Assessing changes in avian communities

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ASSESSING CHANGES IN AVIAN COMMUNITIES

By

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B.A., University of California, Berkeley, CA, 2007

Thesis

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Assessing changes in avian communities

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INTRODUCTION

The loss of biodiversity is a formidable challenge facing the world today. Species extinction rates are currently higher than they have been in the past 540 million years (Barnosky et al. 2011). Many conservation objectives are centered on the preservation of biodiversity because it supports both ecosystem functioning and human well-being (Margule and Pressey 2000; Hooper et al. 2005; Mittlebach 2012; Naeem et al. 2009). Given limited time and resources, conservation practitioners often monitor a single focal species or a species of conservation concern (Caro 2012). However, knowledge on a single species provides limited and biased information about biodiversity (Chao et al. 2006; Caro 2012). Therefore, to effectively conserve biodiversity, it is essential to have reliable models to predict changes in abundance of multiple species exposed to natural or anthropogenic changes (Buckland et al. 2005; Wiens et al. 2008; Tylianakis et al. 2008; Tulloch et al. 2010).

Recent quantitative advances provide new methods to accurately measure the abundance of multiple species while accounting for one of the main sources of error in abundance surveys - imperfect detection (Iknayan et al. 2014). Multispecies abundance models (MSAM) use a Bayesian N-mixture structure (Kéry et al. 2005), which relies on repeated counts, to estimate detection and calculate adjusted abundance estimates for multiple species. MSAMs incorporate sources of variation from both the biological processes that determine abundance on a landscape and observational processes to estimate detection and predict abundance. They have been used to assess various components of biodiversity, including the response of biological communities to different types of land-use practices (Yamura et al. 2012; Chandler et al. 2013). Current MSAMs
still fail to account for false positives, the detection of an individual that is not present because of either misidentification or double count of another individual (Iknayan et al. 2014). False positives can inaccurately inflate abundance and biodiversity estimates. Although they are well known errors, particularly in multispecies survey data, they are seldom accounted for in survey design or analysis (Royle and Link 2006; Miller et al. 2011). Nichols et al. (2000) provides a dependent-double observer (DDO) survey method to account for imperfect detection. Because it relies on two observers working collaboratively to identify individuals, the DDO method is suggested to reduce the occurrence of false positives will occur. To date, the DDO approach has not been combined with MSAMs.

Livestock grazing is a disturbance mechanism that affects biodiversity. Livestock grazing is of special concern because it is one of the most common land uses worldwide (Raven 2002). In the United States, grazing occurs on approximately 40 percent of total land (Holechek et al. 1998) and approximately 70 percent of land in the West (Fleischner 1994). Researchers have documented grazing effects on wildlife species of all vertebrate classes; grazing has been shown to both increase and decrease vertebrate species abundance, as well as alter species composition in communities (Fleischner 1994). Grazing can alter community dynamics and reduce an ecosystem’s resilience to environmental change (Folke et al. 2004). However, many studies that compare grazing effects focus on a single species and compare the effects of grazing techniques to greatly reduced or removed grazing. Much is still unknown about the whether the effects of grazing are similar across multiples species within a community (Krausman et al. 2009). In addition, although grazing has predictable effects on vegetation, it still remains unknown if these effects translate into changes in the abundance of multiple species. Given the economic and cultural importance of grazing to humans, these comparisons of existing grazing systems to
reduced or removed grazing are unrealistic. Because the persistence of grazing is likely in the future, it is important to close this gap in knowledge and understand how different grazing systems affect multiple wildlife species.

In this thesis I explore a derivation of the MSAM using the DDO survey method to create a multispecies dependent double-observer abundance (MDAM) model. I use this tool to explore how two widely used grazing systems affect the abundance of eight songbird species with varying reliance on grassland vegetation in a sagebrush ecosystem.
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CHAPTER 1: A MULTISPECIES DEPENDENT DOUBLE-OBSERVER MODEL: A NEW METHOD TO ASSESS CHANGES IN BIOLOGICAL COMMUNITIES

INTRODUCTION

Effective conservation of biodiversity, the abundance of individuals and species within a given area, requires reliable models to predict changes in the abundance of multiple species. Species have different life history strategies and often respond differently to natural and anthropogenic disturbances (Buckland et al. 2005; Wiens et al. 2008; Tylianakis et al. 2008; Tulloch et al. 2010). The underlying cause of changes in biodiversity may be complex. For example, abundance of one species may vary in response to changes in abiotic conditions. This can lead to changes in other species abundance through other biotic interactions. Multispecies abundance information can help disentangle these complex responses (Dorazio and Connor 2014; Ockendon et al. 2014; Barnaguard et al. 2014).

However, collecting multispecies abundance data can be time and effort intensive. Therefore, managers often rely on information about a single species that is thought to reflect the biodiversity of a community. Although these strategies can be cost-effective, they provide limited and potentially biased information about biodiversity (Chao et al. 2006; Caro 2012), as they are often selected for non-biological reasons (Simberloff 1998). Multispecies data, on the other hand, is thought to reflect larger ecosystem processes (Lambeck 1997). Empirical evidence suggests that if the multiple species are selected based similar life history traits (i.e., they are limited by the same biological processes), they can represent what is occurring in the community (Lindenmayer et al. 2014). Although multispecies approaches are useful, many multispecies studies fail to account for imperfect detection, which is particularly important when considering a wide variety of species with different detection probabilities. As the world continues to lose biodiversity at unprecedented rates (Hooper et al. 2005), it is essential for conservation
practitioners to have an accessible multispecies abundance modeling framework that addresses these issues.

One of the main challenges associated with any abundance estimate is imperfect detection (Seber 1986; Seber 1992; Schwarz and Seber 1999). Detection has two components, availability and detectability. Availability refers to whether a species or individual of interest is present at a given site. Detectability is the probability an observer detects an individual during a survey. Imperfect detection results from two processes governing the components of detection (Table 1-1): (1) biological processes that influence abundance and determine availability; and (2) observation processes that determine detectability, which can be affected by species, observer experience, time of day, and other factors (Farnsworth et al. 2002; Simons et al. 2007; Alldredge et al. 2007; Pacifici et al. 2008).

Failing to account for imperfect detection when monitoring multiple species can lead to incorrect inferences about drivers of change in abundance or biodiversity (Buckland et al. 2005; Kéry and Schaub 2012; Iknayan et al. 2014). Imperfect detection from different sources can produce similar abundance patterns that result from entirely different mechanisms. For example, a common species may be consistently available (i.e., present), but have a low detectability because of cryptic behavior. A rare species, on the other hand, may be mostly unavailable across sites (i.e., present only in a low density), but have high detectability as a result of conspicuous vocalization. All of these factors can differentially affect the observation of each species, producing different observed counts, and ultimately abundance estimates. When quantifying biodiversity it is important to keep this in mind and avoid unrealistic assumptions that detection of all species is a result of the same processes. However, this is beyond the consideration of most traditional biodiversity estimation methods (Iknayan et al. 2014).
Recent abundance estimation methods based on N-mixture models have expanded from a single species (Royle 2004) to a multispecies context (Kéry et al. 2005). N-mixture models produce adjusted abundance estimates by using information contained within repeated counts to estimate detection. The structure is hierarchical and uses information from the biological process and observational process to estimate detection and predict abundance. Multispecies abundance models (MSAMs) are an emerging method that use this N-mixture framework to estimate abundance and detection of multiple species from spatially and temporally replicated counts (Kéry and Schaub 2012). MSAMs can incorporate species-specific or site-specific covariates, such as habitat type, as part of the biological or observation process, and account for differences in these processes for each species (Iknayan et al. 2014). As a result, MSAMs are being used to assess various components of biodiversity, including the response of forest bird biodiversity to different types of land-use practices (Yamura et al. 2012; Chandler et al. 2013), community assembly of forest birds (Barnagaud et al. 2014), and species interactions (Dorazio and Connor 2014).

One of the major limitations of current MSAMs is that they do not address imperfect detection in the form of false positive errors (i.e., the detection of an individual that is not present because of either misidentification or double count of another individual; hereafter “false positives”) (Iknayan et al. 2014). False positives have been documented in many different types of ecological survey data (Miller et al. 2015). Royle and Link (2006) suggested that false positives due to misidentification can be particularly prevalent in multispecies data. If not accounted for, even small rates of false positives can lead to substantial biases (Royle and Link 2006; Fitzpatrick et al. 2009; Miller et al. 2011; Connors et al. 2014). There are design-based (e.g., Miller et al. 2012; Molinari-Jobin et al. 2012) and statistical methods (e.g., Royle and Link
2006) to account for sources of variation that lead to false positives. However, the use of these methods is not widespread. Most often, researchers assume that false positives do not occur (Nichols et al. 2000; Royle and Link 2006; Miller et al. 2012).

The dependent double-observer (DDO) method is a survey method that reduces false positive observations by using removal-based methodology to calculate detectability (Nichols et al. 2000). The method uses two observers with different roles. The primary observer dictates all individuals he/she observes during a survey. The secondary observer notes the identity and location of the individuals observed by the primary observer. In addition, the secondary observer notes individuals missed by the primary observer. This process relies on the secondary observer verifying the observations of the primary observer, making an incorrect detection in the majority of the observations less likely than with a single observer acting alone (Nichols et al. 2000). The observation outcomes, primary observer detects an individual or secondary observer detects an individual that the primary missed, must be correctly recorded. Once that occurs, the observers have flexibility to collaborate to identify characteristics of the individuals (e.g., species, sex). The DDO method has been successfully applied in arid and woodland environments to estimate avian abundance (Nichols et al. 2000; Kissling and Garton et al. 2006, Tipton et al. 2009) and occupancy (Tipton et al. 2008).

Although recent studies have used MSAMs to track biodiversity in response to different land use types (Yamura et al. 2012; Chandler et al. 2013), none have provided design-based methods to reduce false positives. Here, I provide an expansion of the MSAM framework to account for false positives by incorporating the design-based DDO method in a multispecies, multi-season framework. I simulated abundance and count data for four species data to develop this multispecies dependent double-observer abundance model (MDAM). I then applied the MDAM
to case study data collected on prairie songbirds over multiple years on private and public lands in eastern Montana. Songbirds are becoming increasingly important indicators in biodiversity monitoring (Iknayan et al. 2014). Studies have shown that changes in songbird abundance and biodiversity are reliable indicators of impacts resulting from anthropogenic disturbance and land management in numerous ecosystems (e.g., Mac Nally 1997; Bradford et al. 1998; Canterbury et al. 2000; Schulze et al. 2004; Coppedge et al. 2006; Coppedge et al. 2008). With the reduction in false positives, the MDAM can provide more reliable estimates and rigorous inference about changes in communities than previously available. Additionally, MDAM opens up the possibility of large-scale, multispecies, multi-season biodiversity monitoring.

**METHODS**

**Bayesian Statistics Terms**

Bayesian statistical inference is based on three primary pieces of information: a *prior distribution* (hereafter “prior”), which is a probability distribution that represents what is known about a parameter prior to conducting a study; a *likelihood*, which is a probabilistic statement relating observed data to unknown model parameters; and a *posterior distribution*, which is the probability distribution representing a parameter estimate and is proportional to the product of the prior and likelihood. The information from the density of the distribution can be used to determine how much support there is for a point estimate (i.e., the most support is shown by the highest density of the distribution). The density also provides information about how likely it is that an estimate is within a given range of values. In Bayesian inference, this range is known as a credible interval (CRI). A Bayesian CRI of 95% means that there is a 0.95 probability that the true value of the estimated parameter is within the given range.
MDAM Basic Structure

To develop the MDAM, I extended previous approaches to similar multispecies abundance problems (e.g., Yamura et al. 2012; Chandler et al. 2013). The basic structure of the MDAM includes two hierarchical processes: a biological and observation process. The biological process estimates the true abundance of multiple species on a landscape. This process determines whether an individual or species is present at a given location. The observation process estimates the probability of detection using the outcome of two observers using the DDO method and the true abundance from the biological process. The MDAM accounts for imperfect observation by estimating detectability, or the probability that observer detects an individual during a survey. This is calculated from the different observation outcomes between the two observers in the DDO method. The structure of each hierarchical process within the MDAM is described below.

Modeling Abundance

I considered the likelihood for the latent, or true, abundance of species $i$ at plot $j$ ($N_{ij}$) to be a function of a Poisson random variable with mean abundance per plot ($\lambda_{ij}$) (Equation 1). I used a Poisson distribution because I assumed that individuals and species of interest were randomly distributed across plots (Royle 2004).

