

DISSERTATION

TOOLS FOR IMPROVED MANAGEMENT OF SAGEBRUSH AVIFAUNA AND
SAGEBRUSH RANGELANDS

Submitted by

Jennifer Marie Timmer

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2017

Doctoral Committee:

Advisor: Cameron L. Aldridge

David J. Augustine

Monique E. Rocca

Maria E. Fernandez-Gimenez

Copyright by Jennifer Marie Timmer 2017

All Rights Reserved

ABSTRACT

TOOLS FOR IMPROVED MANAGEMENT OF SAGEBRUSH AVIFAUNA AND SAGEBRUSH RANGELANDS

The sagebrush biome of western North America once encompassed over 60 million hectares, but now occupies approximately 55% of its former range due to cultivation, energy and urban development, changing fire regimes, and other factors. As a result, many avifauna species in this ecosystem, such as greater sage-grouse (*Centrocercus urophasianus*) and Brewer's sparrows (*Spizella breweri*), have experienced population declines during the last fifty years. Understanding mechanisms behind changes in bird populations first requires an understanding of how resources may be affected by changes on the landscape. State-and-transition models (STM) are one tool managers could use to portray rangeland dynamics and predict the impact of state changes on ecosystem services, such as wildlife habitat. As conceptual models, STMs are a useful communication tool for land managers and landowners and they can easily be updated with new information. However, STMs are often criticized for a lack of statistical rigor in defining transition probabilities between states, and a lack of spatial context to inform potential transitions and illustrate ecosystem services. They also should include a combination of ecological data and local stakeholder input to improve model quality and relevance. Therefore, my research objectives were to: 1) include additional ecosystem services in one locally developed STM by predicting species richness and avifauna density for common sagebrush songbirds and greater sage-grouse in the states and community phases, 2) use the same collaborative STM and map the states across the study area with a new approach for sagebrush

rangelands, and 3) investigate the use of greater sage-grouse as an umbrella for several sagebrush-associated species (i.e., Brewer's sparrow, sage thrasher [*Oreoscoptes montanus*], sagebrush sparrow [*Artemisiospiza nevadensis*]), and green-tailed towhee [*Chlorura chlorura*]). These research objectives were part of a larger collaborative effort to develop STMs in a participatory approach with local stakeholders in Northwest Colorado. For all three objectives, I collected vegetation, soils, and avifauna abundance data in randomly distributed sampling plots in three project areas in 2013-2015.

For the first objective, I included additional ecosystem services in one recently developed STM by predicting species richness and avifauna density for common sagebrush songbirds and greater sage-grouse in the states and communities. I modeled songbird and sage-grouse pellet count data and species richness with fine-scaled vegetation predictors, like shrub cover and shrub height. I then used the average vegetation values per state or community phase to predict avifauna density and richness with the top models. Moderate or increasing amounts of shrub cover were important predictors for most species, as were bare ground and shrub heights, although responses varied by species. In the STM, I predicted higher species richness and greater densities for sagebrush and shrub-obligate species in the shrub-dominated states and phase and higher densities for grassland-associated species in the state and phase lacking shrub cover. This approach can assist local land managers and landowners gauge impacts of disturbances, such as fire, on avifauna populations, and it also illustrates the effect of managing for only one state on other species and services.

For the second objective, I used the same STM and multinomial logistic regression with the state classification as the response variable and several remotely sensed biotic and abiotic predictors, such as bare ground and elevation. I then predicted the best model to all pixels within

the study area and summarized spatial information about each mapped state, such as average patch size. The best model included big sagebrush cover and elevation. Classification accuracy (based on external and internal validation) was 71-74%, and individual component accuracy varied across the four states. Two shrubland states comprised approximately 67% of the study area, while an exotic grassland state comprised the lowest proportion (1%). The shrubland states were also the most contiguous while the exotic grassland state was the least. To my knowledge, this is the first attempt to use a locally developed STM and map states across the landscape in a sagebrush rangeland. Predicting and mapping states across a landscape could guide monitoring and restoration efforts, inform ecosystem service values per state, elucidate landscape patterns, and forecast transitions within STMs.

For the third objective, I examined count-based regression models for songbirds and logistic regression models for sage-grouse with multi-scaled biotic predictors to evaluate sage-grouse as an umbrella species. I determined the correlation between apparent sage-grouse occurrence and estimated songbird densities per plot to represent a fine-scaled approach. I also mapped model-predicted songbird densities within areas likely to contain sage-grouse to examine the efficacy of sage-grouse as an umbrella at a larger scale. Shrub or sagebrush height and a form of sagebrush cover were important predictors for all species, although the spatial extents varied. I determined that correlation between sage-grouse occurrence and density of all four songbirds at the plot-level was positive but weak. In contrast, higher predicted Brewer's sparrow and green-tailed towhee densities were captured in areas likely to contain sage-grouse across the study area. Sage thrasher densities were similar in areas likely to contain sage-grouse compared to the entire study area, and average sagebrush sparrow density was lower in areas likely to contain sage-grouse. In this study, sage-grouse may be an effective umbrella for

Brewer's sparrows and green-tailed towhees, but sage-grouse habitat does not appear to capture habitat promoting higher sagebrush sparrow densities. A multi-species focus may be the best management and conservation strategy for multiple species of concern.

In combination, these objectives are meant to improve management of sagebrush rangelands and avifauna species. All three objectives illustrate the value of managing for landscape heterogeneity, which is best achieved by managing for a landscape mosaic of different states, rather than for a single state, species, or ecosystem service. Specifically, the STM illustrates services provided by every state and how management for only one state could be detrimental to other services or avifauna species. Local management efforts for sage-grouse populations and habitat should also be improved with a greater understanding of multi-scaled habitat needs for other sagebrush-associated species. Further, I illustrate that by including input from local landowners and managers, the resulting STM should be more relevant and likely to be used as a management tool.

ACKNOWLEDGMENTS

I need to first thank my advisor, Cam Aldridge, for his endless support, encouragement, patience, and never-ending ability to make time for his students. I am grateful for his ability to make mistakes seem manageable and for providing numerous professional development opportunities. Maria Fernandez-Gimenez provided additional support with meetings, workshops, and chapter edits. I owe a big thanks to committee members, David Augustine and Monique Rocca, for encouragement and helpful feedback on dissertation chapters. My time at CSU would not have been nearly as enjoyable or fulfilling without lab mates Kristin Davis, Chris Dickey, Kevin Jablonksi, Danny Martin, Shelley Spear, Crystal Tipton, Nick Van Lanen, Greg Wann, Hailey Wilmer, and Shawna Zimmerman. Thanks for the intellectual feedback, encouragement, birding, trail runs, bike rides, dog walks, happy hours, political grumblings, Cards Against Humanity, and laughs!

I owe a huge thanks to Retta Bruegger for her support, encouragement, and merriment in the field, team meetings, and in between. The project would not have been as successful or enjoyable without her and I will always think of “baby got gap” when I hear Sir Mix A Lot. I am also grateful to Crystal Tipton and Chris Dickey for collaboration in the field and meetings, organization with data, and long car rides not talking about vegetation. Jake Schas, John Wendt, and Luke McCartney also provided sanity and invaluable help in the field.

I greatly appreciated the time, participation, questions, answers, and land access from several landowners involved with the project, and in particular, Wes McStay, Gary Visintainer, Keith Pankey, Cal and Penny Howe, Heather Stirling, and Ryan Wattles. Several agency personnel also contributed time, expertise, questions, and support during the project, and in

particular: Todd Hagenbuch and JD Sexton with Extension, Hunter Seim with the BLM, James Pritchett with CSU Extension, and Emily Kachergis with the BLM. Mike O' Donnell, Brian Cade, Adrian Monroe, and Collin Homer with CSU and USGS provided prompt and valuable feedback on GIS questions or analytical techniques. Spencer Schell, also with the USGS, outfitted me for three field seasons with GPS units, rangefinders, meter sticks, water jugs, and then some.

I owe another big thanks to friends for their support and encouragement over the last 4.5 years and for checking in with me to make sure I wasn't yet another grad school casualty: Renaldo Arroyo, Chip Cariappa, Jaclyn Comeau, Sherrie Davis, Brady Dunn, Kristina Kasik, and Erika Smith. David Knight kept me in good spirits while working at coffee shops the last two years and I appreciate the impromptu air guitar lessons, even when I didn't want them. Ray and Carolee have been more than neighbors to me, Mollie, and Abby since I moved to Fort Collins. They have entertained the three of us on an almost daily basis and provided treats for no reason at all. They have also faithfully watched Abby when I gone for work or for fun.

My family has always been supportive of my academic endeavors, although with some helpful prodding to get it done and get a real job. Hopefully soon....The random cards and care packages are always much appreciated. My immediate family grew during my PhD with the addition of Mollie, and Abby couldn't be happier with her little sister. I am pawsitive that my mental stability is somewhat intact because of these two—and for their not-so-subtle hints that work is just work, but kibble and playtime are what really matter.

