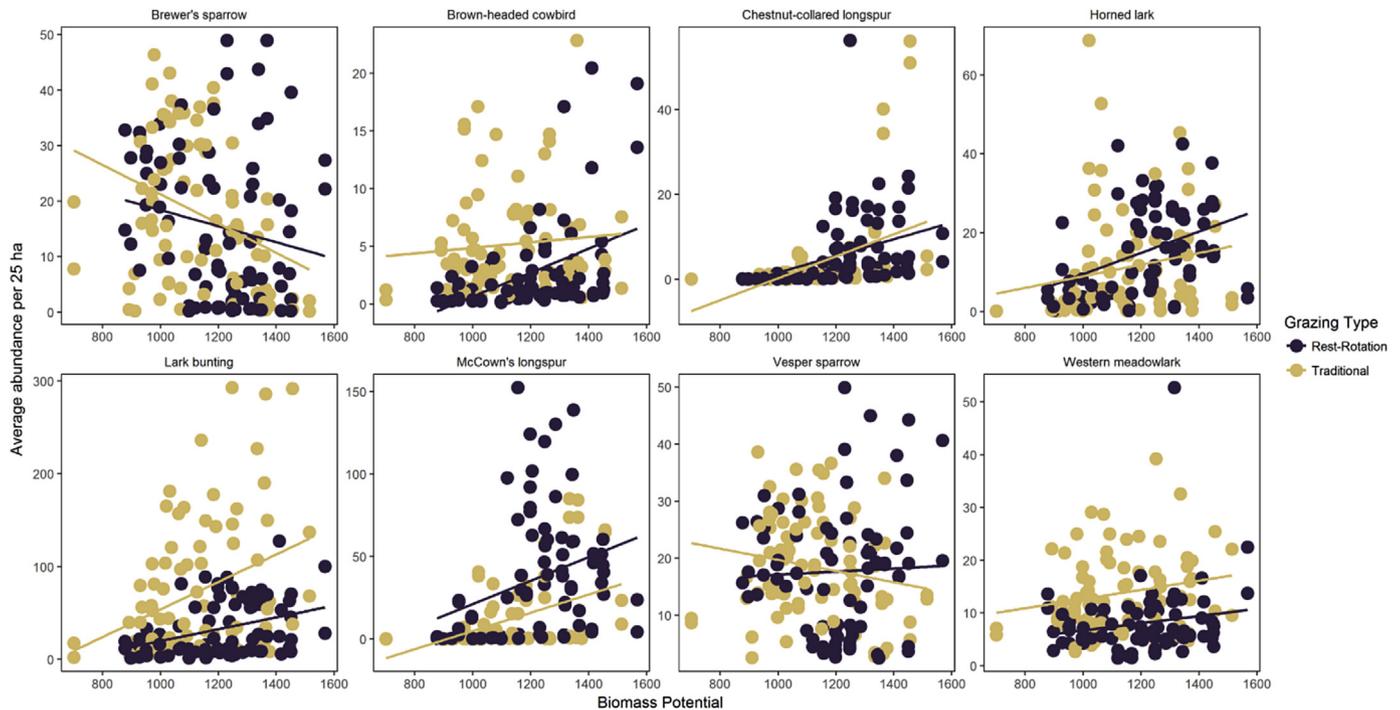


Fig. 4. The average estimated abundance per 25 ha (y-axis) and the values of biomass potential (x-axis). Estimates are derived from the multispecies dependent double-observer abundance model from data collected near Roundup, Montana in 2013. Regression lines show the trend within each grazing system. The distance between the lines reflects the grazing effect for each species, whereas the slopes of the lines reflect the effect of biomass potential on each species.

communities.

5. Conclusions

Our study provides an initial step in comparing two grazing systems, rest-rotation and season-long, in sagebrush ecosystems. We used a group of eight species that were largely representative of the grassland obligate songbirds in this community because we predicted these grazing systems have minimal effects on sagebrush obligate species. The responses of sagebrush obligates suggest that their vegetation preferences may be closely tied to breeding activity or foraging opportunity, which is similar to what other authors have found (Chalfoun, 2006). Future work that measures total reproductive output (a product of nest density and nest success) in these grazing systems may illuminate underlying processes driving changes in abundance.

Livestock grazing is often assumed to have universal consequences for an ecosystem. However, our study demonstrates that any single grazing system is unlikely to have similar consequences for all species. Natural resource managers should consider how a broad, widely applied conservation strategy like livestock grazing can support numerous species. The implications of our study suggest that grazing systems can be used to alter the abundance of individual songbird species closely tied to grass vegetation. However, if conservation goals revolve around maintaining a community of sagebrush songbirds, implementing a single grazing system, either season-long or rest-rotation, is not likely to achieve those goals. Instead, a mosaic of numerous grazing systems on the landscape may better maintain the abundance and distribution of the songbird community and some of the ecological functions of sagebrush ecosystems.

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