Equation 1: Biological process

$$N_{ij} \sim \text{Poisson} (\lambda_{ij})$$

Modeling Observations

The DDO survey method produces observations with three possible outcomes: 1) the primary observer detects an individual; 2) the secondary observer detects an individual that the primary
observer misses; and 3) both the primary and secondary observer fail to detect an individual. Each of these outcomes has a different probability of occurring because they are based on a combination of events resulting from two observers. Outcome 1 is based only on the primary observer’s ability to detect an individual \(p_1\). Outcome 2 is a product of the probability that the primary observer did not detect an individual \((1 - p_1)\) and the secondary observer’s ability to detect an individual \(p_2\). Outcome 3 is a product of neither observer detecting an individual \((1 - p_1) \times (1 - p_2)\). Because this process has multiple outcomes with multiple probabilities, I considered it a multinomial process. I modeled the observed abundance of species \(i\) at plot \(j\) at survey replicate \(k\) \(y_{ij}^k\) as a multinomial random variable that is a function of latent abundance \(N_{ij}\) (Equation 1), and three multinomial cell probabilities \(\pi_{ijk}\) that represent the DDO survey outcomes (Equation 2).

Equation 2: Observation process

\[ y_{ij}^k \sim \text{Multinomial} \left( N_{ij}, \pi_{ijk} \right) \]

**Simulated Data Set**

I simulated data to assess the performance of the MDAM. I used a random Poisson distribution to model true abundance for four hypothetical species randomly distributed across 20 plots. Count data were generated using a random multinomial distribution with the three cell probabilities that corresponded to the outcomes of the DDO process, described above. The count data reflected two observers using the DDO method on three replicate visits at each of the 20 plots over a single season. Detection was held constant at 0.3 for the primary observer and 0.5 for the secondary observer. I considered differences in individual observer effect as the only source of variation in detectability in the observation process. I assumed that all four species were available and observed on each plot during each survey replicate.
MDAM Performance

I used program R (version 3.2.0) and JAGS (Plummer 2013) to run the MDAM with this simulated data in a Bayesian hierarchical framework (see Appendix 1 for code). I generated three Markovian chains for 50,000 iterations with a period of 5,000 burn-in iterations that were discarded. I specified over-dispersed starting values for three Markovian chains, which allows for more reliable information about model performance and aids in diagnosing convergence (King et al. 2010). To assess chain convergence, I used two diagnostics from three independent Markovian chains: (1) trace plots, which show all of the values of the Markovian chains during the 50,000 iterations, to visually inspect chain mixing (King et al. 2010); and (2) the \( R \) statistic, an estimate of the ratio of the among-chain variance to the within-chain variance (Brooks and Gelman 1998). Chain mixing indicates how well multiple, independent Markovian chains converge on a similar range of values.

I used simulated data to examine the precision and accuracy of the MDAM. I compared true abundance and detection values I generated to the MDAM estimates of abundance and detection to measure precision and determine if the abundance values from the simulations contained the true abundance values. To assess the ability of the model to recover truth, I measured coverage, or the percent of time the 95% CRI of the MDAM estimates of abundance and detection included the known true values of abundance and detection. I measured accuracy by calculating the mean absolute percent error of the MDAM parameter estimates for abundance and detection. The mean absolute percent error was calculated as the absolute value of the difference between the true parameter value and MDAM parameter estimates divided by the true parameter value, all multiplied by 100. To ensure that the MDAM could accurately predict parameters under a wide range of possible survey outcomes, I ran the MDAM 100 times with different starting values.
each time. I summarized the results of the 100 simulations to assess overall MDAM performance.

**MDAM Extension**

Real world data often include more variation in both the biological and observational process than the basic MDAM structure describes. The MDAM can accommodate a wide variety of extensions to account for this variation, which allows for more accurate and precise inference about multispecies communities.

**Applying the MDAM Extension**

To test the applicability of potential MDAM extensions, I applied the MDAM to a two-year case study using eight avian species of prairie songbird communities in eastern Montana. I selected the eight species to represent the spectrum of vegetation use present in sagebrush ecosystems. They range from: species dependent entirely on sagebrush, Brewer’s sparrow (*Spizella breweri*); to species dependent entirely on grassland vegetation, chestnut-collared longspur (*Calcarius ornatus*), horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), McCown's longspur (*Rhynchophanes mccownii*), vesper sparrow (*Pooecetes gramineus*), and western meadowlark (*Sturnella neglecta*); to a species dependent on both sagebrush and grassland vegetation, the brown-headed cowbird (*Molothrus ater*). The structure of the MDAM extension is described below.

**Modeling Abundance**

True abundance of species *i* at plot *j* in year *y* (*N_{ijy}*), was modeled as a Poisson random variable with mean species abundance per plot in each year (*λ_{ijy}* (Equation 3). I included land ownership as a categorical covariate to account variation in the abundance of these eight species...
because it has been shown that variation in land management associated with land ownership can change the potential of a landscape to support biological communities (Scott et al. 2001). I let the effect of land ownership vary by species \( i \) to capture the variation in species’ responses to land-use practices or other variables associated with ownership. I used a log link function to relate land ownership to abundance using a linear predictor of mean species abundance per plot in each year \( (\lambda_{ijk}) \). I modeled the mean species abundance per plot in each year as a function of the linear combination of a species-specific intercept \( (\beta_{0i}) \), plus a fixed-effect of land ownership that varied by species \( (\beta_{1i}) \), a fixed effect for year that varied by species \( (\beta_{2i}) \), plus a random effect for plot \( (\alpha_j) \) to account for variation not otherwise explained (Equation 4).

Equation 3: Biological process

\[
N_{ijy} \sim \text{Poisson} \left( \lambda_{ijy} \right)
\]

Equation 4: Mean species abundance

\[
\log(\lambda_{ijy}) = \beta_{0i} + \beta_{1i} \times \text{land ownership} + \beta_{2i} \times \text{year} + \alpha_j
\]

I used vague normal distributions \( N(0, 1,000) \) for the priors of the coefficients of the linear predictor of the mean species abundance per plot in each year \( (\lambda_{ijy}) \). For the random plot effect, I used a uniform distribution ranging from 0 to 100 for the prior on the dispersion parameter.

**Modeling Observations**

I used the basic MDAM structure to model observations for the case study data. I modeled the observed abundance of species \( i \) at plot \( j \) in year \( y \) at survey replicate \( k \) \( (y_{ijk}) \) as a
multinomial random variable that is a function of true abundance ($N_{ijy}$) (Equation 3) and cell probabilities ($\pi_{ijk}$) based on the DDO surveys described above (Equation 2).

Equation 5: Observation process

$$y_{ijk} \sim \text{Multinomial} \left( N_{ijy}, \pi_{ijk} \right)$$

I accounted for variation in the observation process by including both individual observer effects and species effects. I did not include additional explanatory covariates in the observation process because additional sources of variation were reduced by using timing and weather restrictions for all DDO surveys, described in Case Study Data Set below. I used vague normal distributions N (0, 10,000) for the priors of detectability for each observer that informed the multinomial cell probabilities.

Case Study Data Set

Observers collected counts of the eight sagebrush songbird species described above using the DDO method during the peak songbird breeding season (May through July) in 2013 and 2014. The surveys were conducted on approximately 1,000 ha of private and public rangelands. This included 25 ha plots with 40 on private land and 40 on public land (a total of 80 plots) in Golden Valley and Musselshell counties, Montana, USA. The area is dominated by sagebrush (Artemisia tridentata spp. wyomingensis) and native grassland. The plot size was based on covering 125 m from a survey transect at all times (Figure 1-1), because $\geq 95\%$ of songbird detections are within 125 m of the observer (Ralph et al. 1995). Observers surveyed each plot three times (approximately once a month in May, June, and July) over the breeding season within a year. Surveys were conducted between approximately 0600 and 1100 hours. Surveys were not conducted during inclement weather or when winds were greater than 15 mph.
MDAM Extension Performance

I used the same specifications (three Markovian chains run for 50,000 iterations with a period of 5,000 burn-ins) as the basic MDAM to run the MDAM extension. Using program R and JAGS (see Appendix 1 for code), I generated over-dispersed starting values for three Markovian chains and ran them for 50,000 iterations with a period of 5,000 burn-in iterations that were discarded. I used visual inspection trace plots (King et al. 2010) and the $\hat{R}$ statistic (Brooks and Gelman 1998) to examine parameter convergence. I also examined the posterior density distributions to check for smooth, uni-modal posterior distributions. A uni-modal posterior distribution indicates that a single, predicted value of a parameter (the parameter estimate where the peak of the distribution occurs) has the highest probability of support.

MDAM Assumptions

Three main assumptions, based on the assumptions of the N-mixture model, underlie the MDAM: (1) the sampled population remains closed to immigration, emigration, birth and death for the duration of sampling activities; (2) individual and species’ detectability is constant among repeated sampling occasions; and (3) the data of the biological and observation processes are adequately described by the chosen distribution. To address assumption 1, I considered each period of time where it was biologically relevant to assume closure separately. For the simulated data, that was a single breeding season. For the case study data, I considered each breeding season separately and surveyed only adults during the peak breeding season for migratory songbirds in Montana (May through July) (Montana Bird Distribution Committee 2012). I modeled detectability as constant to address assumption 2 for simulated data. For the case study, I addressed assumption 2 by sampling over a short period of time, where it is likely that detection remained constant, and using standardized timing and weather restrictions for all DDO surveys
to minimize variation in detection probability. I addressed assumption 3 with the simulated data by simulating data that reflected the assumption of the distributions (i.e., animals were randomly distributed on the landscape). For the case study data I added covariates that explained extra variation not accounted for by the Poisson and multinomial distributions.

In addition to the two MDAM general assumptions, there are three associated with the DDO method: (3) primary observer detects individuals independent of the secondary observer; (4) each observer’s ability to detect individuals is the same for both the primary and secondary observer roles; and (5) primary and secondary observer have the same range of distance in which they can detect individuals (Nichols et al. 2000). I used a walking transect with the DDO method. This helped ensure independent detection by the primary observer and address assumption 3 because the primary observer was always walking in front of the secondary observer (Figure 1-1). I addressed assumption 4 by having the primary and secondary observers switch roles during consecutive surveys. Therefore, each observer spent roughly equal amounts of time in each role. To address assumption 5, I confined surveys to a fixed area, 125 m on either side of the survey transect (Figure 1-1), as suggested by Nichols et al. (2000).

**RESULTS**

**Basic MDAM**

The MDAM performed well with simulated data. The Markovian chain convergence was reached for abundance and detection by the 5,000 iteration burn-in period. Figure 1-2 (A) shows an example of the Markovian chain convergence for the abundance estimates for each hypothetical species. Good convergence is represented by chains with considerable overlap, so that all chains appear almost indistinguishable from one another. In addition, all \( \hat{R} \) values were near one (\(< 1.01\)). Values of \( \hat{R} \) close to 1 indicate that the Markovian chains have converged on
the single posterior value. Coverage for all abundance estimates for 100 repeated simulations was 0.943, meaning that 94.3% of the 95% CRI s of the predicted abundance values from the simulations contained the true abundance value. Coverage for detection was similarly high at 0.945. The MDAM also provided accurate estimates. The vast majority of abundance estimates (92.2%) had a mean absolute percent error between 0 and 20% (Table 1-2). The mean absolute percent errors for detection estimates were less than or equal to 5% (Table 1-3).

**MDAM Extension**

The MDAM extension performed well with the case study data. The Markovian chains convergence was reached for all parameters: abundance, detection, and effect of private land. Figure 1-2 (B) shows the chains for the predicted abundance of the avian species. In addition, all $\hat{R}$ values were near one (< 1.01). Posterior distributions were smooth and uni-modal, suggesting good model performance and predictive power. Figure 1-3 shows the posterior density distributions of the abundance estimates for the eight avian species that were analyzed with the MDAM.

The case study data consisted of 11,267 observations in 2013 and 12,175 observations in 2014 of the eight sagebrush songbird species (Table 1-4). In both 2013 and 2014 total observations were higher on private land (6,080 and 6,878, respectively) than public land (5,187 and 5,297, respectively), although this pattern differed by species. In 2013 and 2014, observers recorded more Brewer’s sparrows, brown-headed cowbird, lark bunting, vesper sparrow, and western meadowlark on public land than on private land. In contrast, in 2013 and 2014 there were more horned larks and McCown’s longspurs observed on private land than public land. The observed number of chestnut-collared longspurs was similar between land ownership and years.
Average detection probabilities varied greatly between observers and species, ranging from 0.006 to 0.79 (Figure 1-4). Lark buntings had the lowest average detection probability (0.05), followed by brown-headed cowbird (0.23), chestnut-collared longspur (0.27), vesper sparrow (0.37), western meadowlark (0.37), Brewer’s sparrow (0.39), horned lark (0.51), and McCown’s longspur (0.58).

Predicted abundance patterns were similar for 2013 and 2014 (Figure 1-5; Table 1-5). There were significantly more (i.e., CRIs did not overlap) individuals predicted on public land in 2013 for lark bunting and western meadowlark than private land. However, this pattern did not remain in 2014. The difference in abundance for both lark bunting and western meadowlark was not significant between public and private lands. On the other hand, there were significantly more McCown’s longspurs per 25 ha predicted on private land in 2013 and 2014 than public land. For all other species, brown-headed cowbird, Brewer's sparrow, chestnut-collared longspur, horned lark, and vesper sparrow, there was no significant difference in 2013 and 2014 between public land and private land (Table 1-5).