I need to thank running and beer for helping maintain my sanity during my time at CSU. Finally, thanks to the birds for making everything I do (for work or fun) better.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	vi
LIST OF TABLES	ix
LIST OF FIGURES	xi
CHAPTER I. INTRODUCTION	1
LITERATURE CITED	11
CHAPTER II. MULTIPLE ECOSYSTEM SERVICES IN A STATE-AND-TRANSITION MODEL FOR SAGEBRUSH RANGELANDS	16
LITERATURE CITED	67
CHAPTER III. A SPATIAL APPROACH TO MAP STATES IN A STATE-AND- TRANSITION MODEL FOR SAGEBRUSH RANGELANDS	77
LITERATURE CITED	109
CHAPTER IV. MANAGING FOR MULTIPLE SPECIES: GREATER SAGE-GROUSE AND SAGEBRUSH SONGBIRDS	116
LITERATURE CITED	156
CHAPTER V. CONCLUSION	163
LITERATURE CITED	170
APPENDIX I	173

LIST OF TABLES

Table 2.1- Definitions of fine-scaled predictors used in count-based regression models for greater sage-grouse and sagebrush-associated songbirds in Northwest Colorado, 2013-2015.....46

Table 2.2- Count-based regression models for greater sage-grouse pellets and songbirds in Northwest Colorado, 2013-2015. We report log-likelihood (LL), number of parameters (K), Bayesian Information Criterion (BIC), difference in BIC compared to lowest BIC of the model set (Δ BIC), BIC weight (w), pseudo- R^2 value, prediction error from five-fold cross validation, and p-value from likelihood ratio test for models with Δ BIC < 4.....47

Table 2.3- Beta coefficient estimates (β), standard errors (SE), and 95% confidence intervals for variables in the top (i.e., Δ BIC < 2) count-based regression models for greater sage-grouse pellets and songbirds in Northwest Colorado, 2013-2015.....50

Table 2.4- Predicted densities of songbirds and greater sage-grouse pellets and species richness for states and community phases in Northwest Colorado, 2013-2015, for a locally developed state-and-transition model (Tipton 2015, Appendix I). 95% confidence intervals for each density estimate are in parenthesis.....53

Table 3.1- Top multinomial logistic regression models considered for predicting states identified from a state-and-transition model in Northwest Colorado, 2013-2015 (Tipton 2015). For each model, we report log-likelihood (LL), number of parameters (K), Bayesian Information Criterion (BIC), difference in BIC compared to lowest BIC of the model set (Δ BIC), and BIC weight (w) for all models <7 Δ BIC.....104

Table 3.2- Model statistics from the top multinomial logistic regression model for predicting states identified from a state-and-transition model in Northwest Colorado, 2013-2015 (Tipton 2015). Statistics are presented relative to the diverse shrubland state and include parameter probabilities, 95% confidence intervals in parentheses, and relative risk ratios (RRR).....105

Table 3.3- Landscape metrics for spatially explicit states identified from a state-and-transition model in Northwest Colorado, 2013-2015 (Tipton 2015) and predicted with multinomial logistic regression.....106

Table 4.1- Definitions of multi-scaled predictors used in logistic and count-based regression models for greater sage-grouse and sagebrush-associated songbirds in Northwest Colorado, 2013-2015.....141

Table 4.2- Logistic and count-based regression models for greater sage-grouse use and sagebrush-associated songbird density in Northwest Colorado, 2013-2015. For each model, we report log-likelihood (LL), number of parameters (K), Bayesian Information Criterion (BIC), difference in BIC compared to lowest BIC of the model set (Δ BIC), BIC weight (w), pseudo- R^2

value, prediction error from five-fold cross validation, p-value from likelihood ratio test, and receiver operating characteristic score (ROC) for sage-grouse logistic regression models.....142

Table 4.3- Beta coefficient estimates (β), standard errors (SE), and 95% confidence intervals for predictors in the top (i.e., $\Delta\text{BIC} < 4$) logistic and count-based regression models for greater sage-grouse use and sagebrush-associated songbird density in Northwest Colorado, 2013-2015.....144

LIST OF FIGURES

Figure 2.1- Locations of avifauna, vegetation, and soil surveys, 2013-2015, in Northwest Colorado with three study areas outlined and labeled (West Moffat, East Moffat, and Routt). We collected vegetation, soil, and avifauna abundance data at all three areas to quantify avifauna habitat relationships, but predicted avifauna densities in just the East Moffat state-and-transition model.....	54
Figure 2.2- Generalized state-and-transition model created for eastern Moffat County on Sandyland, Rolling Loam, Claypan, Deep Loam, and Sandy Foothills ecological sites in Northwest Colorado, 2013-2015 (Tipton 2015) with average and minimum-maximum vegetation values for each state and community phase. Solid lines around boxes indicate states while dotted lines indicate community phases within a state. Production estimates include grasses and forbs. See Tipton (2015) and Appendix I for full description of possible transition drivers and determination of states and phases.....	55
Figure 2.3- Predicted variable relationships and 95% confidence intervals for Brewer’s sparrows for the third best negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).....	56
Figure 2.4- Predicted variable relationships and 95% confidence intervals for green-tailed towhees for the top negative binomial model in Northwest Colorado, 2013-2015.....	57
Figure 2.5- Predicted variable relationships and 95% confidence intervals for sagebrush sparrows for the top negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).....	58
Figure 2.6- Predicted variable relationships and 95% confidence intervals for sage thrashers for the third best negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).....	59
Figure 2.7- Predicted variable relationships and 95% confidence intervals for greater sage-grouse single pellets for the top negative binomial model in Northwest Colorado, 2013-2015.....	60
Figure 2.8- Predicted variable relationships and 95% confidence intervals for greater sage-grouse roost piles for the best negative binomial model (sagebrush and herbaceous cover) and the fifth best model (grass height and forb cover) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).....	61

Figure 2.9- Predicted variable relationships and 95% confidence intervals for horned larks for the top negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).....62

Figure 2.10- Predicted variable relationships and 95% confidence intervals for vesper sparrows for the second best negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).....63

Figure 2.11- Predicted variable relationships and 95% confidence intervals for western meadowlarks for the top negative binomial model in Northwest Colorado, 2013-2015.....64

Figure 2.12- Predicted variable relationship and 95% confidence intervals for the top Poisson model for avifauna species richness (all common species in top figure and shrub-obligate species only in bottom figure) in Northwest Colorado, 2013-2015.....65

Figure 2.13- Range of songbird and pellet densities based on minimum and maximum vegetation values per state or community phase in a generalized state-and-transition model created for eastern Moffat County in Northwest Colorado, 2013-2015 (Tipton 2015). Total richness includes all eight avifauna species and shrub-species richness includes Brewer’s sparrows, green-tailed towhees, sagebrush sparrows, sage thrashers, and greater sage-grouse. See Tipton (2015) and Appendix I for full description of possible transition drivers and determination of states and phases.....66

Figure 3.1- Study area extent for making a spatially explicit state-and-transition model in Moffat County, Northwest Colorado (Tipton 2015). Included are focal ecological sites, high intensity traverse (HIT) and low intensity traverse (LIT) sampling plots, recent fires, and past mechanical shrub treatments. Transparent areas within the study area boundaries (i.e., to the north of the Yampa River, to the east of the Little Snake River, and to the eastern Moffat county border) indicate no data.....107

Figure 3.2- Map of multinomial logistic regression model predictions for states in a state-and-transition model in Moffat County, Northwest Colorado (Tipton 2015, Appendix I). Included are four states (native grassland, crested wheatgrass, needle-and-thread shrubland, and diverse shrubland) as predicted by a multinomial logistic regression model. Transparent areas within the outlined study area boundaries (i.e., to the north of the Yampa River, to the east of the Little Snake River, and to the eastern Moffat county border) indicate no data.....108

Figure 4.1- Study area for songbird and greater sage-grouse pellet surveys, 2013-2015, with two study sites outlined and labeled (West Moffat on the left and East Moffat to the right) and the overall greater sage-grouse range north of the Yampa River only represented by stippling (Colorado Parks and Wildlife 2011).....146

Figure 4.2- Predicted variable relationships and 95% confidence intervals for the top negative binomial models of Brewer’s sparrows and multi-scaled predictors in Northwest Colorado, 2013-2015. Variable relationships were similar across top three models (see Table 4.3).....147

Figure 4.3- Predicted variable relationships and 95% confidence intervals for the top negative binomial model of green-tailed towhees and multi-scaled predictors in Northwest Colorado, 2013-2015.....148

Figure 4.4- Predicted variable relationships and 95% confidence intervals for the top Poisson models of sagebrush sparrows and multi-scaled predictors in Northwest Colorado, 2013-2015.....149