Land ownership had positive, negative, and neutral effects on the eight species examined (Figure 1-6). The results in the remainder of this section are presented as an estimate from the MDAM (on the link scale) and a 95% CRI in brackets. There was no significant effect (i.e., the CRI overlapped with 0 and the most support in posterior distribution was for values at or near 0 on the link scale) on the estimated abundance for two of the eight species examined: Brewer's sparrow (-0.05 [-0.30 – 0.18]) and vesper sparrow (-0.03 [-0.27 – 0.21]). Private land ownership had a significant positive effect on the predicted abundance of chestnut-collared longspur (0.43 [0.16 – 0.70]), horned lark (0.37 [-0.13 – 0.62]), and McCown's longspur (1.26 [1.02 – 1.51]). Private land ownership had a significant negative effect on three species: brown-headed cowbird
(-0.49 [-0.79 – -0.20]), lark bunting (-0.74 [-1.01 – -0.48]), and western meadowlark (-0.49 [-0.73 – -0.23]).

**DISCUSSION**

The MDAM extends previous MSAM models to include a removal-based survey method that reduces the rate of false positives. It provides flexibility for synthesizing multiple sources of data that are hindered by imperfect detection from biological (e.g., differences in abundance that arise from different land use) and observation process (e.g., observer performance). It does this all in a framework that accounts for imperfect detection. Although it is similar to the multinomial abundance model published by Kéry and Royle (2010) and the MSAM published by Chandler et al. (2013), it is the first to implement the DDO methodology to reduce the rate of false positives in the MSAM structure.

All performance diagnostics indicated that the MDAM was an accurate and faithful model. This is likely a result of the large amount of information from the DDO method used to model the observation process. This method provided detailed encounter history information for each individual that was detected during surveys. In the MDAM extension, each encounter history incorporated individual observer effects and species effects. The MDAM consistently predicted precise values that contained the true parameters the majority of the time when it was run 100 times with different starting values, indicating that the predications are reliable. Similarly, the convergence diagnostics and posterior distributions of the MDAM extension indicated that the MDAM extension converged well on posterior distribution estimates.

The predictions of the MDAM extension were biologically sound and congruent with other studies. The community composition of this prairie system predicted by the MDAM extension is similar to songbird communities in nearby sagebrush and mixed-grass communities (Bradford et
al. 1998; Reinkensmeyer et al. 2007; Jones et al. 2010). The most abundant species, McCown’s
longspur, western meadowlark, vesper sparrow, and Brewer’s sparrow, were consistent with
other findings (Bradford et al. 1998; Jones et al. 2010). I found that land ownership had a neutral
or positive effect on predicted abundance for the majority of species, five of eight, which I
investigated. The positive effect of private land on chestnut-collared longspur, horned lark, and
McCown’s longspur abundance was consistent with other findings about private lands, which
often support more species than public or protected lands (Scott et al. 2001).

The MDAM provides many benefits that resulted from both the MDAM model structure and
the DDO survey method. The MDAM structure does not require replication at some sample plots
like other MSAMs because of the detectability information contained within the DDO
observations. Therefore, it is possible that field efforts could be reduced with similar information
yield, which is useful when trying to allocate limited personnel and financial resources. Using
the DDO method, observers can work together to identify a bird and ensure double counting is
not occurring, which has the ability to reduce false positives. The ability of the observers to work
together on identification, with the stipulation that the observation outcome has to be correctly
recorded, also allows new observers to be quickly trained in bird identification. In addition,
working in pairs for the DDO method in remote field locations provides a safety advantage.

The MDAM structure is generalizable and can be applied to many different systems to
estimate multispecies abundance. The multispecies abundance data from the MDAM can be used
to derive abundance-based biodiversity metrics that summarize species richness and evenness, or
relative abundance to other species. It is possible to relax many of the assumptions of the
MDAM presented in this paper. For example, the assumption that every species is available for
sampling during the observation process is unrealistic (Dorazio and Royle 2005). However, this
can be addressed in the MDAM by adding in another level to the hierarchical model that represents the animal’s availability, as described by Kéry and Schaub (2012). In my case study example, the only explanatory covariate for latent abundance is land ownership, which may not be realistic in many ecosystems (Lovett-Doust and Kuntz 2001). The MDAM can accommodate additional biotic or abiotic covariates that might be plot- and ecosystem-specific and help explain variation in abundance. In addition, the reliable abundance estimates from the MDAM can be used in an integrated population model (Kéry and Schaub 2012). This can provide a much clearer picture of the mechanisms driving changes in abundance and biodiversity. The MDAM can also be used to concurrently track the abundance of a single species and a biodiversity parameter of interest. If monitored over multiple seasons, this can provide a potential method to determine if a focal species reliably tracks changes in a community. Finally, although the DDO was developed as a bird survey method (Nichols et al. 2000), it can be used on additional taxa. Double-observer methods have already been used for marine and terrestrial mammals (Buckland et al. 2010; Griffin et al. 2013; Hoef et al. 2014) and amphibians (Becker et al. 2013).

There are some important limitations of the MDAM to consider. First, I was not able to quantify the extent to which the DDO method reduces false positives. As Nichols et al. (2000) stated, two observers, rather than a single observer making a decision about the identity or presence of a species, is an improvement in reducing false positives. In addition, the assumption that detection probability is the same for an observer whether they are in the role of primary or secondary observer (assumption 5) may not be true. Mills and Knowlton (1989) showed that observer performance improves when observers are aware they are being monitored.

The patterns of abundance of multiple species are fundamental to understanding biodiversity. The MDAM provides a framework of reliable multispecies abundance predictions, which I have
shown using simulated and case-study data, and can accommodate extensions that have important implications for conservation. The MDAM has the flexibility to incorporate long-term, large-scale, and multi-taxon data. It can provide data-driven solutions to reduce cost and effort put into biodiversity monitoring while still providing accurate, high-resolution data. In addition, there may be further extensions of the MDAM, such as methods to quantify the rates of false positives, which would allow for an unprecedented accuracy in multispecies monitoring. Given the field and data benefits of the MDAM and its ability to accommodate extensions, the MDAM can be an instrumental tool for the future of biodiversity conservation.
Literature Cited


**FIGURES AND TABLES**

**Figure 1-1.** Dependent double-observer method. The primary (open circle) and secondary observer (dashed circle) walk single-file along the transect (dotted line) within a 500 m x 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.
Figure 1-2. Trace plots showing all of the values of the three Markovian chains during the 50,000 iterations run for eight avian species. The x-axis represents the number of iterations after a burn in period of 5,000 iterations (not pictured) and the y-axis represents the value of the chain. A) Trace plots of abundance estimates (lambda) for four species (identity represented by the number in brackets []) derived from simulated data. B) Trace plots of non-transformed (log) mean abundance value for each species ($\lambda_{ijk}$) from data collected near Roundup, Montana in 2013 and 2014.
Figure 1-3. The posterior distribution estimates of average abundance in 2013 on public land for eight avian species. Estimates are derived using the multispecies dependent double-observer abundance model and data collected near of Roundup, Montana in 2013.
Figure 1-4. The average probability (right y-axis) that an individual observer (x-axis) detected each avian species (left y-axis) during dependent double-observer surveys conducted on public and private lands near Roundup, Montana, in 2013 and 2014. Black bars represent the 95% Bayesian credible intervals of the estimate.
Figure 1-5. The average estimated abundance per 25 ha on public and private land for eight avian species. Black bars represent the 95% Bayesian credible intervals of the estimate. Predictions are derived from the multispecies dependent double-observer abundance model using data collected near Roundup, Montana in 2013 and 2014.
Figure 1-6. The effect of private land ownership on average abundance compared to public land ownership for eight songbird species on public and private lands near Roundup, Montana, in 2013 and 2014. The effect values are on the link scale.
Table 1-1. Two processes, biological and observation, influence the two components of detection, availability and detectability. Detection error results from two specific combinations of these two processes.

<table>
<thead>
<tr>
<th>Biological Process</th>
<th>Observation Process</th>
<th>Detection error present?</th>
<th>Detection Outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Availability¹</td>
<td>Detectability²</td>
<td>Observation</td>
<td></td>
</tr>
<tr>
<td>Available (present)</td>
<td>Detected</td>
<td>No</td>
<td>True positive</td>
</tr>
<tr>
<td></td>
<td>Not detected</td>
<td>Yes</td>
<td>False negative</td>
</tr>
<tr>
<td>Not available (not present)</td>
<td>Detected</td>
<td>Yes</td>
<td>False positive</td>
</tr>
<tr>
<td></td>
<td>Not detected</td>
<td>No</td>
<td>True negative</td>
</tr>
</tbody>
</table>

¹The probability that an individual is present and available for observation at a plot. Independent of detectability.
²The probability an observer detects an individual. Dependent on availability.
**Table 1-2.** Mean absolute percent error for abundance estimates from the multispecies dependent double-observer abundance model. Data were simulated 100 times for four species surveyed on 20 plots three times over a season by two observers.

<table>
<thead>
<tr>
<th>Mean absolute percent error</th>
<th>% of simulations$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-20</td>
<td>92.2</td>
</tr>
<tr>
<td>21-40</td>
<td>5.7</td>
</tr>
<tr>
<td>41-60</td>
<td>1.1</td>
</tr>
<tr>
<td>61-80</td>
<td>0.5</td>
</tr>
<tr>
<td>81-100</td>
<td>0.2</td>
</tr>
<tr>
<td>&gt;100</td>
<td>0.3</td>
</tr>
</tbody>
</table>

$^1$% of simulations represents the percent of simulations out of 8,000 that fall within the given range.
Table 1-3. Mean absolute percent error for detection probability estimates from the multispecies dependent double-observer abundance model. Data were simulated 100 times for four species surveyed on 20 plots three times over a season by two observers.

<table>
<thead>
<tr>
<th>Mean absolute percent error</th>
<th>% of simulations¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>51.0</td>
</tr>
<tr>
<td>2</td>
<td>30.5</td>
</tr>
<tr>
<td>3</td>
<td>14.5</td>
</tr>
<tr>
<td>4</td>
<td>3.5</td>
</tr>
<tr>
<td>5</td>
<td>0.5</td>
</tr>
</tbody>
</table>

¹% of simulations represents the percent of simulations out of 200 that fall within the given range.
Table 1-4. Summary of observations of eight sagebrush songbirds surveyed using the dependent double-observer method in 2013 and 2014 near Roundup, MT. Plots refers to the number of plots out of 40 in which the species was detected. Observed refers to the total number of individuals observed during the three sampling occasions.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>2013 Public</th>
<th>2013 Private</th>
<th>2014 Public Land</th>
<th>2014 Private</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plots</td>
<td>Observed</td>
<td>Plots</td>
<td>Observed</td>
</tr>
<tr>
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<td>35</td>
<td>979</td>
<td>27</td>
<td>804</td>
</tr>
<tr>
<td>Brown-headed cowbird</td>
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<td>200</td>
<td>17</td>
<td>90</td>
</tr>
<tr>
<td>Chestnut-collared longspur</td>
<td>16</td>
<td>168</td>
<td>19</td>
<td>272</td>
</tr>
<tr>
<td>Horned lark</td>
<td>33</td>
<td>597</td>
<td>37</td>
<td>1,015</td>
</tr>
<tr>
<td>Lark bunting</td>
<td>17</td>
<td>345</td>
<td>17</td>
<td>113</td>
</tr>
<tr>
<td>McCown’s longspur</td>
<td>18</td>
<td>1,037</td>
<td>31</td>
<td>2,450</td>
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<tr>
<td>Vesper sparrow</td>
<td>39</td>
<td>1,066</td>
<td>39</td>
<td>936</td>
</tr>
<tr>
<td>Western meadowlark</td>
<td>40</td>
<td>795</td>
<td>40</td>
<td>400</td>
</tr>
<tr>
<td>Totals</td>
<td>5,187</td>
<td>6,080</td>
<td>5,297</td>
<td>6,878</td>
</tr>
</tbody>
</table>
Table 1-5. The average estimated abundance ($\bar{N}$) and ninety-five percent credible intervals (CRI) per 25 ha on public and private land for eight avian species. Predictions are derived from the multispecies dependent double-observer abundance model using data collected near Roundup, Montana in 2013 and 2014.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
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<th></th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{N}$</td>
<td>95% CRI</td>
<td>$\bar{N}$</td>
<td>95% CRI</td>
<td>$\bar{N}$</td>
<td>95% CRI</td>
<td>$\bar{N}$</td>
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<td>3.9-6.9</td>
<td>3.2</td>
<td>2.3-4.3</td>
<td>6.8</td>
<td>4.1-11.0</td>
<td>4.2</td>
<td>2.5-6.9</td>
</tr>
<tr>
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<td>3.0</td>
<td>2.3-3.7</td>
<td>4.6</td>
<td>3.7-5.7</td>
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<td>1.4-2.9</td>
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<td>2.2-4.5</td>
</tr>
<tr>
<td>Horned lark</td>
<td>11.3</td>
<td>9.4-13.4</td>
<td>16.4</td>
<td>13.6-19.5</td>
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<td>11.5-17.9</td>
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<td>16.7-26.0</td>
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<tr>
<td>Lark bunting</td>
<td>21.5</td>
<td>15.1-30.8</td>
<td>10.2</td>
<td>6.9-15.0</td>
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<td>1.1-3.6</td>
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<tr>
<td>McCown’s longspur</td>
<td>13.0</td>
<td>10.8-15.5</td>
<td>46.2</td>
<td>38.8-54.6</td>
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<td>Vesper sparrow</td>
<td>18.2</td>
<td>15.1-21.7</td>
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<td>14.6-21.0</td>
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<tr>
<td>Western meadowlark</td>
<td>16.0</td>
<td>13.1-19.4</td>
<td>9.8</td>
<td>8.0-12.0</td>
<td>24.9</td>
<td>18.8-32.6</td>
<td>15.3</td>
<td>11.5-20.1</td>
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</tbody>
</table>
CHAPTER 2: ASSESSING SONGBIRD RESPONSE TO COMMON GRAZING PRACTICES

INTRODUCTION

Livestock grazing is one of the most common land uses worldwide (Raven 2002). In the United States, grazing occurs on approximately 40 percent of total land (Holechek et al. 1998) and approximately 70 percent of land in the west (Fleischner 1994). Livestock grazing directly affects vegetation by altering plant species composition and physical plant structure (Olff and Ritchie 1998; Briske et al. 2008; Lwiwski et al. 2015). Through the consumption of vegetation, livestock directly and indirectly affect the amount of vegetation available in an ecosystem. This has led some to suggest that livestock function as “ecosystem engineers” (Derner et al. 2009). Livestock grazing offers many benefits to a variety of stakeholders ranging from conservation practitioners to private land owners. In many landscapes with no formal protection, the continued use of landscapes for grazing represent a favorable alternative for native wildlife when compared with other land uses such as cropland. In addition, livestock grazing can provide both economic and cultural benefits to land owners. As a result, grazing easements and federal programs that support livestock grazing are quickly becoming a widely used conservation management tool. For example, in the western United States, grazing programs that are thought to be beneficial to wildlife are being implemented on over 2 million acres in 11 states (NABCI 2013).

Despite these known advantages, the effects of different grazing systems, or how domestic livestock are moved throughout a landscape, on native wildlife remain relatively unexplored (Krausman et al. 2009). It is important to understand these effects in ecosystems that have been extensively fragmented. In these ecosystems, often the only remaining native vegetation persists on lands that are grazed by livestock. Sagebrush (Artemisia spp.) ecosystems have undergone extensive conversion to fragmentation from factors such as cropland conversion and urbanization (Knick et al. 2003). The remaining sagebrush landscapes are almost entirely grazed by livestock.
Knick et al. (2003) reported that “virtually all sagebrush lands are managed principally for livestock grazing.” Species that depend on this sagebrush ecosystems must therefore exist on lands with livestock grazing. In addition, large-scale grazing management programs, such as the Sage Grouse Initiative funded by the Natural Resource Conservation Service (NRCS) have implemented grazing management over a large portion of the western United States (NRCS 2015).

Unfortunately, there are few comparisons of the relative effects of different livestock grazing systems on wildlife. Many studies that examine the effect of livestock grazing on wildlife tend to compare livestock grazing in an area to an area without livestock grazing (e.g., Bock and Webb 1984; Harrison et al. 2010; Nelson et al. 2011). Many of these investigations focus on the abundance of a single species (Krausman et al. 2009), providing only a partial measure of grazing impacts to wildlife (Briske et al. 2008). Using multiple species to assess grazing is important because different livestock grazing systems are likely to differentially affect a variety of species with diverse life history strategies (Bock et al. 1993; Krausman et al. 2009). For example, in a summary of grazing studies, Bock et al. (1993) noted that a group of ten songbird species showed a positive response to moderate levels of livestock grazing but a negative response to heavy grazing, dependent on the type of grassland vegetation. In addition, studies often do not consider multiple types of land ownership, which can have a significant effect on management practices (Sorice et al. 2014). This is important in arid lands, including sagebrush ecosystems, where ownership in the lower 48 states of the United States is 39% privately owned and 54% publically owned (NABCI 2013). Finally, many livestock grazing assessments do not measure attributes relevant to land managers. Studies often use vegetation metrics related to wildlife, whereas rangeland managers are typically interested in larger-scale metrics related to
livestock production (Henderson and Davis 2014). A multispecies, multiple land-ownership comparison of livestock grazing systems based on common livestock grazing practices in sagebrush ecosystems offers much needed information.

Songbirds in sagebrush ecosystems are an excellent study system to explore the effects of different livestock grazing systems for many reasons. Songbirds are widespread and accessible for monitoring throughout sagebrush ecosystems, sensitive to habitat change, respond to grazing, and have declined concurrently with the increase of livestock production on rangelands (Bradford et al. 1998; Canterbury et al. 2000; Fuhlendorf and Engle 2001; Coppedge et al. 2006; Coppedge et al. 2008). Changes in songbird abundance are also ecologically important because they play an integral role in ecological communities: they interact with other species as predators, prey, pollinators and seed dispersers (Murphy and Romanuk 2012). In addition, many sagebrush ecosystem birds are designated as species of conservation concern by local, regional, or national organizations (Rich et al. 2004; Montana Natural Heritage Program 2014; IUCN 2015). Overall, many sagebrush songbirds have been steadily declining (Knick and Rotenberry 1995; Knick et al. 2003). Since 2010, bird populations in sagebrush ecosystems and other arid lands have been declining faster than in any other ecosystem in the lower 48 states of the United States (NABCI 2014). Finally, sagebrush ecosystem songbirds exhibit a varying degree of reliance on grassland vegetation, an important component of sagebrush ecosystems (Rich et al. 2005). They range from: grassland obligates, species that use grassland for the majority of their life history needs; to facultative grassland species, which use grassland in addition to other vegetation to meet their life history needs; to sagebrush obligates, species that use sagebrush for the majority of their life history needs.
A large body of evidence suggests that grassland obligate songbirds respond to structural heterogeneity in grassland vegetation (Davis and Duncan 1999; Fisher and Davis 2010). Structural heterogeneity provides an advantage to grassland birds by offering a range of conditions for nest concealment and foraging (Henderson and Davis 2014). Different grazing systems affect the structural heterogeneity of grassland vegetation (Fuhlendorf and Engle 2001). However, it is unclear if differences in structural heterogeneity produced by different grazing systems are large enough to change songbird abundance. Given this uncertainty, the fact songbirds in sagebrush ecosystems depend almost exclusively on landscapes that are grazed by livestock, and the large-scale grazing programs in sagebrush ecosystems that implement conservation grazing, I address the question: how does grazing system influence songbird communities in sagebrush ecosystems?

To answer this question, I use two grazing systems known to result in differences in vegetative structural heterogeneity. Traditional and rest-rotation are two widely implemented grazing systems in the United States (Briske et al. 2008; Holechek et al. 1999). Traditional grazing involves the continuous presence of livestock in the same pasture during a growing season (e.g., May through November) repeatedly over multiple years. Rest-rotation grazing, in contrast, involves alternating 15 to 18 month rotations of continuous grazing and rest within a pasture. Traditional grazing results in higher vegetation structural heterogeneity than rest-rotation grazing on both local- and broad-scales (Fuhlendorf and Engle 2001). 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.
I use eight songbird species that represent varying degrees of grassland use in sagebrush ecosystems ranging from grassland to sagebrush obligates (Paige and Ritter 1999) (Table 2-1): Brewer’s sparrow (*Spizella breweri*), brown-headed cowbird (*Molothrus ater*), chestnut-collared longspur (*Calcarius ornatus*), horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), McCown's longspur (*Rhynchophanes mccownii*), vesper sparrow (*Pooecetes gramineus*), and western meadowlark (*Sturnella neglecta*). I test the hypothesis that songbirds respond to grazing (i.e., the structural heterogeneity caused by grazing) based on their reliance on grassland vegetation. I predict that grassland obligate species are more abundant in the grazing system that produced more structural heterogeneity, traditional grazing. In addition, I predict that the strength of the effect of traditional grazing on the difference in abundance depends on how much species depends on grassland. Thus grassland obligates will show a stronger response than facultative species or generalists. Finally, I predict that sagebrush obligate species show no difference in abundance between the two grazing systems because they are not closely tied to changes in grassland structural heterogeneity and livestock grazing is not known to affect sagebrush shrubs (Veblen et al. 2015).

Songbird abundance may be affected by a variety of other factors operating independent of variability in grassland 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, I consider an index of biomass potential produced by NRCS. The index relates abiotic factors, including soil and climate, to the ability of the land to produce biomass. Preliminary analysis determined that biomass potential was different between traditional and rest-rotation grazing systems (Appendix 2); thus, the influence of biomass
potential was included as a covariate to account for additional sources of heterogeneity within grazing systems. To account for additional spatial and temporal variation in abundance, I include parameters for sampling plot and year. Many species respond to management actions differently because of different life history requirements (Lindenmayer et al. 2002). Therefore, I assume the effects of grazing and these additional covariates on abundance each vary by species, as described below. I use a modified multispecies abundance model, the multispecies dependent-double observer abundance model (MDAM), to track changes in abundance of multiple sagebrush songbird species. The MDAM uses removal methodology in a Bayesian framework to estimate detection and adjusted abundance estimates of multiple species (see Chapter 1). With this study, I provide a critical comparison for land managers on how a group of wildlife species respond to two widely used grazing systems.

METHODS

Field Methods

Study Area

I conducted this study across 89,000 ha of sagebrush grassland habitat in Golden Valley and Musselshell Counties near Roundup, Montana. I 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 0.34 m and the highest amount of precipitation occurring in May. 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 habitat.

**Field Sampling**

I randomly selected 40 sampling plots that were 500 m x 500m (25 ha) in each of the two grazing systems, for a total of 80 sample plots. A size of 25 ha was chosen following Tipton et al. (2008 and 2009). My goal was to obtain a sample of plots that were representative of grassland and sagebrush songbird habitat in the study area. Therefore, I 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, I excluded plots that included county roads. If a plot was excluded, I selected another random plot to sample so that I maintained 40 sampling plots in each grazing system. Traditional grazing plots were located on public lands managed by US Department of Interior Bureau of Land Management (BLM). Rest-rotation plots were located on private lands that are enrolled in a conservation program that employs rest-rotation grazing.

Bird survey data were collected during the peak songbird breeding season in Montana from May through July in 2013 and 2014. Sampling plots were surveyed three times (approximately once a month in May, June, and July) to capture the beginning, middle, and end of the breeding season. I used dependent double-observer transect (DDOT) survey method to obtain abundance estimates of eight bird species.

The DDOT survey method involved two observers who walked along a transect: a primary observer who walked in front, and a secondary observer, who walked approximately 3 to 5 m behind the primary observer. The observers started the survey on the southeast transect corner of each plot and walked along the transect surveying 125 m on either side of the transect (Figure 2-1). I chose a distance of 125 m because ≥95% of songbird detections occur within 125 m of an
observer (Ralph et al. 1995). Following Nichols et al. (2000), 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 the primary observer missed. If an auditory detection occurred, an observer was required to get visual confirmation of the bird. The observers switched roles after each survey. Surveys were conducted between approximately 0600 and 1100 hours. Surveys were not conducted during inclement weather or when winds were greater than 15 mph.

Statistical Analysis

Modeling Abundance

I modeled true 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 \( (\lambda_{ijy}) \) (Equation 1). I used a log link function to relate grazing and additional explanatory covariates to abundance using a linear predictor of mean species abundance \( (\lambda_{ijy}) \) (Equation 2). I modeled the mean species abundance per plot in each year as a function of the linear combination of a species-specific intercept \( (\beta_0) \), plus a fixed-effect of grazing system that varied by species, \( (\beta_1) \), a fixed effect for biomass potential that varied by species \( (\beta_2) \), a fixed effect for year that varied by species \( (\beta_3) \), plus a random effect for plot \( (\alpha_j) \) to account for variation not otherwise explained (Equation 2).

Equation 1: Biological process

\[ N_{ijy} \sim \text{Poisson} (\lambda_{ijy}) \]
Equation 2: Mean species abundance

\[ \log(\lambda_{ijy}) = \beta_{0i} + \beta_{1i} \times \text{grazing type} + \beta_{2i} \times \text{biomass potential} + \beta_{3i} \times \text{year} + \alpha_j \]

I used vague normal distributions \( N(0, 1,000) \) for the priors of the coefficients of the linear predictor of mean species abundance \( \lambda_{ijy} \). For the random plot effect \( \alpha_j \), I used a uniform distribution ranging from 0 to 100 for the prior on the dispersion parameter.