Figure 4.5- Predicted variable relationships and 95% confidence intervals for the top negative binomial models of sage thrashers and multi-scaled predictors in Northwest Colorado, 2013-2015, excluding the intercept-only model.....150

Figure 4.6- Predicted species richness for Brewer’s sparrows, green-tailed towhees, sagebrush sparrows, and sage thrashers within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52 and richness was calculated based on a minimum density to support a songbird territory (i.e., 0.42 Brewer’s sparrows/ha, 1.11 green-tailed towhees/ha, 0.59 sage thrashers/ha, and 0.14 sagebrush sparrows/ha; Boyle and Reeder 2005, Poole 2005).....151

Figure 4.7- Predicted Brewer’s sparrow density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52.....152

Figure 4.8- Predicted green-tailed towhee density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52.....153

Figure 4.9- Predicted sagebrush sparrow density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52.....154

Figure 4.10- Predicted sage thrasher density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52.....155

CHAPTER I. INTRODUCTION

The sagebrush biome of western North America once encompassed over 60 million hectares, but now occupies approximately 55% of its former range (Miller et al. 2011). As a result, many avifauna species in this ecosystem, such as greater sage-grouse (*Centrocercus urophasianus*) and Brewer's sparrows (*Spizella breweri*), have experienced population declines during the last fifty years (Knick et al. 2003). Understanding mechanisms behind changes in bird populations first requires an understanding of how habitat resources may be affected by changes on the landscape. State-and-transition models (STM) are one tool managers could use to portray rangeland dynamics and predict the impact of state changes on ecosystem services, such as avifauna habitat or populations (Bestelmeyer et al. 2003, Holmes and Miller 2010). However, STMs could include both ecological data and local knowledge to improve model quality and relevance (Kachergis et al. 2013). They should also include spatial context to inform potential transitions and illustrate ecosystem services (Bestelmeyer et al. 2011, Steele et al. 2012).

Ecological Sites & State-and-Transition Models

Ecological sites are defined by ecological site descriptions (ESDs) within climate-based Major Land Resource Areas (Bestelmeyer et al. 2003). An ecological site includes distinctive soil and hydrologic properties, topography, and landform features that produce a characteristic plant community. Each ecological site is characterized by a state-and-transition model (STM), which describes the dynamics between potential states for a particular site based on management activities or natural events. Alternate states are described relative to a site's reference state, which is often a state that is considered desirable for optimizing forage production for livestock the desirable state (Bestelmeyer et al. 2009, Twidwell et al. 2013). Within a state, plant communities may vary among phases and shift along reversible pathways due to drought, fire,

grazing, or other events, reflecting the natural dynamics of plant communities (Stringham et al. 2003). Transitions between states, however, are triggered by natural disturbances or management activities, resulting in structural and/or functional change and are not easily reversible (Westoby et al. 1989, Bestelmeyer et al. 2003). In order for one state to transition to another, a threshold must be crossed (Friedel 1991, Stringham et al. 2003). A threshold represents a spatial and/or temporal boundary between states, and management intervention may not be enough to allow a change back to the initial state (Friedel 1991, Laycock 1991, Briske et al. 2005). Bestelmeyer et al. (2009) stress the utility of STMs for communicating to land managers about thresholds between reference and alternate states in a system in order to identify and prevent transitions to undesirable alternate states. Simulated STMs can also be used to forecast vegetation dynamics based on transition probabilities and drivers within a system or management unit (Daniel and Frid 2011).

The Natural Resource Conservation Service (NRCS) and several federal agencies have adopted the use of ESDs and STMs for current rangeland assessment, monitoring, and management (Bestelmeyer et al. 2003). Bestelmeyer et al. (2009) outlined several steps to develop data-driven, iterative STMs based on expert knowledge, spatial stratification, multiple intensity field surveys, multivariate analyses, monitoring, and model refinement. Kachergis et al. (2013) also outlined how to develop STMs in a multidisciplinary context to include multiple sources of knowledge. However, STMs are often criticized for a lack of statistical rigor and exclusion of spatial scale and context (Bestelmeyer et al. 2011, Twidwell et al. 2013). Transition probabilities are usually described by qualitative or observational studies rather than experimental approaches, and measuring vegetation characteristics in a few plots will not characterize patterns within a region or allow inference to a larger landscape (Briske et al. 2005).

Further, a hierarchy of processes can interact to produce what is observed in one plot by influencing transitions between states (Bestelmeyer et al. 2011). Vegetation patterns also depend on scale. At a small scale, a plot might show heterogeneity in grazed and ungrazed grasses from livestock selectivity, but at a larger scale, the landscape could be homogenous because season-long grazing does not usually result in heavily used or unused areas (Fuhlendorf and Engle 2001).

Sagebrush Rangelands

STMs may be especially useful in arid and unpredictable communities, such as sagebrush rangelands where multiple stable states occur (Friedel 1991). The sagebrush biome of western North America once encompassed over 60 million hectares but has experienced a range reduction of approximately 45% (Knick et al. 2003, Miller et al. 2011). The invasion of exotic grasses such as cheatgrass (*Bromus tectorum*) and changing fire intervals have been implicated in the loss of diverse sagebrush rangelands, in addition to energy development and livestock grazing (West 2000, Miller et al. 2011). Fire in sagebrush rangelands can result in a state change through complete shrub cover loss, but unburned patches may remain depending on fire severity and landscape heterogeneity (Pyke 2011). Sagebrush recovery following a fire is dependent on initial species composition, completeness of the burn, and presence of obligate seeders (Davies et al. 2012). Few sagebrush species re-sprout following fire and recovery of shrub cover following a fire may take decades or even centuries (Knick et al. 2005, Baker 2006).

In addition to exotic plants and fire, other drivers of change in sagebrush rangelands include livestock grazing and mechanical treatment of shrubs. Grazing is currently the most common land-use on public and private sagebrush rangelands (Knick et al. 2011). Grazing

pressure by domestic livestock can impact water and nutrient availability, soil stability, and plant composition and thus, cause community phase and/or state transitions (Friedel 1991, Pyke 2011, Porensky et al. 2016). Moderate grazing pressure may not cause a state change, but heavy or continuous grazing during late spring-early summer can reduce perennial bunchgrasses and lead to a state or community phase with denser sagebrush cover (Pyke 2011). Sagebrush and other shrubs have often been viewed as competitors with palatable grasses and forbs, and sagebrush removal via mechanical or chemical methods was initially intended to improve herbaceous cover for livestock forage (Connelly et al. 2000, Beck et al. 2012). However, mechanical treatment to reduce shrub cover may have unintended consequences, such as an increase in annual forbs or exotic grasses with no increase in perennial cover (Davies et al. 2011).

Sagebrush Avifauna

Given the fragmentation and deterioration of sagebrush rangelands, many avifauna species in this ecosystem have experienced population declines (Dobkin and Sauder 2004). Some species rely entirely on sagebrush ecosystems for activities such as nesting and foraging (e.g., sagebrush sparrow [*Artemisiospiza nevadensis*], Brewer's sparrow [*Spizella breweri*], sage thrasher [*Oreoscoptes montanus*], and sage-grouse [*Centrocercus spp.*]), whereas others rely partially on sagebrush (e.g., green-tailed towhees [*Chlorura chlorura*], vesper sparrows [*Pooecetes gramineus*]; Braun et al. 1976). Greater sage-grouse (*C. urophasianus*) populations in North America have declined range-wide within the last fifty years (Connelly and Braun 1997, U.S. Fish and Wildlife Service [USFWS] 2015). Their distribution is closely associated with sagebrush distribution because sage-grouse are completely or partially dependent on sagebrush during all their various life stages (Patterson 1952). Therefore, many of the same factors implicated in the loss, degradation, or fragmentation of sagebrush communities in western North

America (e.g., invasive plant species, livestock grazing, and changing fire return intervals) are also associated with sage-grouse population and other sagebrush avian species declines range-wide (Connelly and Braun 1997, USFWS 2015).

Sage-grouse have been proposed as an umbrella species for other sagebrush-obligate species because they have a large annual range that overlaps with many other species, they are fairly sensitive to anthropogenic activity, their biology is well-known, and many habitat recommendations have been evaluated and published for sage-grouse (Rowland et al. 2006). However, this approach is often assumed and rarely tested (Simberloff 1998). Given a reduction in sage-grouse populations range-wide, large and small-scale conservation efforts (e.g., Sage Grouse Initiative) are underway to promote sagebrush habitat and prevent further declines in sage-grouse populations (USFWS 2015). However, it is unclear how efforts to promote sage-grouse habitat will affect other species which are also dependent on sagebrush. Sagebrush rangelands are heterogeneous and features relevant to sage-grouse may not be relevant to species with smaller home ranges (Hanser and Knick 2011). For example, one study found an increase in Brewer's sparrow and green-tailed towhee abundance three years following juniper (*Juniperus* spp.) removal to restore sage-grouse habitat (Sage Grouse Initiative 2015). Another study found that mechanical treatments to improve Gunnison sage-grouse (*C. minimus*) habitat reduced Brewer's sparrow density and green-tailed towhee occupancy in treated areas (Lukacs et al. 2016).

Ecological Sites and Wildlife Habitat

Several studies examined the occurrence of sagebrush fauna within ESDs and STMs (e.g., Holmes and Miller 2010) or evaluated the potential for ESDs and STMs to incorporate

measures that assess wildlife habitat (e.g., Williams et al. 2011). Range conditions across soil types (i.e., NRCS range site index) influence vegetation characteristics, which in turn, influence songbird abundance (Vander Haegan et al. 2000). Similarly, abundance of grasshopper sparrows (*Ammodramus savannarum*) was greatest in native perennial communities in the Columbia Basin, and any shift from this community was projected to decrease sparrow abundance (Holmes and Miller 2010).

To characterize ecological sites and states within STMs, protocols usually include measuring standard indicators, such as foliar and basal cover by species or functional group, species richness, plant production, and soil properties (Herrick et al. 2005, Bestelmeyer et al. 2009). In Wyoming, current ESD metrics did not inform predictions of greater sage-grouse nest occurrence or success beyond other habitat variables measured at a local or landscape scale (Doherty et al. 2011). The authors suggested including field metrics related to nest occurrence or success, such as sagebrush canopy cover, grass height and visual obstruction reading, in the standard ESD measures. Horizontal and vertical shrub structure differentiated ecological sites and songbird habitat in Northwest Colorado, and modified monitoring methods rather than standard ESD metrics best characterized shrub structure (e.g., shrub density, shrub canopy gaps, and shrub height; Williams et al. 2011).

The aforementioned studies illustrate a disconnect between rangeland management and wildlife habitat management. Ecological sites in the sagebrush biome provide different levels of habitat quality for different wildlife species, yet traditional ESD metrics do not differentiate vegetation structure attributes that influence wildlife habitat quality (Doherty et al. 2011, Williams et al. 2011). In particular, ESDs do not adequately characterize the horizontal and vertical shrub structure of sagebrush rangelands, which determine the quality of nesting and

cover habitat for multiple wildlife species (Doherty et al. 2011, Williams et al. 2011). They also do not account for the influence of spatial heterogeneity on wildlife habitat, such as arrangement of shrub patches (e.g., clumped or dispersed) within a site or surrounding management activities (Bestelmeyer et al. 2011).

However, ESDs and STMs have the potential to incorporate multiple ecosystem services, such as wildlife habitat and livestock forage, which would increase their appeal to a variety of stakeholders, such as government land agencies and private landowners (Bestelmeyer and Briske 2012). Land managers could then use STMs to predict how wildlife habitat and livestock forage would change in response to a state change. Further, by associating monetary value to ecosystem services, like livestock grazing and sage-grouse habitat, landowners can understand the economic impact and trade-off of managing for different states or objectives (Boyd et al. 2014). STMs also illustrate the value of landscape heterogeneity. If land managers only promote the reference state in STMs (Bestelmeyer et al. 2003), then species that thrive in seemingly degraded states may decline. For example, mountain plover (*Charadrius montanus*) nesting habitat is comprised of bare ground, and if the short grass prairie is only managed for livestock forage and greater grass cover, mountain plover populations could decline (Augustine and Derner 2012). Instead, STMs could promote an ecosystem approach whereby the objective is to maintain a functioning, intact system long-term, which may include seemingly degraded or disturbed states (Boyd et al. 2014).

Spatially Explicit STMs

STMs could be further improved if they included spatial context and scale. As currently constructed, they merely represent descriptions of states without acknowledgment of spatial variation in transition drivers, soil, and topography (Bestelmeyer et al. 2011). They also do not

incorporate scale dependent patterns or processes, which can influence transitions (Bestelmeyer et al. 2011). Spatially represented states could improve understanding of ecosystem services on the landscape, such as connectivity of wildlife habitat, and they could also enhance assessment, monitoring, and management of rangelands in a hierarchical or probabilistic framework (Briske et al. 2005, Bestelmeyer et al. 2009).

Bestelmeyer et al. (2011) suggest that STM development consider three scales (patch, site, and landscape) and three classes of spatial processes that produce spatial heterogeneity: spatial variation in driver histories, spatial dependence in response to drivers, and spatial contagion and feedbacks, such as the spread of transitions to nearby areas (Bestelmeyer et al. 2011). By examining patch size, arrangement, and other landscape patterns, managers can better identify and predict factors influencing transitions between states. Managers could also target states to test transition assumptions over time or with experiments to improve the rigor of STMs (Steele et al. 2012). Similarly, managers could combine simulated state-and-transition modeling (Daniel and Frid 2011) with spatially explicit states to forecast potential outcomes for management actions or disturbances within a region (Provenchar et al. 2007).

A logical starting place is to develop a STM (see Bestelmeyer et al. 2009) for one ecological site or similar ecological sites. States can be generalized across similar ecological sites because different states should represent differences in structure and ecological processes rather than differences in species composition (Steele et al. 2012). Ecological sites as defined by USDA-NRCS are already represented spatially via third order soil mapping units (Bestelmeyer et al. 2009). However, each soil map unit may contain multiple soil components or ecological sites due to fine-scale variation that cannot be mapped (Forbis et al. 2007). The map unit is named according to the major soil component or the dominant ecological site within the unit. For

regions with coarser variation in soil attributes and less bare ground, mapping states with their associated ecological site(s) is probably a reasonable approach. However, in more arid regions, approaches that incorporate fine-scaled variability in soil properties may need to be preserved. For example, Steele et al. (2012) mapped states by digitally editing the soil map units to represent multiple ecological sites within a map unit for the Chihuahuan Desert. They then used a manual classification system based on monitoring data, aerial imagery, and field visits to link vegetation state with the appropriate ecological site. Regardless of the approach, mapping states needs to be accessible to managers in order to increase their utility. Starting with a locally developed STM that is more accurate and relevant to local concerns and stakeholders would also increase the model's quality and utility (Steele et al. 2012, Bruegger et al. 2016).

Objectives

Given the need for effective management of multiple avifauna species within sagebrush rangeland and current limitations with STMs, I had several objectives for my dissertation. These research objectives were part of a larger collaborative effort to develop STMs in a participatory approach with local stakeholders in Northwest Colorado. My overall goal was simply to improve management efforts for sagebrush rangelands and their associated avifauna. My first objective was to include additional ecosystem services in a recently developed STM by predicting species richness and avifauna density for common sagebrush songbirds and greater sage-grouse in the states and community phases. This approach also resulted in a management tool that allowed landowners or biologists to gauge the impact of state changes on avifauna density, and it elucidated important habitat relationships for avifauna species in Northwest Colorado. In Chapter II, I model indices of songbird and sage-grouse abundance with fine-scaled vegetation predictors, like shrub cover and shrub height collected in three project areas. For my second objective, I use

the same previously developed STM and mapped states across the study area with a new approach applicable in sagebrush rangelands. In Chapter III, I use multinomial logistic regression with the state classification as the response variable and apply several remotely sensed biotic and abiotic predictors, such as bare ground and elevation, to predict states. I then predict the best model to all pixels within the study area and summarize spatial information about each mapped state, such as average patch size. For my last objective, I investigate the use of greater sage-grouse as an umbrella for several sagebrush-associated species (i.e., Brewer's sparrow, sage thrasher, sagebrush sparrow, and green-tailed towhee). In Chapter IV, I examine count-based regression models for songbirds and logistic regression models for sage-grouse with multi-scaled biotic predictors. I evaluate the correlation between apparent sage-grouse occurrence and estimated songbird densities per sampling plot, and map model-predicted surfaces for each species to determine if higher songbird densities are captured in areas likely to contain sage-grouse. Chapters II, III, and IV reflect each of these specific objectives and are intended for publication in peer-reviewed journals.

LITERATURE CITED

- Augustine, D. J., and J. D. Derner. 2012. Disturbance regimes and mountain plover habitat in shortgrass steppe: large herbivore grazing does not substitute for prairie dog grazing or fire. *Journal of Wildlife Management* 76:721-728.
- Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34:177-185.
- Beck, J. L., J. W. Connelly, and C. L. Wamboldt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. *Rangeland Ecology Management* 65:444-455.
- Bestelmeyer, B. T., and D. D. Briske. 2012. Grand challenges for resilience-based management of rangelands. *Rangeland Ecology and Management* 65:654-663.
- Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114-126.
- Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, Jr., D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology and Management* 62:1-15.
- Bestelmeyer, B. T., D. P. Goolsby, and S. R. Archer. 2011. Spatial perspectives in state-and-transition models: a missing link to land management? *Journal of Applied Ecology* 48: 746-757.