**Modeling Observations**

The DDOT survey method produces observations with three possible outcomes: 1) the primary observer detects an individual; 2) the secondary observer detects an individual the primary observer misses; and 3) both the primary and secondary observer do not detect an individual. Each of these outcomes has a different probability of occurring because they are based on a combination of events resulting from two observers. Outcome 1 is based only on the primary observer’s ability to detect an individual \( p_1 \). Outcome 2 is a product of the probability that the primary observer did not detect an individual, \( 1 - p_1 \), and the secondary observer’s ability to detect an individual \( p_2 \). Outcome 3 is a product of neither observer detecting an individual \( (1 - p_1) \times (1 - p_2) \). Because this process has multiple outcomes with multiple probabilities, I considered it a multinomial process. I modeled the observed abundance, \( y_{ijky} \), of species \( i \) at plot \( j \) in year \( y \) at survey replicate \( k \) as a function of a multinomial random variable that is a function of latent abundance, \( N_{ijy} \) (Equation 1), and three multinomial cell probabilities \( \pi_{ijk} \) that represent the DDOT survey outcomes described above (Equation 3).

Equation 3: Observation process

\[ y_{ijky} \sim Multinomial \left( N_{ijy}, \pi_{ijk} \right) \]
I accounted for variation in the observation process by including both individual observer effects and species effects. I used vague normal distributions N (0, 10,000) for the prior distributions of detectability for each observer and species that informed the multinomial cell probabilities.

**Results**

Two-person field teams completed a total of 478 DDOT surveys in 2013 and 2014. Each year, teams conducted 240 surveys per grazing system, with the exception of rest-rotation grazing in 2013, when there were 238 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 prairie avian species (Table 2-2). In both 2013 and 2014, total observations were higher in rest-rotation (6,080 and 6,878, respectively) than traditional grazing (5,187 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 traditional 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 traditional grazing. There was no clear pattern for chestnut-collared longspur: more were observed in rest-rotation grazing in 2013, but this was reversed in 2014.

The effect of year was neutral (i.e., the CRI overlapped with 0 and the most support in posterior distribution was for values at or near 0 on the link scale) for most species considered (Table 2-3; Figure 2-2). Therefore, the results presented in this section are based on the 2013 sampling year. Compared to traditional grazing, the effect (presented on a log scale) of rest-rotation grazing on abundance was neutral for half of the species examined (Table 2-3): Brewer’s sparrow, chestnut-collared longspur, horned lark, and vesper sparrow. 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 (presented on a log scale) of biomass potential on abundance was positive for six of the eight species examined (Table 2-3): brown-headed cowbird, chestnut-collared longspur, horned lark, lark bunting, McCown’s longspur, and western meadowlark. The effect was negative for Brewer’s sparrow. For vesper sparrow the effect was neutral (Figure 2-3).

Songbird abundance differed between the two grazing systems (Figure 2-4) when accounting for the effect of biomass potential and year. All abundance estimates presented in this section are the average predicted number of individuals of a species per 25 ha sampling plot. I considered abundance to be different between the two grazing systems if the CRI’s for the predicted abundance did not overlap (i.e., it was 100% likely that the abundances were different) (Figure 2-5). 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 2-3; Figure 2-4). Three species were on average more abundant per 25 ha in traditional grazing than rest-rotation grazing: brown-headed cowbird, lark bunting, and western meadowlark. McCown’s longspur, on the other hand, was more abundant per 25 ha in rest-rotation grazing than traditional grazing systems. The remaining four species showed no difference (i.e., CRI’s 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 (Figure 2-6). Overall, grazing system appeared to have a larger effect on abundance than biomass potential (i.e., the difference between the predicted abundance for each grazing system was
larger than the difference in abundance predicted over all of the biomass potential values present) for brown-headed cowbird (at low values of biomass potential), 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.

**DISCUSSION**

My findings, in general, support my predictions. Overall facultative and grassland obligate species were either more abundant on traditional grazing systems 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 my predictions. McCown’s longspur, a grassland obligate, was more abundant on rest-rotation that is suggest to have less grassland structural heterogeneity than on traditional grazing. Biomass potential had a positive effect on six out of the eight species and the relative role compared to grazing varied by species. This is consistent with other studies in sagebrush and grassland ecosystems, which suggest abiotic factors play an important role in determining abundance (Wiens and Rotenberry 1980), interact with grazing, and vary by individual species (Lipsey 2015). It is important to note that survey teams observed all species in both grazing treatments, although there were differences in the number observed between the two grazing systems.

Some grassland obligate species, lark bunting and western meadowlark, were more abundant on traditional grazing systems, where there is more grassland vegetation structural heterogeneity. This is consistent with other work on grassland birds (Fisher and Davis 2010). Both of these species nest and forage on the ground; a wide variety of grassland 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 traditional grazing systems. 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 songbirds. Thus, my findings were consistent with what I predicted that this species would be most abundant in areas where grassland songbirds are likely to be more abundant (i.e., traditional grazing systems).

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 traditional grazing. This may represent the incredible variability grassland 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 birds. This variation may also explain why the strength of the influences of traditional grazing did not follow my prediction that grassland obligate species would respond more strongly than facultative grassland species.

The response of McCown’s longspur is counter to my predictions. McCown’s longspur showed a clear difference in abundance between the two grazing systems: on average it was more than twice as abundant per 25 ha in rest-rotation grazing than traditional grazing. Based on observations, it would seem that McCown’s longspur are not as widespread on traditional grazing systems. Over two years of the study, McCown’s longspurs were only seen on roughly half of the plots in traditional grazing systems, whereas they were seen on roughly 75% of the
plots in rest-rotation grazing systems. 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. I consistently observed large colonies of nesting McCown’s longspurs in the study area with few other songbird species present. In addition, McCown’s longspurs prefer very short grassland vegetation (Knopf 1996; Sedgwick 2004). Although they appear to have the same requirements as other grassland songbirds in the study (e.g., require grassland vegetation for nesting and foraging, nest on the ground), the need for short grass may override the need for structural heterogeneity that other grassland birds require. 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 will nest in areas where individuals are already present).

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 one species, Brewer’s sparrow, showed a negative response to biomass potential. This is likely because Brewer’s sparrow depend completely on sagebrush, a shrub known for growing in poor, unproductive soil. For vesper sparrow the effect of range quality was essentially neutral, which is consistent with the description of this species as a generalist (Jones and Cornley 2002).

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 these grazing systems. The long term effects of vegetation changes and songbird associations are likely complex in sagebrush ecosystems. For example, Rotenberry and Wiens (2009) found that vegetation associations of
sagebrush songbirds from a six year study were not predictive of habitat associations in the same study area 14 years later. Secondly, although I attempted to capture a range of avian responses with the eight species I selected, eight species may not capture all of the variety of breeding songbirds within the sagebrush grassland bird community. Given that grazing primarily effects grassland and not sagebrush vegetation, the choice of species was a good representation of the community of species likely to be affected by grazing. Finally, pasture size is an important component of grazing management (McGranahan et al. 2013). I did not consider this as part of my study because of the variability that was present in both grazing systems. Given this variability, I did not expect that on average pasture size would be different between the two grazing systems.

This study provided an important first step in comparing rest-rotation and traditional grazing in sagebrush ecosystems. I used a group of eight species that were largely representative of the grassland obligate songbirds in this community. Although I do not expect these grazing systems to have much of an effect on sagebrush species, future work should continue to explore sagebrush obligates. The responses of these species suggest that their vegetation preferences are closely tied to breeding activity, which I did not investigate. Future work that measures total reproductive output (a product of nest density and nest success) in these grazing systems may illuminate underlying processes driving these changes in abundance. I used a novel modeling and survey approach, the MDAM, which can incorporate this type of extension. Grazing is often assumed to have universal consequences for an ecosystem. However, this study demonstrates that any grazing system is unlikely to have similar consequences for all species. This represents an important consideration for managers thinking about how a broad, widely applied activity like grazing can support numerous species.
**LITERATURE CITED**


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http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/geo/?cid=nrcs142p2_05361


**Figure 2-1.** 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 x 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.
Figure 2-2. The posterior distributions of the estimated effect of rest-rotation grazing (log scale on the x-axis) compared to traditional grazing on abundance of species per 25 ha eight sagebrush songbird species. The percentages in each distribution represent the percent chance that the effect of rest-rotation grazing is positive. Estimates are derived from data collected near Roundup, Montana, in 2013 using the multispecies dependent double-observer abundance model.
Figure 2-3. The posterior distributions of the estimated effect of biomass potential (log scale on the x-axis) on abundance of species per 25 ha for eight sagebrush songbird species. The percentages in each distribution represent the percent chance that the effect of biomass potential is positive. Predictions are derived from data collected near Roundup, Montana, in 2013 using the multispecies dependent double-observer abundance model.
Figure 2-4. The estimated abundance of species per 25 ha for eight sagebrush songbird species in rest-rotation and traditional grazing systems. Estimates are derived from data collected near Roundup, Montana, in 2013 using the multispecies dependent double-observer abundance model.
**Figure 2-5.** The posterior distributions of the estimated abundance per 25 ha for eight sagebrush songbird species in rest-rotation and traditional grazing systems. Predictions are derived from data collected near Roundup, Montana, in 2013 using the multispecies dependent double-observer abundance model.
Figure 2-6. The log of 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.
Table 2-1. Eight sagebrush ecosystem songbird species, their vegetation association, uses for grassland vegetation, and predicted response of rest-rotation compared to traditional grazing systems on public and private land near Roundup, Montana, in 2013 and 2014.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Vegetation association</th>
<th>Uses for grassland vegetation</th>
<th>Predicted response to grazing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brewer’s sparrow</td>
<td><em>Spizella breweri</em></td>
<td>Sagebrush obligate²</td>
<td>Occasional foraging</td>
<td>Neutral</td>
</tr>
<tr>
<td>Brown-headed cowbird</td>
<td><em>Molothrus ater</em></td>
<td>Facultative grassland¹</td>
<td>Occasional nesting, foraging</td>
<td>Neutral to negative</td>
</tr>
<tr>
<td>Chestnut-collared longspur</td>
<td><em>Calcarius ornatus</em></td>
<td>Grassland obligate¹</td>
<td>Nesting, foraging</td>
<td>Negative</td>
</tr>
<tr>
<td>Horned lark</td>
<td><em>Eremophila alpestris</em></td>
<td>Grassland obligate¹</td>
<td>Nesting, foraging</td>
<td>Negative</td>
</tr>
<tr>
<td>Lark bunting</td>
<td><em>Calamospiza melanocorys</em></td>
<td>Grassland obligate¹</td>
<td>Nesting, foraging</td>
<td>Negative</td>
</tr>
<tr>
<td>McCown’s longspur</td>
<td><em>Rhynchophanes mccownii</em></td>
<td>Grassland obligate¹</td>
<td>Nesting, foraging</td>
<td>Negative</td>
</tr>
<tr>
<td>Vesper sparrow</td>
<td><em>Pooecetes gramineus</em></td>
<td>Generalist³</td>
<td>Occasional nesting*, foraging</td>
<td>Neutral</td>
</tr>
<tr>
<td>Western meadowlark</td>
<td><em>Sturnella neglecta</em></td>
<td>Grassland obligate¹</td>
<td>Nesting, foraging</td>
<td>Negative</td>
</tr>
</tbody>
</table>

¹ Vickery et al. 1999.
² Paige and Ritter 1999.
³ Jones and Cornley 2002.
**Table 2-2.** Summary of observations of eight birds surveyed using the dependent double-observer transect method in 2013 and 2014 in rest-rotation and traditional grazing systems near Roundup, MT.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Brewer’s sparrow</td>
<td>35</td>
<td>979</td>
<td>27</td>
<td>804</td>
</tr>
<tr>
<td>Brown-headed cowbird</td>
<td>30</td>
<td>200</td>
<td>17</td>
<td>90</td>
</tr>
<tr>
<td>Chestnut-collared longspur</td>
<td>16</td>
<td>168</td>
<td>19</td>
<td>272</td>
</tr>
<tr>
<td>Horned lark</td>
<td>33</td>
<td>597</td>
<td>37</td>
<td>1,015</td>
</tr>
<tr>
<td>Lark bunting</td>
<td>17</td>
<td>345</td>
<td>17</td>
<td>113</td>
</tr>
<tr>
<td>McCown’s longspur</td>
<td>18</td>
<td>1,037</td>
<td>31</td>
<td>2,450</td>
</tr>
<tr>
<td>Vesper sparrow</td>
<td>39</td>
<td>1,066</td>
<td>39</td>
<td>936</td>
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<tr>
<td>Western meadowlark</td>
<td>40</td>
<td>795</td>
<td>40</td>
<td>400</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>5,187</td>
<td>6,080</td>
<td><strong>5,297</strong></td>
<td><strong>6,878</strong></td>
</tr>
</tbody>
</table>
Table 2-3. 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 traditional grazing near Roundup, Montana in 2013 and 2014.