- Boyd, C. S., D. D. Johnson, J. D. Kerby, T. J. Svejcar, and K. W. Davies. 2014. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? *Rangeland Ecology and Management* 67:358-368.
- Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. *Wilson Bulletin* 88:165–171.
- Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management* 58:1–10.
- Bruegger, R. A., M. E. Fernandez-Gimenez, C. Y. Tipton, J. M. Timmer, and C. L. Aldridge. 2016. Multi-stakeholder development of state-and-transition models: a case study from northwestern Colorado. *Rangelands*. doi: 10.1016/j.rala.2016.10.008.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines for management of sage grouse populations and habitat. *Wildlife Society Bulletin* 28:967–985.
- Daniel, C. J., and L. Frid. 2011. Predicting landscape vegetation dynamics using state-and-transition simulation models. Pages 5-22 *in* First Landscape State-and-Transition Simulation Modeling Conference.
- Davies, G. M., J. D. Bakker, and A. M. Nafus. 2011. Are there benefit to mowing Wyoming big sagebrush plant communities? An evaluation in Southeastern Oregon. *Environmental Management* 48:539-546.
- Davies, G. M., J. D. Bakker, E. Dettweiler-Robinson, P. W. Dunwiddie, S. A. Hall, J. Downs, and J. Evans. 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecological Applications* 22:1562–1577.

- Dobkin, D. S., and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy: distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, OR, USA.
- Doherty, K. E., J. L. Beck, and D. E. Naugle. 2011. Comparing ecological site descriptions to habitat characteristics influencing greater sage-grouse nest site occurrence and success. *Rangeland Ecology and Management* 64:344–351.
- Forbis, T. A., L. Provenchar, L. Turner, G. Medlyn, J. Thompson, and G. Jones. 2007. A method for landscape-scale vegetation assessment: application to Great Basin rangeland ecosystems. *Rangeland Ecology and Management* 60:209-217.
- Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management* 44:422–426.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625-632.
- Garton, E. O., J. W. Connelly, J. S. Horne, C. S. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pp 293–382 *in* S. T. Knick and J. W. Connelly (editors). *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Hanser, S. E., and S. T. Knick. 2011. Greater Sage-Grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. Pp 473–487 *in* S. T. Knick and J. W. Connelly (editors). *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Herrick, J. E., J. W. Van Zee, K. M. Havstad, Burkett L. M., and W. G. Whitford. 2005.

- Monitoring manual for grassland, shrubland and savanna ecosystems. USDA-Agricultural Research Service, Jornada Experimental Range, Las Cruces, USA.
- Holmes, A. L., and R. F. Miller. 2010. State-and-transition models for assessing grasshopper sparrow habitat use. *Journal of Wildlife Management* 74:1834–1840.
- Kachergis, E. J., C. N. Knapp, M. E. Fernandez-Gimenez, J. P. Ritten, J. G. Pritchett, J. Parsons, W. Hibbs, and R. Roath. 2013. Tools for resilience management: multidisciplinary development of state-and-transition models for northwest Colorado. *Ecology and Society* <http://dx.doi.org/10.5751/ES-05805-180439>.
- Knick, S. T., A. L. Holms, and R. F. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. Pages 63–75 in V. A. Saab and H.D.W. Powell, editors. *Fire and avian ecology in North America. Studies in Avian Biology*, University of California-Press, Berkeley, USA.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.
- Knick, S. T., S. E. Hanser, R. F. Miller, D. A. Pyke, M. J. Wisdom, S. P. Finn, E. T. Rinkes, and C. J. Henny. 2011. Ecological influence and pathways of land use in sagebrush. Pages 203–251 in S. T. Knicks and J.W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology*, University of California-Press, Berkeley, USA.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.

- Lukacs, P. M., A. Seglund, and S. Boyle. 2015. Effects of Gunnison sage-grouse habitat treatment efforts on associated avifauna and vegetation structure. *Avian Conservation and Ecology* 10(2):7. <http://dx.doi.org/10.5751/ACE-00799-100207>.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 in S. T. Knicks and J.W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Patterson, R. L. 1952. *The Sage Grouse in Wyoming*. Sage Books, Denver, CO, USA.
- Porensky, L., K. Mueller, D. J. Augustine, and J. Derner. 2016. Thresholds and gradients in a semi-arid grassland: long-term grazing treatments induce slow, continuous and reversible vegetation change. *Journal of Applied Ecology* 53: 1013-1022.
- Provencher, L., Forbis, T., Frid, L., and G. Medlyn. 2007. Comparing alternative management strategies of fire, grazing, and weed control using spatial modeling. *Ecological Modelling*. 209: 249–263.
- Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. Pages 531–548 in S. T. Knicks and J.W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press Berkeley, USA.
- Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323-335.
- Sage Grouse Initiative. 2015. Sagebrush songbirds benefit from sage grouse habitat restoration. Science to Solutions Series Number 9. Sage Grouse Initiative. 4pp.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83:247-257.

- Steele, C. M., B. T. Bestelmeyer, L. M. Burkett, P. L. Smith, and S. Yanoff. 2012. Spatially explicit representation of state-and-transition models. *Rangeland Ecology and Management* 65:213-222.
- Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.
- Twidwell, D., B. W. Allred, and S. D. Fuhlendorf. 2013. National-scale assessment of ecological content in the world’s largest land management framework. *Ecosphere* 4:1-27.
- U.S. Fish and Wildlife Service. 2015. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition to List Greater Sage-grouse (*Centrocercus urophasianus*) as an Endangered or Threatened Species. FWS–R6–ES–2015–0146.
- Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, U.S.A. *Conservation Biology* 14:1145–1160.
- West, N. E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. Pages 15–26 *in* P. G. Entwistle, A. M. DeBolt, J. H. Kaltenecker, and K. Steenhof (editors). Sagebrush Steppe Ecosystems Symposium. U.S. Department of Interior (USDI) Bureau of Land Management Publication No. BLM/ID/PT-001001+1150. USDI Bureau of Land Management, Boise, Idaho.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:265–273.
- Williams, M. I., G. B. Paige, T. L. Thurow, A. L. Hild, and K. G. Gerow. 2011. Songbird relationships to shrub-steppe ecological site characteristics. *Rangeland Ecology and Management* 64:109–118.

CHAPTER II. MULTIPLE ECOSYSTEM SERVICES IN A STATE-AND-TRANSITION MODEL FOR SAGEBRUSH RANGELANDS

Summary

State-and-transition models (STM) describe multiple stable states and non-linear vegetation dynamics as conceptual models, and they usually include amount of livestock forage provided by each state. STMs can be improved by addressing multiple ecosystem services, such as wildlife habitat, so land managers can predict how wildlife populations might change in response to vegetation dynamics and drivers of change. Our objective was to incorporate avifauna density and species richness into a recently developed STM for sagebrush rangelands in Northwest Colorado. We stratified our study areas by ecological site or sagebrush cover and elevation where developed ecological sites were lacking. We surveyed randomly distributed plots for songbirds and greater sage-grouse (*Centrocercus urophasianus*) pellets, collected a suite of vegetation indicators at each plot, and quantified avifauna habitat relationships with count-based regression models. We then used the habitat models to predict songbird and sage-grouse pellet density based on average vegetation values per state or community phase. Moderate or increasing shrub cover were important predictors for most species, as were bare ground and shrub height, although responses varied by species. In the STM, we predicted higher densities for sagebrush and shrub-obligate species in the shrub-dominated states and phase and higher densities for grassland-associated species in the state and phase lacking shrub cover. We also predicted greater species richness for the shrub-dominated states and community phase. Our approach can assist local land managers and landowners gauge impacts of land-use decisions on avifauna populations, especially for species of conservation concern.

Introduction

State-and-transition models (STM) are conceptual models that describe rangeland dynamics, allowing both alternate stable states and conventional succession-retrogression dynamics (Bestelmeyer et al. 2003). STMs are composed of a reference state and often several alternate states (Bestelmeyer et al. 2003). Within a state, plant composition can shift among phases and along reversible pathways in response to weather or disturbance events reflecting the natural dynamics of variations in different plant communities (Bestelmeyer et al. 2003, Stringham et al. 2003). Transitions between states, however, imply crossing spatial and/or temporal boundaries (i.e., thresholds) in which significant ecological processes have been altered; transitions are the trajectories or drivers of change (Stringham et al. 2003).