<table>
<thead>
<tr>
<th>Species</th>
<th>Grazing(^1)</th>
<th>Biomass potential(^2)</th>
<th>Year(^3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brewer’s sparrow</td>
<td>0.122 (-0.109–0.355)</td>
<td>-0.192 (-0.308–0.075)</td>
<td>-0.200 (-0.310–0.091)</td>
</tr>
<tr>
<td>Brown-headed cowbird</td>
<td>-0.713 (-1.000–0.429)</td>
<td>0.371 (0.224–0.519)</td>
<td>0.211 (-0.052–0.489)</td>
</tr>
<tr>
<td>Chestnut-collared longspur</td>
<td>0.121 (-0.146–0.39)</td>
<td>1.219 (1.064–1.377)</td>
<td>-0.446 (-0.656–0.238)</td>
</tr>
<tr>
<td>Horned lark</td>
<td>0.177 (-0.052–0.408)</td>
<td>0.344 (0.226–0.462)</td>
<td>0.244 (0.149–0.339)</td>
</tr>
<tr>
<td>Lark bunting</td>
<td>-0.961 (-1.215–0.707)</td>
<td>0.441 (0.314–0.568)</td>
<td>-1.660 (-2.030–1.316)</td>
</tr>
<tr>
<td>McCown’s longspur</td>
<td>0.914 (0.685–1.143)</td>
<td>0.704 (0.587–0.821)</td>
<td>0.082 (0.011–0.154)</td>
</tr>
<tr>
<td>Vesper sparrow</td>
<td>0.072 (-0.159–0.303)</td>
<td>-0.002 (-0.117–0.113)</td>
<td>0.064 (-0.042–0.171)</td>
</tr>
<tr>
<td>Western meadowlark</td>
<td>-0.582 (-0.820–0.346)</td>
<td>0.181 (0.061–0.302)</td>
<td>0.402 (0.277–0.529)</td>
</tr>
</tbody>
</table>

\(^1\) = The effect of rest-rotation relative to traditional grazing.  
\(^2\) = The effect of a one unit increase in biomass potential relative to average biomass potential.  
\(^3\) = The effect of 2014 relative to 2013.
Table 2-4. The average predicted abundance ($\bar{N}$) and ninety-five percent credible intervals per 25 ha for eight avian species in rest-rotation and traditional grazing systems. Predictions are derived from the multispecies dependent double-observer abundance model from data collected near Roundup, Montana in 2013 and 2014.

<table>
<thead>
<tr>
<th>Species</th>
<th>2013</th>
<th></th>
<th>2014</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rest-rotation</td>
<td>Traditional</td>
<td>Rest-rotation</td>
<td>Traditional</td>
</tr>
<tr>
<td></td>
<td>$\bar{N}$</td>
<td>95% CRI</td>
<td>$\bar{N}$</td>
<td>95% CRI</td>
</tr>
<tr>
<td>Chestnut-collared longspur</td>
<td>2.26</td>
<td>1.77–2.84</td>
<td>2.00</td>
<td>1.55–2.55</td>
</tr>
<tr>
<td>Lark bunting</td>
<td>8.28</td>
<td>5.73–11.70</td>
<td>21.62</td>
<td>15.57–29.54</td>
</tr>
<tr>
<td>McCown’s longspur</td>
<td>33.18</td>
<td>28.15–38.78</td>
<td>13.30</td>
<td>11.19–15.69</td>
</tr>
</tbody>
</table>
APPENDIX 1: R Code

# Multispecies dependent double-observer model
# Author: Jessie Golding
# 7/31/2015

# Load required R packages

require(plyr)
require(dplyr)
require(car)
require(R2jags)
require(raster)
require(rgdal)
require(stringr)
require(ggplot2)
require(wesanderson)
require(gridExtra)
require(reshape2)
require(RColorBrewer)
require(RODBC)
require(mcmcplots)

### Simulated data ###

# Function to simulate data (sim.fun) and run simulation (sim.fun.rep)
# Create function to simulate dependent double-observer data for multiple species
# and multiple sites and multiple repeated surveys for a single season

sim.fun <- function(n.sites){

## Setup the logistics of sampling

# Number of sites
n.sites <- n.sites
# Number of visits to each site
n.reps <- 3
# Number of observers
n.observers <- 2
# Number of species
n.sp <- 4
# Number of observations
n.obs <- n.sites * n.reps * n.sp

# Indices for long format
#prim = primary observer
#sec = secondary observer
prim <- sample(1:2, n.sites*n.reps*n.sp, replace = T)
sec <- ifelse(prim == 1, 2, 1)

# A quick check that it worked
all((prim + sec) == 3)

#Generate site info
site <- rep(1:n.sites, each = n.reps*n.sp)

#Generate survey replicate information
reps <- rep(rep(1:n.reps, n.sites), n.sp)

#Generate species information
sp <-rep(1:n.sp, each = n.sites*n.reps)

# Detection probability of primary observer
P <- vector("numeric")
P[1] <- 0.3
# Detection probability of secondary observer
P[2] <- 0.5

# Sum of p's should be less than 1, where the remainder represents the
# proportion of the sampled population not observed
stopifnot((P[1] + P[2]) < 1)
"n\n")

## Biological Parameters

# Mean abundance across sites, one for each species
# The numbers are meant to be very different so we can see how the model handles them
lambda <- c(20, 150, 300, 1000)

# Proportion of the population captured at each session

# Proportion of population not captured at each session
p.nocap <- 1 - p.cap

## Simulation
# Initialize matrices to hold values of abundance corrected for availability
N <- array(NA, dim = c(n.sites, n.reps, n.sp))

# Initialize matrices to hold values of observations and probability of detection
# Columns are outcomes of the multinomial
y <- cp <- matrix(NA, nrow = n.obs, ncol = n.observers)

# Initialize matrix to hold values of true abundance
M <- matrix(NA, n.sites, n.sp)
for(i in 1:n.sites){
    M[i,] <- rpois(n.sp, lambda)
}

# Abundance corrected for availability during each survey rep
for(i in 1:n.sites){
    for(j in 1:n.reps){
        for(k in 1:n.sp){
            N[i,j,k] <- rbinom(1, M[i,k], p.cap)
        }
    }
}

# Number observed
for(i in 1:n.obs){
    cp[i,] <- c(P[prim[i]], P[sec[i]] * (1 - P[prim[i]]))
    y[i,] <- cmultinom(1, N[site[i], reps[i], sp[i]], cp[i,])
}

# Put the data together in long format
input <- data.frame(cbind(y[,1:2], y[,1]+y[,2], site, reps, sp, prim, sec))
colnames(input)[1:3] <- c("y1", "y2", "ncap")

# JAGS model to estimate parameters
sink("model_multinomial_multisp_sim.txt")
cat("model{
# Priors
# Linear predictor on abundance, setup for species variation only,
# abundance assumed the same at every site
for(i in 1:n.sp){
    log.n[i] ~ dnorm(0, 0.001)
    mu.lambda[i] <- exp(log.n[i])
")
# Population size of each species at each site
# (JAGS -> dnegbin(p,r))
for(i in 1:n.sites){
  for(k in 1:n.sp){
    N[i,k] ~ dpois(mu.lambda[k])
  }
}

# Individual observer detection probability, no variation
for(i in 1:n.observers){
  p[i] ~ dbeta(1, 1)
}

# Likelihood
for(i in 1:n.obs){
  # Indices always follow site, reps, species order
  # Capture probabilities
  # Seen by observer #1
  cp[i,1] <- p[prim[i]]
  # Seen by observer #2 and not seen by observer #1
  cp[i,2] <- p[sec[i]] * (1 - p[prim[i]])
  # Seen by somebody
  pcap[i] <- sum(cp[i,])
  # Not seen by either observer
  pnocap[i] <- 1 - pcap[i]
  # Adjust the prob of capture to the prop available
  # 2 is for number of outcomes (probabilities for obs1 and obs2)
  for(j in 1:2){
    muc[i,j] <- cp[i,j]/pcap[i]
  }
  # Realizations
  # Number captured (ncap) and population size (N)
  ncap[i] ~ dbin(pcap[i], round(N[site[i],sp[i]]))
  y[i,] ~ dmulti(cp[i,1:2], ncap[i])
}

# Format JAGS data
data <- list("y" = input[,1:2],
              "prim" = input$prim,
              "sec" = input$sec,
"n.obs" = nrow(input),
"n.observers" = n.observers,
"n.sites" = length(unique(input$site)),
"site" = input$site,
"n.sp" = length(unique(input$sp)),
"ncap" = input$ncap,
"sp" = input$sp)

#R2jags requires the data is in the global environment. Because this is in a
#function need to write it to the global environment each time.
list2env(data, envir=globalenv())

require(R2jags)
inits <- function(){list(
  log.n = log(lambda),
  p = c(0.3, 0.5),
  N = M*2 )}
parms <- c("p", "N", "mu.lambda", "pcap")
out <- jags.parallel(data=names(data), inits, parms, "model_multinomial_multisp_sim.txt", 3,
50000, 1000, 1)

summ <- list("P" = round(cbind(P, out$BUGS$mean$p, 100 * abs(P - out$BUGS$mean$p)/P),
2),
  "N" = round(cbind(M, out$BUGS$mean$N, 100 * abs(M - out$BUGS$mean$N)/M),
2))

coverage<-list("Pcov" = ifelse(P>(quantile(out$BUGS$sims.list$p,.025)) &
P<(quantile(out$BUGS$sims.list$p,.975)), 1, 0),
  "Ncov" = ifelse(M>(quantile(out$BUGS$sims.list$N,.025)) &
M<(quantile(out$BUGS$sims.list$N,.975)), 1, 0))

data<-list(summ,coverage)

}

#Create function to specify the number of times and for how many sites the sim.fun
#should run
sim.fun.rep<-function(n.times, n.sites){
  replicate(n.times, sim.fun(n.sites), simplify = F)
}

### Function to format and plot simulated data for MDAM to assess mean absolute percent error
and coverage ###
sim.form<-function(sim.out,n.times,n.sp.n.sites){
    #Absolute mean percent error of detection (p)
    p.err <- unlist(lapply(sim.out, function(x){
        x[[1]][[1]][,3]
    })))
    #Absolute mean percent error of abundance (n)
    n.err <- unlist(lapply(sim.out, function(x){
        x[[1]][[2]][9:12]
    })))
    #Coverage (does 95% CRI include true value) of detection (p)
    p.cov<-numeric(length = 0)
    for(i in 1:n.times){
        tmp<-as.numeric(unlist(sim.out[[i]][[2]][1]))
        p.cov[i]<-sum(tmp)
    }
    #Coverage (does 95% CRI include true value) of abundance (n)
    n.cov <- unlist(lapply(sim.out, function(x){
        x[2][[2]][1:4]
    })))
    #Create data frames of absolute mean percent errors
    p.est<-as.data.frame(p.err)
    n.est<-as.data.frame(n.err)
    #Calculate coverage values. The number that the sums are divided by are the total # number of samples from the sim.fun function
    p.coverage<-(sum(p.cov)/(n.times*2))*100
    n.coverage<-(sum(n.cov)/(n.sites*n.sp*n.times))*100
    #Info for table of percent errors - n
    n.est$cat<-ifelse(n.est$n.err<21,1,
        ifelse(n.est$n.err>21 & n.est$n.err<40,2,
            ifelse(n.est$n.err>41 & n.est$n.err<60,3,
                ifelse(n.est$n.err>61 & n.est$n.err<80,4,
                    ifelse(n.est$n.err>81 & n.est$n.err<100,5,
                        6)))))
    n.est<-as.data.frame(ddply(n.est,.(cat), nrow))
    n.est$percent <-round((n.est$V1/(n.sites*n.sp*n.times))*100,1)
    #Info for table of percent errors - p
    p.est$cat<-ifelse(p.est$p.err<=1,1,
        ifelse(p.est$p.err>1 & p.est$p.err<=2,2,
            ifelse(p.est$p.err>2 & p.est$p.err<=3,3,
                ifelse(p.est$p.err>3 & p.est$p.err<=4,4,
                    ifelse(p.est$p.err>4 & p.est$p.err<=5,5,
                        ifelse(p.est$p.err>5 & p.est$p.err<=6,6,
                            7)))))
    p.est<-as.data.frame(ddply(p.est,.(cat), nrow))
    p.est$percent <-round((p.est$V1/(n.sites*n.sp*n.times))*100,1)
`ifelse(p.est$p.err>2 & p.est$p.err<=3,3,
ifelse(p.est$p.err>3 & p.est$p.err<=4,4,
ifelse(p.est$p.err>4 & p.est$p.err<=5,5,
ifelse(p.est$p.err>5,6,
6))))`

`p.est<-as.data.frame(ddply(p.est,(cat), nrow))`

`p.est$percent <- (p.est$V1/(n.times*2))*100`

```r
### MDAM Extension Chapter 1 ###

#Code for writing and running MDAM extension described in Chapter 1

```
ifelse(p.est$p.err>2 & p.est$p.err<=3,3,
ifelse(p.est$p.err>3 & p.est$p.err<=4,4,
ifelse(p.est$p.err>4 & p.est$p.err<=5,5,
ifelse(p.est$p.err>5,6,
6))))

p.est<-as.data.frame(ddply(p.est,(cat), nrow))
p.est$percent <- (p.est$V1/(n.times*2))*100

```
for (k in 1:2)

# Site abundance
N[i,j,k] ~ dpois(mu.lambda[i,j,k])

# Individual observer detection probability
for (i in 1:n.observers)
for (j in 1:n.sp)
p[i,j] ~ dnorm(0, 0.001)

# Primary likelihood
for (i in 1:n.obs)
# Capture probabilities
# Seen by observer #1
cp[i,1] <- p[prim[i],sp[i]]
# Seen by observer #2 and not seen by observer #1
cp[i,2] <- p[sec[i],sp[i]] * (1 - p[prim[i],sp[i]])
# Seen by observer #1 or observer #2
pcap[i] <- 1 - ((1-cp[i,1])*(1-cp[i,2]))
# Not seen by either observer
pnocap[i] <- 1 - pcap[i]

# Realizations
# Number captured (ncap) and population size (N)
cap[i] ~ dbin(pcap[i], round(N[site[i],sp[i],year[i]]))
# Detection probabilities
y[i,] ~ dmulti(cp[i,1:2], ncap[i])

"", fill = T)
sink()

# Data
jags.dat <- list("y" = input_big8[,5:6],
                   "prim" = input_big8$prim,
                   "sec" = input_big8$sec,
                   "n.obs" = nrow(input_big8),
                   "n.observers" = n.observers,
                   "n.sites" = length(unique(input_big8$site)),
                   "site" = input_big8$site,
"n.sp" = length(unique(input_big8$sp)),
"sp" = input_big8$sp,
"ncap" = input_big8$ncap,
"grazed" = grazed,
"rangeq" = rangeq,
"year" = input_big8$year)

# Monitor parameters

pars <- c("loglam", "graze.eff",
          "year.eff", "p")

# Initial values
Nst <- matrix(NA, n.sites, n.sp)
lambda <- 175
for (i in 1:n.sites) {
  Nst[i,] <- rpois(n.sp, lambda)
}
Nst <- array(c(Nst, Nst), dim = c(n.sites, n.sp, 2))

p <- runif(n.observers)
p <- cbind(p, p, p, p, p, p, p, p, p)
pst <- matrix(p, ncol = ncol(p), dimnames = NULL)

init.vals <- function() {list(
  N = Nst, p = pst)
}

# Call
out <- jags(jags.dat,
            init.vals,
pars,
            "model_multinomial_multisp_MDAMext.txt",
            n.chains = 3,
            50000,
            5000,
            1)

### MDAM Chapter 2 ###

# Code for writing and running MDAM described in Chapter 2
# JAGS model to estimate parameters

sink("model_multinomial_multisp_RE_cov_Ch2.txt")
cat(""
   model{
      # Priors
      # RE on site to account for overdispersion
      sd.site ~ dunif(0, 100)
      tau.site <- 1/(sd.site^2)
      for(i in 1:n.sites){
         site.eff[i] ~ dnorm(0, tau.site)
      }

      # Fixed effect on year and biomass potential
      for(i in 1:n.sp){
         year.eff[i] ~ dnorm(0, 0.01)
         biom.eff[i]~ dnorm(0, 0.01)
      }

      # Grazing effect and mean abundance prior (i.e. intercept)
      for(i in 1:n.sp){
         graze.eff[i] ~ dnorm(0, 0.01)
         loglam[i] ~ dnorm(0, 0.01)
         lambda[i] <- exp(loglam[i])
      }

      # Site abundance linear predictor
      for(i in 1:n.sites){
         for(j in 1:n.sp){
            for (k in 1:2){
                       + year.eff[j]*(k-1))
            }
         }
      }

      # Site abundance
      N[i,j,k] ~ dpois(mu.lambda[i,j,k])
   }
}

# Individual observer detection probability, treat like a regression
# similar to the calculation of N above if covariates desired
for(i in 1:n.observers){
   for (j in 1:n.sp){
      
   }
}
p[i,j] ~ dnorm(0, 0.001)

\# Primary likelihood
for(i in 1:n.obs){
\# Indices always follow site, reps, species order
\# Capture probabilities
\# Seen by observer #1
cp[i,1] <- p[prim[i],sp[i]]
\# Seen by observer #2 and not seen by observer #1
cp[i,2] <- p[sec[i],sp[i]] * (1 - p[prim[i],sp[i]])
\# Seen by somebody
pcap[i] <- 1-((1-cp[i,1])*(1-cp[i,2]))
\# Not seen by either observer
pnocap[i] <- 1 - pcap[i]
\# Realizations
\# Number captured (ncap) and population size (N)
ccap[i] ~ dbin(pcap[i], round(N[site[i],sp[i],year[i]]))
\# Detection probabilities
y[i,] ~ dmulti(cp[i,1:2], ncap[i])
}

"", fill = T)
sink()

# Data
jags.dat <- list("y" = input_big8[,5:6],
    "prim" = input_big8$prim,
    "sec" = input_big8$sec,
    "n.obs" = nrow(input_big8),
    "n.observers" = n.observers,
    "n.sites" = length(unique(input_big8$site)),
    "site" = input_big8$site,
    "n.sp" = length(unique(input_big8$sp)),
    "sp" = input_big8$sp,
    "ncap" = input_big8$ncap,
    "grazed" = grazed,
    "biom"=biom,
    "year"=input_big8$year)

# Monitor parameters
pars <- c("loglam","graze.eff","rq.eff",
    "year.eff","p","N")
# Initial values
Nst <- matrix(NA, n.sites, n.sp)
lambda <- 175
for (i in 1:n.sites){
  Nst[i,] <- rpois(n.sp, lambda)
}
Nst <- array(c(Nst, Nst), dim = c(n.sites, n.sp, 2))

p <- runif(n.observers)
p <- cbind(p, p, p, p, p, p, p, p)
pst <- matrix(p, ncol = ncol(p), dimnames = NULL)

init.vals <- function(){list(
  N = Nst, p = pst)
}

# Call
out <- jags(jags.dat,
  init.vals,
  pars,
  "model_multinomial_multisp_RE_cov_Ch2.txt",
  n.chains = 3,
  50000,
  5000,
  1)
Songbird Research Study: Addressing the Issue of Range Quality

WILD 596: Independent Study (30794)

Jessie Golding

9/29/2014
Introduction
My master’s research examines the effects of grazing management and environmental factors on songbird community structure. There are two grazing management systems that I am investigating: season-long grazing and rest-rotation grazing. Season-long grazing involves keeping livestock in the same pasture for an entire grazing season, which usually lasts from May through November method, and rest-rotation grazing involves rotating livestock through multiple pastures over the grazing season. Each of these grazing systems in my study area is exclusively associated with a land ownership type: season-long grazing occurs only on public lands owned by the Bureau of Land Management (BLM); rest-rotation grazing occurs only on private land as part of the Sage Grouse Initiative (SGI), a program run by the National Resource Conservation Service (NRCS). I am interested in separating out the effects of grazing system and environmental factors, which relies on the assumption that the land potential, or potential to produce a certain set of vegetation characteristics, are equal. On multiple occasions, various parties have brought up the point that the landownership (and associated land use history) tied to each type of grazing may be reflective of an inherent difference in potential or quality. In particular, there is concern that public land is often more degraded than private land; a commonly held belief is that private land boundaries were delineated based on productivity and what was not desired was absorbed into the public land system. My goal is to address this underlying assumption, through answering these two questions:

Question 1: Is there a difference between land potential on private and public land in my study area outside of Roundup, Montana?

Question 2: If there is a difference, how large is that difference and is it statistically significant? I would like to quantify the difference so that I can account for this in future analysis of changes in avian communities.

I initiated an independent study project to address these objectives in the beginning of Spring semester of 2014 at the University of Montana. This report is designed to serve as a summary of the course during the spring and summer of 2014 and present the final results of the analysis.

Independent Study Course Summary
This course was a multi-month collaborative process that drew from many experts and data sources. My advisor, Dr. Victoria Dreitz, assistant professor and director of the Avian Science Center at the University of Montana oversaw the progress of the study to make sure it adhered to University of
Montana standards. Mary Manning, regional vegetation ecologist with the United States Forest Service (USFS), was the primary point of contact for rangeland science. Mrs. Manning and I met multiple times over the Spring 2014 semester to review information on rangeland science, methods for assessing range quality, ecological site descriptions, and to develop a method address this question. Mrs. Manning assigned reading and two written assignments, a formal write up of my course objectives and a write up about different ways to measure vegetation cover to provide a foundation in rangeland ecology. I sought additional input from rangeland experts Krist Walstad and Kirt Waltstead, rangeland management specialist with NRCS in Roundup and Bozeman, respectively. They advised me on current NRCS methods, including similarity indices, and provided supplemental information about the data available in the NRCS Soil Data Viewer 6.1. In addition, William Drummond, soil scientist with NRCS in Bozeman, provided guidance on landscape productivity metrics from the NRCS Soil Data Viewer 6.1. Dr. Paul Lukacs, professor at the University of Montana, provided advice on sampling design and statistical problems. Finally, Joe Smith, Ph.D. student at the University of Montana, provided assistance in spatial analysis.

Over the course I explored two general methods of addressing these questions. The first was looking at range quality metrics that are based on all land use history to date. The second was looking at range quality metrics based on land potential derived from physical characteristics of the landscape. Rangeland health assessments and similarity index calculations are two methods in this first category that were developed by NRCS. Both use current conditions compared with a reference state, which is described by an ecological site description (ESD), to determine range quality. ESDs are classifications of rangeland and forest soils and vegetation, and are widely used by a variety of federal agencies. Rangeland health assessments and similarity indices differ in how they calculate departure from reference state; the former uses a qualitative assessment (outlined in Interpretting Indicators of Rangeland Health version 4 (Pellant et al. 2005)) and the latter uses a quantitative assessment (calculated as vegetation percent similarity). I decided not to use these because I had no way of accurately accounting for the difference in land use history between the two land types I was comparing. In addition, the logistics of implementing these methods were challenging. Both of these metrics rely on the mapping of ecological sites prior to evaluation, which takes a considerable amount of effort. With 21 possible ecological sites within my study area (NCRS 2014), mapping these ecological sites and then performing this analysis would have been unrealistic given the timeline of my master’s research.
Due to these constraints I selected two methods in the second category, based on land potential, to use in my analysis. Land productivity and wetness index calculations are methods that use physical characteristics to estimate potential of the land to produce vegetation. They inherently do not heavily rely on metrics that include past land use or management because they are primarily based on physical properties resulting from soil or topography. Rangeland productivity is defined by the NRCS as “the amount of vegetation that can be expected to grow annually in a well-managed area (NRCS 2011).” The measurement is given as pounds per acre of dry vegetation and is highly dependent on soil type in areas where climate and topography are similar, like my study area. The compound topographic index (CTI) is a steady state wetness index that takes into account soil type (and the associated soil attributes that contribute to water holding properties), topography, and upstream water availability. This is a useful metric because water availability is an important determinant for range productivity (Humphrey 1962).

My final goal in this course was to take these two metrics and use them to assess whether there was a difference in range quality, measured as land potential, between private and public land in my study area.

**Study Area**

The study area for this project is located in rangelands outside of Roundup, Montana, on private and public lands. I had access to 44,019 ha of public land and 25,566 ha of private land and for the initial sampling set up of my project. I randomly selected a total of 1,000 ha from each land type (in the form of 80 25 ha plots). This provided two spatial scales for inference: the regional scale and local scale, respectively. Cattle are the primary domestic livestock that use these lands, although sheep are common as well. The vegetation in the study area includes areas dominated by sagebrush (*Artemsia tridentata*), as well as those dominated by native and non-native grassland vegetation. Appendix 1 contains an overview map of the study area, as well as pictures of the vegetation types present in the study area.

**Methods**

I conducted a series of visual summary and statistical tests to test if private and public land differed in my study area. I used histograms, boxplots, and bar graphs to compare productivity metrics and CTI by land ownership. I used a t-test in addition to these visual comparisons to test if the means of these metrics were significantly different. I conducted these analyses for productivity at the two spatial scales, regional and local, mentioned above. Complete CTI data was not available for both scales, so I
only used the local scale for this analysis. All analyses were conducted with the program R version 3.1.1 (R Core Team 2012). Appendix 2 contains the annotated R code for these summaries and tests.

**Results**

The results show that on average private land is more productive and has a higher moisture content than public land (Table 1). Results of visual comparisons using histograms showed that in both the productivity and the CTI that there is considerable overlap between the range of values for public and private lands in this area (Figure 1A – 1C). Results using boxplots showed a similar pattern: both productivity and the CTI showed a large amount of overlap but private land produced higher values for both metrics than public land (Figure 2A – 2C). I analyzed the productivity data at multiple scales and although the values were higher at the local scale than at the regional scale, the values showed the same pattern based on land ownership: private land has a statistically significant (P-value <0.0005) higher average productivity than public land (Table 1). Data for the CTI was limited to the local scale; however, because the local scale was a random sample of the regional scale, I am confident that the local scale is representative of the regional scale. Data for the CTI showed a similar pattern to that of the productivity. The histogram comparison revealed considerable overlap between the range of values (Figure 1C), but boxplot comparison (Figure 2C) and the t-test showed that the means were significantly different (P-value <0.0005) and higher on private land (Table 1).

**Discussion**

Private land is higher quality than public land when multiple productivity metrics are considered. This is most likely due to a history of land use, where private land was selected because it was the most productive, and land put under public management was often unproductive and unclaimed land. It is important to note that these metrics used have little to do with past land use because they focused potential defined by physical characteristics. There are multiple additional metrics that could be used, but the agreement of these two provides solid evidence that private land is of higher quality. In addition, the agreement of the multiple scales suggests this is a pattern that occurs beyond the local scale.
References

NRCS. 2011. Soil Data Viewer 6.1. Available online at:

NRCS. 2014. Ecological Site Descriptions. Available online at:


Tables and Figures

Table 1. Comparison of Rangeland Quality Metrics by Ownership. A comparison of range productivity (published by NRCS in the Soil Data Viewer 6.1) and the compound topographic index (CTI) by land ownership. The mean, standard deviation (SD), 95% confidence interval (CI), and results of the t-test are presented. The p-value associated with the t-test measures how significant the difference in means between the two groups is (< 0.05 is considered significant). The comparison of rangeland productivity is presented for both the regional scale and local scale. The comparison of CTI is presented only for the local scale due to limited data availability.

<table>
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<th>Public Land</th>
<th>Private Land</th>
<th>T-Test</th>
<th>p-value</th>
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<td>Mean</td>
<td>SD</td>
<td>95% CI</td>
<td>Mean</td>
</tr>
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<td>Range Productivity</td>
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<td>329.46</td>
<td>1036.89-1040.01</td>
<td>1182.53</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range Productivity</td>
<td>1129.22</td>
<td>253.34</td>
<td>1121.38-1137.06</td>
<td>1209.75</td>
</tr>
<tr>
<td>(local scale)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>CTI (local scale)</td>
<td>8.126</td>
<td>1.896</td>
<td>0.02997</td>
<td>8.354</td>
</tr>
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</table>


Figure 1A. Comparison of Rangeland Productivity by Land Ownership at the Regional Scale.

Rangeland productivity (measured in pounds of dry vegetation produced per acre) as reported by the NRCS Soil Data Viewer 6.1 on public and private lands outside of Roundup, Montana.
Figure 1B. Comparison of Rangeland Productivity by Land Ownership at the Local Scale.

Rangeland productivity (measured in pounds of dry vegetation produced per acre) as reported by the NRCS Soil Data Viewer 6.1 on public and private lands outside of Roundup, Montana.
Figure 1C. Comparison of CTI by Land Ownership at the Local Scale. Compound topographic index (CTI) on public and private lands outside of Roundup, Montana.
Figure 2A. Comparison of Mean Rangeland Productivity by Land Ownership at the Regional Scale. Rangeland productivity (measured in pounds of dry vegetation per acre) as reported by the NRCS Soil Data Viewer 6.1 on public and private lands outside of Roundup, Montana. The values shown are as follows: white dots represent the mean; the horizontal black line represents the median; the box contains the first through third quartiles; the vertical black lines represent the smallest and largest values in the data set; and the solid black dots outside represent outliers in the data sets.
Figure 2B. Comparison of Mean Rangeland Productivity by Land Ownership at the Local Scale. 
Rangeland productivity (measured in pounds of dry vegetation produced per acre) as reported by the NRCS Soil Data Viewer 6.1 on public and private lands outside of Roundup, Montana. The values shown are as follows: white dots represent the mean; the horizontal black line represents the median; the box contains the first through third quartiles; the vertical black lines represent the smallest and largest values in the data set; and the solid black dots outside represent outliers in the data sets.
Figure 2C. Comparison of CTI by Land Ownership at the Local Scale. Compound topographic index (CTI) on public and private lands outside of Roundup, Montana. The values shown are as follows: white dots represents the mean; the thick black line represents the median; the box contains the first through third quartiles; the black vertical lines represent the smallest and largest values in the data set; and the solid black dots outside represent outliers in the data sets.
Appendix 1: Study Area Figures

Figure 1. Overview of the study area. An overview of the study area, including the relative position in Montana. BLM lands are shown in yellow. I am not able to disclose the exact location of the private lands because of information sharing agreements, but the study area polygon shows the general area examined.
Figure 2. Habitat variability in the study area. An example of the mix of sagebrush and grassland vegetation in the study area.

Figure 3. Non-native species in the study area. An example of the crested wheat grass vegetation in the study area.
Figure 4. *Short grass in the study area.* An example of the short grass vegetation in the study area.

Figure 5. *Sagebrush in the study area.* An example of the sagebrush vegetation in the study area.
Appendix 2: Annotated R-Code

# Code to quantify differences in land condition/range quality between public and private land in study area
# For 2014 independent study project.
# Spatial code developed with Joe Smith on 8/27/14

# Load necessary packages
library(raster)
library(rgdal)

# Load productivity (prod) raster file created in ArcMap 10.0
# Created raster file of merged soil productivity data (for GV and MS counties) in R
prod <- raster("C:/Users/jessie.golding/Documents/Songbird Research/2014 Field/2014 GIS/rangeprod_65and66_raster.tif")

# Set wd so you don't have to continually type out that long file path...
setwd("C:/Users/jessie.golding/Documents/Songbird Research/2014 Field/2014 GIS")

# Commands to look at the raster dataset
plot(prod)
class(prod)
str(prod)
extent(prod)
hist(prod)

# Create raster of land ownership file. The advantage of doing this here rather than in ArcMap is that this uses the template of the productivity raster (prod) to create the new raster so that you easily directly compare them.
own <- shapefile("ppclipped.shp")
ownr <- rasterize(own, prod, field="OWNER_TYPE")
plot(ownr)

# Summarize productivity by land ownership type. 0=private, 1=public
prod_private <- prod[ownr == 0]
str(prod_private)
hist(prod_private)
plot(density(prod_private))
prod_blm <- prod[ownr == 1]
summary(prod_blm)
summary(prod_private)

# Combine data into a single data frame (prod) for easier plotting
d1<-data.frame(prod_blm)
d1$own <- "BLM"
names(d1)[1]<-"prod"

d2<-data.frame(prod_private)
d2$own <-"Private"
names(d2)[1]<-"prod"

prod <-rbind(d1,d2)

#Plot results
#Plot both histograms on one graph
#The scale commands were put in there to adjust the scale and the expand command makes it so there are not weird spaces around the edge of the plot
library(ggplot2)
ggplot(prod, aes(x=prod, fill=own)) +
  geom_histogram(binwidth=100, alpha=.5, position="identity")+
  scale_x_continuous(limits=c(0,2500),expand=c(0,0))+
  scale_y_continuous(expand=c(0,0))+
  xlab("Productivity (lbs. per acre)")+
  ylab("Frequency")+
  scale_fill_discrete(name="Ownership")+
  ggtitle("Rangeland Productivity by Land Ownership") +
  theme_bw()

#Create a boxplot to visually compare difference in means
ggplot(prod, aes(x=own, y=prod, fill=own)) +
  geom_boxplot() +
  stat_summary(fun.y = "mean", geom = "point", shape= 23, size= 3, fill= "white") +
  xlab("Ownership")+
  ylab("Productivity (lbs. per acre)")+
  ggtitle("Rangeland Productivity by Land Ownership") +
  guides(fill=FALSE)+
  theme_bw()

#Summary statistics using a summary function from online for summary stats
#http://www.cookbook-r.com/Graphs/Plotting_means_and_error_bars_(ggplot2)/
summarySE <- function(data=NULL, measurevar, groupvars=NULL, na.rm=FALSE, conf.interval=.95, .drop=TRUE) {
  require(plyr)

  # New version of length which can handle NA's: if na.rm==T, don't count them
  length2 <- function (x, na.rm=FALSE) {
    if (na.rm) sum(!is.na(x))
    else length(x)
  }

  # This does the summary. For each group's data frame, return a vector with
  # N, mean, and sd
```r
datac <- ddply(data, groupvars, .drop=.drop,
  .fun = function(xx, col) {
    c(N    = length2(xx[[col]], na.rm=na.rm),
      mean = mean   (xx[[col]], na.rm=na.rm),
      sd   = sd     (xx[[col]], na.rm=na.rm)
    )
  },
  measurevar
)