A STM usually corresponds to one ecological site, which has distinctive soil, climatic, and topographical properties that determine a site's characteristic plant community (Bestelmeyer et al. 2003). Range condition was initially described in terms of palatable species for grazing and succession was described in terms of grazing pressure (Dyksterhuis 1949, Westoby et al. 1989). Now, ecological sites and states are described in terms of species richness, composition, structure, and ecological function (Stringham et al. 2003, Twidwell et al. 2013). A broader description of states could allow a broader inclusion of the services a state provides, such as wildlife habitat. Land managers could then use STMs to predict how wildlife habitat, and thus populations, may change in response to changing vegetation conditions (Holmes and Miller 2010). For example, Cagney (2009) described nesting and brood-rearing habitat quality for greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) and amount and quality of livestock forage among various states on a sandy ecological site. Further, by associating monetary value to ecosystem services, like sage-grouse habitat or livestock forage, landowners

can understand the economic impact and trade-off of managing for different states or objectives (Pritchett et al. 2012, Boyd et al. 2014).

Many of the threats facing wildlife populations are complex because animals use large landscapes and select habitat features at multiple scales (Johnson 1980). Therefore, these threats require equally complex solutions at the ecosystem level rather than species-specific approaches (Boyd et al. 2014). STMs could provide an ecosystem focus for wildlife management because they outline drivers of change that degrade range condition and ecological function, which may threaten wildlife habitat (Boyd et al. 2014). Conversely, STMs define the management actions that can maintain or restore desirable states to improve range condition and improve or restore wildlife habitat. For example, sage-grouse require intact sagebrush (*Artemisia* spp.) systems, yet pinyon-juniper (*Pinus-Juniperus* spp.) tree encroachment can be one factor limiting sage-grouse habitat (Miller et al. 2011). Fire is a natural mechanism to promote a sagebrush-dominated state and reduce pinyon-juniper establishment and encroachment, but fire also temporarily removes the sagebrush that sage-grouse require. Using a STM approach in this example could help stakeholders identify the best solution to maintain not just sage-grouse habitat, but a functioning, intact system long-term, which includes periodic fire and burned and unburned states (Boyd et al. 2014). Promoting multiple states across a larger landscape would also benefit multiple services and stakeholders rather than promoting a single state.

Because STMs could improve rangeland management by addressing multiple ecosystem services and promoting an ecosystem approach (Boyd et al. 2014), our objective was to create a decision support tool for local managers by incorporating avifauna densities and species richness as additional ecosystem services into a previously developed STM (Tipton 2015). Specifically, we collected vegetation and avifauna abundance data in three study areas dominated by

sagebrush, used the vegetation data to model sage-grouse and songbird habitat, and then used the habitat models to predict avifauna density and species richness for states and community phases in a STM developed with a participatory approach for one of the study areas (Bruegger et al. 2016). The STM we used for demonstration purposes included field data and local knowledge, which should result in a model that is more complete, better reflects local conditions and concerns, and is more likely to be used by those who help developed it (Knapp et al. 2011, Kachergis et al. 2013). Because the Natural Resource Conservation Service (NRCS) and other land management agencies have adopted STMs and ecological sites as the basis for rangeland assessment, monitoring, and management (Bestelmeyer et al. 2003), the need for locally relevant STMs addressing multiple ecosystem services is a necessity.

STMs may be especially useful in arid and semiarid systems, such as sagebrush rangelands, where multiple, persistent states occur (Laycock 1991). The sagebrush biome of western North America once encompassed over 60 million hectares but now occupies approximately half of its former distribution (Knick et al. 2003, Miller et al. 2011). The invasion of exotic grasses, such as cheatgrass (*Bromus tectorum*) and changing fire intervals have been implicated in the loss of diverse sagebrush rangelands, in addition to increasing energy development and persistent livestock grazing (Miller et al. 2011). Given the fragmentation and deterioration of sagebrush rangelands, many avifauna species in this ecosystem have undergone population declines (Dobkin and Sauder 2004). Some species rely entirely on sagebrush ecosystems for activities such as nesting and foraging (e.g., sagebrush sparrow [*Artemisiospiza nevadensis*], Brewer's sparrow [*Spizella breweri*], sage thrasher [*Oreoscoptes montanus*], and sage-grouse [*Centrocercus* spp.]), whereas others rely on shrub cover in general (e.g., green-tailed towhees [*Chlorura chlorura*]; Braun et al. 1976). Long-term data for sage-grouse

populations in North America show a decline of 17-47% over the last 30 years (Connelly and Braun 1997) and several songbird species that rely on sagebrush during the breeding season have also declined in all or part of their range (Dobkin and Sauder 2004). Therefore, STMs should address habitat for a variety of species, especially avian species of conservation concern, rather than for a single species or taxon (e.g., Doherty et al. 2011, Williams et al. 2011)..

Although multiple indicators (e.g., species richness, plant biomass, foliar cover; Herrick et al. 2005) are used to describe states or ecological sites, other environmental features may need to be included to accurately describe wildlife habitat (Doherty et al. 2011). Indicators such as shrub and grass height and shrub density are not traditionally collected, but may be useful to determine habitat structure for sage-grouse or other avifauna (Doherty et al. 2011, Williams et al. 2011). Horizontal and vertical shrub structure differentiated ecological sites and songbird habitat for several species, as described by modified monitoring methods rather than standard ecological site metrics (e.g., shrub density, shrub canopy gaps, and shrub height; Williams et al. 2011).

Recent studies have examined the occurrence of avifauna within ecological sites and STMs (Doherty et al. 2011) or evaluated the potential for ecological sites and STMs to incorporate measures that assess wildlife habitat (Williams et al. 2011). For instance, abundance of grasshopper sparrows (*Ammodramus savannarum*) was greatest in native perennial communities, and any shift from this community was projected to decrease sparrow abundance (Holmes and Miller 2010). We sought to improve upon previous efforts by integrating density of multiple species and taxa within a recently developed STM. Further, Tipton (2015) developed the STM with field data and local knowledge in a participatory approach (Tipton 2015, Bruegger et al. 2016), so the results of this effort should be more relevant to local managers and landowners (Knapp et al. 2011, Kachergis et al. 2013).

Methods

Study Area

We collected vegetation and avifauna abundance data at three sagebrush-dominated study areas in Northwest Colorado. West Moffat was the most arid and characterized by low sagebrush (*A. arbuscula*)-Wyoming big sagebrush (*A. tridentata wyomingensis*) communities. Soils were highly intermixed and variable with topography. Wyoming big sagebrush communities and loamy or sandy soils dominated East Moffat. Receiving the most moisture, our study area in east-central Routt County was dominated by mountain big sagebrush (*A. t. vaseyana*) on loamy soils and low sagebrush on clayey soils. A bunchgrass (e.g., Sandberg bluegrass [*Poa secunda*]) or western wheatgrass (*Pascopyrum smithii*) dominated the understories in each study area. The study areas (Fig. 2.1) were located across a precipitation gradient from west to east and annual precipitation varied from 20-40 cm for West Moffat, 18-30 cm for East Moffat, and 35-45 cm for Routt (Miller et al. 2011). Cattle grazing occurred on all three study areas and sheep grazing also occurred on one landowner's private property in East Moffat. Stocking rates for all landowners were at or below recommended guidelines. Three wildfires occurred prior to the study in East Moffat: a 2010 wildfire (3,185 ha of which 506 ha were re-seeded with native species in 2011), a 2008 wildfire (10,243 ha), and a smaller 2008 fire (1,505 ha). Past mechanical treatments to reduce shrub density in East Moffat included mow, brush beat, and drag treatments, each < 200 ha in size and 14-20 years old.

Our data collection coincided with data collection for the STM development, which was accomplished using a participatory approach (Tipton 2015, Bruegger et al. 2016). Therefore, where we collected avifauna and vegetation data in each of the three study areas varied based on local stakeholder concerns. For East Moffat, stakeholders were most interested in Sandyland and

Rolling Loam ecological sites and areas of past treatments or disturbances, so we randomly allocated sampling plots (spaced >200 m) within past treatments (e.g., burned and mechanically treated areas) and areas with no known treatments on Sandyland and Rolling Loam sites (using Web Soil Survey Geographic [SSURGO] database). We also allocated a small proportion of plots on Deep Loam, Sandy Foothills, and Claypan ecological sites because they were intermingled with the Sandyland and Rolling Loam sites, and past treatments or disturbances of interest to stakeholders occurred on these sites (Tipton 2015).

For Routt, STMs were developed for Claypan and Mountain Loam ecological sites from a precursor project (Kachergis et al. 2011), so we sampled at established and additional locations in this area. For West Moffat, local stakeholders were most interested in specific vegetation types (i.e., Wyoming big sagebrush and salt shrub communities) rather than ecological sites. Further, ecological sites had not been defined for this area and range sites were poorly defined. Therefore, we stratified the area by elevation and big sagebrush cover using a digital elevation model and a remotely sensed vegetation product (Homer et al. 2012), and allocated sampling plots among the strata with greater effort given to the higher sagebrush cover strata.

We collected vegetation and avifauna data at all three study areas and used these data to quantify avifauna habitat relationships. However, for demonstration purposes, we are only predicting avifauna densities within the STM developed for East Moffat (Tipton 2015). This STM was generalized across multiple ecological sites, mainly due to landowner interest and local observations that plant communities responded similarly to treatments and disturbances across sandy and loamy ecological sites. Further, Tipton (2015) did not find a difference among vegetation clusters or disturbance response based on abiotic characteristics associated with ecological site.

Field Surveys

To incorporate multiple avifauna species into the STM, we surveyed for greater sage-grouse and several songbird species in each project area at 144 randomly generated plots (73 in East Moffat, 52 in West Moffat, and 19 in Routt; Fig. 2.1) mid-May to late June 2013-2015. To estimate sage-grouse relative abundance, we surveyed a 10-m radius area at each plot for sage-grouse pellets. We searched within 2-m increments beginning at plot center to reduce observer error (Dahlgren et al. 2006). We recorded the number of single pellets, roost piles, and number of pellets per roost pile. Single pellets reflected general use areas where grouse were most likely foraging or traveling and roost piles reflected roost areas where groups of birds gather to rest, often defecating in piles (Patterson 1952, Hanser et al. 2011). Pellets were recorded as a roost pile if ≥ 2 pellets were found within a 30-cm diameter area (Hanser et al. 2011). We also calculated a naïve estimate of pellet detectability to ensure we were detecting a majority of the pellets within a plot; we re-surveyed a small subset of plots within 1-2 days of the first survey to determine how many pellets we missed during the initial survey. We used a simple mark-resight equation ($\beta = (n_1 - n_2) / n_1$) to determine pellet detectability where n_1 is the number of pellets or roost piles detected the first survey and n_2 is the number of pellets or roost piles detected on the second survey (Pollock et al. 2002).

To estimate songbird abundance, we conducted standard point count surveys at the center of each plot following a distance sampling protocol (Buckland et al. 2001). The protocol included focusing on detections at and surrounding the point and measuring radial distance with rangefinders to the point where each bird was first detected (Buckland et al. 2001). We identified birds both audibly and visually within a six-minute interval at each point and recorded detected individuals only once. We conducted surveys during the breeding season from sunrise to

approximately four hours after sunrise depending on weather. We did not conduct surveys during inclement weather, such as rain or windy conditions when activity of the birds or detectability of the birds was hindered. We also conducted surveys beginning at lower elevation plots earlier in the breeding season and moved up in elevation as the season progressed to capture the phenology of the birds' breeding activity (Hanni et al. 2013).

We measured a suite of ecological site metrics (e.g., vegetation and soils attributes; Herrick et al. 2005) at all survey plots during the summers following avifauna surveys. These metrics were used in both the STM development and to model avifauna habitat. For predictors in the avifauna habitat models, we primarily used foliar cover by species, litter, rock, dung, and bare ground as measured with the line-point intercept (LPI) method (Bonham 1989) on five parallel transects at 1-m intervals. For further details on the ecological site metrics, see Tipton (2015). We collected several additional metrics to further characterize avifauna habitat. We assessed visual obstruction with a modified Robel pole (Robel et al. 1970). We recorded visual obstruction (VO) at five evenly spaced points along two transects per plot, with VO viewed from four ordinal directions per point. The pole was divided into alternating half decimeters and an observer recorded the lowest visible half decimeter from a distance of four meters from the pole and viewed from a height of one meter. We also measured grass height of the nearest plant to each VO reading and averaged the 10 heights per plot. To further characterize structural diversity, we measured height of the tallest shrub (excluding inflorescences) intercepting the transect when taking LPI measurements.

Data Analyses

Avifauna Detection Probabilities

To estimate songbird density and examine potential variables affecting detectability, we used program Distance 6.0 (Thomas et al. 2010). We excluded outlier detections based on visual inspection of detection histograms and binned distances accordingly (Buckland et al. 2001). Detectability variables included start time, Julian date, observer, how the bird was detected (i.e., calling, singing, or visual), temperature, cloud cover, and wind speed (Hanni et al. 2013). We selected the best detection model for each species using Akaike's Information Criterion (Burnham and Anderson 1998) and used the best model to predict density estimates for each plot. We then used plot-specific density estimates and survey effort (i.e., number of times a plot was surveyed) to generate an offset value to scale counts for site-specific variability in detection (Buckland et al. 2009). We also compared density estimates for the common species on plots surveyed in multiple years to determine if we could combine data from multiple field seasons (Buckland et al. 2001).

Avifauna Model Development and Evaluation

We evaluated count-based regression models (i.e., generalized linear models) for songbird abundance and sage-grouse pellets with the vegetation metrics collected at each plot. We included sampling plots from study areas for a species' model development only if we detected songbirds or pellets in that area (e.g., if a species was only detected in West and East Moffat, we did not include Routt sampling plots in model development to avoid making false inferences). For each songbird model, we excluded songbird counts beyond the truncation distance (as determined by detection histograms) and included an offset term. For the sage-grouse models, we fit models for single pellet counts and roost pile counts to reflect areas where

the birds forage and roost. We hypothesized that shrub-obligate species would respond positively to sagebrush or shrub cover and non-shrub-obligate species would respond negatively, but each species should respond differently to understory components depending on life history traits.

We also examined count-based regression models for the number of common species detected per plot and the number of shrub-obligate species per plot to compare species richness in the STM. Common species included both shrub-obligates (i.e., Brewer's sparrows, green-tailed towhees, sagebrush sparrows, sage thrashers, and sage-grouse) and non-shrub-obligates (i.e., horned larks [*Eremophila alpestris*], vesper sparrows [*Pooecetes gramineus*], and western meadowlarks [*Sturnella neglecta*]). Shrub-obligate species included Brewer's sparrows, green-tailed towhees, sagebrush sparrows, sage thrashers, and sage-grouse. We only calculated richness metrics with these species because we had enough detections for each to estimate detectability. To determine the number of songbirds present at each plot for the richness metrics, we calculated the minimum density to support a songbird territory following Aldridge et al. (2011). We used the model-predicted plot density for each species and the largest territory size recorded for each species in the Birds of North America species' accounts (Poole 2005) or Colorado Parks and Wildlife species' accounts (Boyle and Reeder 2005). For sage-grouse pellets and roost piles in the richness metrics, we classified a plot as containing sage-grouse if ≥ 1 single pellet or roost pile was detected. We used presence/absence of sage-grouse from the raw counts rather than the model-predicted densities due to high pellet detectability. We chose to evaluate species richness per state rather than a diversity index because a diversity index could not account for the indirect relationship between individual counts of songbirds and counts of pellets.

For all count models, we first identified the appropriate distribution (i.e., Poisson and negative binomial) for each species using an intercept-only model and Vuong's test (Hilbe

2011). We examined histograms of raw counts and counts >1 to check for non-linear relationships, outliers, and variables with limited distributions to part or all of the study area. If plots showed evidence for non-linearity, we evaluated a linear and a quadratic model with Bayesian Information Criterion (BIC; Hilbe 2011) to determine which model structure to retain. We used Pearson's correlation coefficient to determine if any of the variables were overly correlated (i.e., $r \geq |0.7|$; Zar 2010). We performed all analyses in Program R 3.3.2 (R Development Core Team 2015).

We then used BIC to compare models for combinations of predictor variables (excluding overly correlated variables) to determine the best models explaining sage-grouse pellet and songbird abundance and species richness. We determined competitive models as a model with $\Delta\text{BIC} \leq 2$. For all species, we included the best shrub structure variable (i.e., sagebrush cover, shrub cover, or VO) and evaluated a shrub structure-only model. Most species included in the analysis are sagebrush- or shrub-obligate species and models without a shrub structure variable would not be as useful for management of sagebrush rangelands. To avoid over-fitting models, we did not include more than one variable per 10% of plots with a songbird or pellet count in any model (Hosmer and Lemeshow 2000) and excluded models when coefficients of variables switched direction.

To assess the fitted models over an intercept-only model, we calculated a McFadden's pseudo- R^2 value (Zar 2010) and used a chi-square likelihood ratio test with the `lrtest` function (in package "lmtest") to determine goodness-of-fit for the top model over an intercept-only (null) model. Because we did not have independent datasets to evaluate the predictive capability of our top models for songbirds, sage-grouse, and species richness, we evaluated predictive success

using five-fold cross validation (Hastie et al. 2009) with the cvFit function (in package “cvTools”).