# Rename the "mean" column
datac <- rename(datac, c("mean" = measurevar))

datac$se <- datac$sd / sqrt(datac$N)  # Calculate standard error of the mean

# Confidence interval multiplier for standard error
# Calculate t-statistic for confidence interval:
# e.g., if conf.interval is .95, use .975 (above/below), and use df=N-1
ciMult <- qt(conf.interval/2 + .5, datac$N-1)
datac$ci <- datac$se * ciMult

return(datac)
}

#Run the summarySE function on the productivity data
prod_summarystats <-summarySE(prod, measurevar="prod", groupvars=c("own"))

#Create a point chart to compare means with SE included
ggplot(prod_summarystats, aes(x=own, y=prod)) +
  scale_y_continuous(limits=c(1030, max(prod_summarystats$prod + prod_summarystats$se)),breaks=c(1050,1100,1150,1200)) +
  geom_errorbar(aes(ymin=prod-se, ymax=prod+se), width=.1) +
  geom_line() +
  geom_point()+
  xlab("Ownership") +
  ylab("Productivity (lbs. per acre") +
  ggtitle("Mean Rangeland Productivity by Land Ownership") +
  theme_bw()

#Use t test to test for difference in means
t.test(prod_private, prod_blm)

#Test for same result on plot scale
#Create raster of land ownership file using the ownwership file with just plots
#This is the same process as above
own_plot <-shapefile("ppclipped_plots.shp")
```

own_plot_r <- rasterize(own_plot, prod, field="OWNER_TYPE")
plot(own_plot_r)

prod_private_plot <- prod[own_plot_r == 0]
prod_blm_plot <- prod[own_plot_r == 1]

#Combine data into a single data frame (prod) for easier plotting
d3<-data.frame(prod_blm_plot)
d3$own <-"BLM"
names(d3)[1]<-"prod"

d4<-data.frame(prod_private_plot)
d4$own <-"Private"
names(d4)[1]<-"prod"

prod_plot <-rbind(d3,d4)

#Plot the results using a histogram
ggplot(prod_plot, aes(x=prod, fill=own)) +
  geom_histogram(binwidth=100, alpha=.5, position="identity")+
  scale_x_continuous(limits=c(0,2500),expand=c(0,0))+scale_y_continuous(expand=c(0,0))+
  xlab("Productivity (lbs. per acre)")+
  ylab("Frequency")+
  scale_fill_discrete(name="Ownership")+
  ggtitle("Rangeland Productivity by Land Ownership")+
  theme_bw()

#Create a boxplot to visually compare difference in means
ggplot(prod_plot, aes(x=own, y=prod, fill=own)) +
  geom_boxplot() +
  stat_summary(fun.y = "mean", geom = "point", shape= 23, size= 3, fill= "white") +
  xlab("Ownership") +
  ylab("Productivity (lbs. per acre)") +
  ggtitle("Rangeland Productivity by Land Ownership") +
  guides(fill=FALSE) +
  theme_bw()

#Run summary stats for final check
prod_plot_summarystats <-summarySE(prod_plot, measurevar="prod", groupvars=c("own"))

#Use t test to test for difference in means
t.test(prod_private_plot, prod_blm_plot)

#CTI - compound topographic index - analysis
cti <-raster("cti_50x50_3.tif")
plot(cti)
#Summarize cti by land ownership type. 0=private, 1=public.
##Use the already pulled in own_plot shapefile but create a raster file based on the new cti raster file
##Remember that the own_plot file is only at the plot-level sampling scale

```r
owner2 <- rasterize(own_plot, cti, field="OWNER_TYPE")
plot(owner2)
```

#Summarize cti by land ownership type. 0=private, 1=public

```r
cti_private <- cti[owner2 == 0]
cti_blm <- cti[owner2 == 1]
```

#Combine data into a single data frame (cti) for easier plotting

```r
d5<-data.frame(cti_blm)
d5$own <- "BLM"
names(d5)[1]<-"cti"

d6<-data.frame(cti_private)
d6$own <- "Private"
names(d6)[1]<-"cti"

citi <- rbind(d5,d6)
```

#Plot the results

```r
ggplot(cti, aes(x=cti, fill=own)) +
  geom_histogram(alpha=.5, position="identity") +
  xlab("CTI") +
  ylab("Frequency") +
  scale_fill_discrete(name="Ownership") +
  ggtitle("CTI by Land Ownership") +
  theme_bw()
```

#Create a boxplot to visually compare difference in means

```r
ggplot(cti, aes(x=own, y=cti, fill=own)) +
  geom_boxplot() +
  stat_summary(fun.y = "mean", geom = "point", shape= 23, size= 3, fill= "white") +
  xlab("Ownership") +
  ylab("CTI") +
  ggtitle("CTI by Land Ownership") +
  guides(fill=FALSE) +
  theme_bw()
```

#Run summary stats for final check

```r
citi_summarystats <- summarySE(cti, measurevar="cti", groupvars=c("own"))
```

#Use t test to test for difference in means of cti

```r
t.test(cti_private, cti_blm)
```