Avifauna Abundance per State or Community Phase

To incorporate avifauna density into the STM for East Moffat (Fig. 2.2; Tipton 2015), we used our best count model(s) for each species to predict the number of individual songbirds per hectare and the number of sage-grouse single pellets and roost piles within 0.03 ha per state or community phase. The STM included two shrub-dominated states (diverse shrubland and needle-and-thread [*Hesperostipa comata*] shrubland), a native grassland state, and a grass-dominated and shrub-dominated phase within a crested wheatgrass (*Agropyron cristatum*) state (Appendix I; Tipton 2015). For each state or phase, we calculated average vegetation conditions for predictor variables (e.g., shrub cover and bare ground) and average offset terms for songbird detectability. We then used the average vegetation values and offset terms per state/phase and predicted songbird or pellet density per state/phase using each species’ best regression model(s). We also used our best species richness models to predict richness per state/phase for common species and for shrub-obligate species only. For species with multiple competitive models, we model averaged predicted densities. We calculated 95% confidence intervals around each predicted value using the estimated standard error and a critical value of 1.96 (Zar 2010). To match the predicted pellet densities per state/phase to the predicted songbird densities per state/phase, we re-scaled our predicted pellets from pellets/0.03 ha to pellets/1 ha. To better reflect variation in vegetation and inform management decisions, we also predicted bird and pellet densities using the minimum and maximum vegetation values for each state/phase. These values were obtained from field sampling and allowed us to predict a range of predicted densities based on the range of vegetation components, such as shrub cover, associated with a state/phase

rather than just an average value. However, the predicted densities do not necessarily reflect maximum and minimum bird or pellet densities per state/phase because a species could prefer greater shrub cover, but less bare ground. Therefore, the predicted densities may reflect multiple vegetation components.

Results

Avifauna Detection Probabilities

We detected a total of 367 Brewer's sparrows on 109 plots, 97 green-tailed towhees on 45 plots, 129 sagebrush sparrows on 49 plots, 103 sage thrashers on 56 plots, 353 horned larks on 93 plots, 166 vesper sparrows on 64 plots, and 230 western meadowlarks on 77 plots. Based on a subset of plots surveyed in >1 season, we did not find a difference in density estimates for the more common songbirds, and therefore, combined data among field seasons. We binned songbird counts into 6 or 7 bins and truncated distances >200-250 m, depending on the species. Average offset value was 0.25 for Brewer's sparrows, 1.29 for green-tailed towhees, 1.27 for sagebrush sparrows, 1.42 for sage thrashers, and 0.66, 0.71, and 1.79 for horned larks, vesper sparrows, and western meadowlarks, respectively. We counted 996 single pellets on 58 plots (mean of 7 pellets per plot), and 242 roost piles on 46 plots (mean of 2 piles per plot) and truncated single pellets to <100 and roost piles to <25 to remove outlier groups. Based on 27 plots we surveyed twice in 2013 and 2014, our naïve estimate of detectability was 0.91 for roost piles and 0.86 for single pellets, so we did not include an offset term to scale pellet counts in subsequent regression models for sage-grouse.

Avifauna Model Development and Evaluation

Based on Vuong's test, the negative binomial distribution was the best model structure for all songbird species, single pellets, and roost piles. For total species richness and shrub-obligate species richness, a Poisson distribution was best, given limited zeroes in the datasets. We did not detect sagebrush sparrows, sage thrashers, or sage-grouse pellets in Routt, so we restricted model development for these species to East and West Moffat (Fig. 2.1). We only detected one horned lark in Routt, so we also restricted model development for this species to East and West Moffat.

Of the 11 variables included (Table 2.1), sagebrush cover, total shrub cover, and VO were highly correlated, so only the best variable was retained for each species. Shrub height and VO and grass and herbaceous cover were positively correlated and bare ground was negatively correlated with litter, grass cover, and total herbaceous cover. For species' models that were restricted to East and West Moffat study areas, shrub height was also overly correlated with sagebrush and shrub cover, and litter and grass were positively correlated. Therefore, we did not include these variables in the same model. We excluded forb cover and exotic plant cover from subsequent models due to limited distribution throughout the study area. However, for species' models that were restricted to East and West Moffat, forb and exotic cover both had a more even distribution across these two areas and were thus, included in models for sage thrashers, sagebrush sparrows, and sage-grouse. For species exhibiting non-linear responses to predictors, see Table 2.3.

Our quantitative models confirmed our hypotheses regarding avifauna habitat relationships. The best model for Brewer's sparrows included shrub cover and shrub height (BIC

= 574.26), a second competitive model included shrub cover, shrub height, and herbaceous cover with a quadratic term (BIC = 574.65), and a third competitive model also included grass height (BIC = 576.06; Table 2.2). Brewer's sparrow counts increased with greater shrub cover and taller shrubs and grasses and peaked at approximately 38% herbaceous cover (Table 2.3; Fig. 2.2). The best model for green-tailed towhees included shrub cover, shrub height, and cover of bare ground (BIC = 288.51; Table 2.3). Green-tailed towhee counts increased with greater shrub cover and shrub height but decreased with more bare ground (Table 2.3; Fig. 2.4). The best model for sagebrush sparrows included shrub cover plus a quadratic term, grass cover, and exotic plant cover (BIC = 308.01; Table 2.2). Sagebrush sparrow counts peaked around 21% shrub cover, and counts increased as grass and exotic plant cover decreased (Table 2.3; Fig. 2.5). The second-best model for sagebrush sparrows was similar but did not include exotic plant cover (BIC = 308.48). Two other competitive models were discarded because they were essentially the same model as the best model (i.e., litter and bare ground were overly correlated with grass cover in the best model; Table 2.2). The best model for sage thrashers included shrub cover plus a quadratic term (BIC = 293.53), a second competitive model included an intercept term only (null model; BIC = 294.18), and the third best model included litter plus shrub cover (BIC = 294.71; Table 2.2). Sage thrasher counts peaked around 30% shrub cover and increased with more litter (Table 2.3; Fig. 2.6).

The best model for sage-grouse general use sites (i.e., single pellets) included sagebrush cover, bare ground, and a quadratic term for bare ground (BIC = 587.63; Table 2.2). Single pellets were positively associated with sagebrush cover and peaked around 22% bare ground (Table 2.3; Fig. 2.7). The second best model for general use sites included only sagebrush cover (BIC = 587.76). The best model for roost sites included sagebrush and herbaceous cover (BIC =

399.35), followed by a model containing sagebrush and forb cover (BIC = 399.69), an intercept-only model (BIC = 400.21), a model containing just sagebrush (BIC = 400.40), and a model containing sagebrush and forb cover and grass height (BIC = 400.4; Table 2.2). Roost piles increased with sagebrush cover and decreased with herbaceous and forb cover and taller grasses (Table 2.3; Fig. 2.8). Two other models were also competitive for roost sites (sagebrush plus grass cover and sagebrush plus bare ground; Table 2.2). However, grass cover and bare ground were correlated with herbaceous cover, so we excluded these models.

The best model for horned larks included shrub cover and litter (BIC = 499.22) and the second best model included shrub cover only (BIC = 500.26; Table 2.2). Horned lark counts decreased with greater shrub cover and litter (Table 2.3; Fig. 2.9). The best model for vesper sparrows included shrub cover and bare ground (BIC = 379.39) and the second best model also included grass height (BIC = 379.98). Vesper sparrow counts increased with less shrub cover and bare ground and taller grasses (Table 2.3; Fig. 2.10). The best model for western meadowlarks included shrub cover and bare ground (BIC = 466.33; Table 2.2) and meadowlarks preferred less shrub cover and bare ground (Table 2.3; Fig. 2.11). All common species richness and shrub-obligate species richness each had one competitive model, shrub cover plus a quadratic term (BIC = 572.63 and 488.68, respectively; Table 2.2). Species richness for common and shrub-obligate species both peaked at approximately 30% shrub cover (Table 2.3; Fig. 2.12). I list model assessment metrics for each species in table 2.2.

Avifauna Abundance per State or Community Phase

We predicted the highest density of Brewer's sparrows, sage thrashers, and green-tailed towhees in the diverse shrubland state (3.3 Brewer's sparrows/ha; 0.9 sage thrashers/ha; 1.1

green-tailed towhees/ha; Table 2.4). The lowest predicted densities occurred in the crested wheatgrass-grassland community phase (0.9 Brewer's sparrow/ha; 0.3 sage thrashers/ha; 0.1 green-tailed towhees/ha). We predicted the greatest density of sagebrush sparrows in the needle-and-thread shrubland state (0.8 sagebrush sparrows/ha) and the lowest in the crested wheatgrass-grassland community phase (0.02 sagebrush sparrows/ha). We predicted the highest single grouse pellet and roost pile densities in the crested wheatgrass-shrubland community phase (545 pellets/ha; 68 roost piles/ha) and the lowest in the native grassland state (114 pellets/ha; 28 roost piles/ha).

For horned larks and vesper sparrows (non-shrub-obligate species), the crested wheatgrass-grassland phase promoted the greatest density (6.4 horned larks/ha; 3.0 vesper sparrows/ha; Table 2.4), and the native grassland state promoted the highest western meadowlark density (4.4 western meadowlarks/ha). The diverse shrubland state promoted the lowest density for horned larks (1.0 horned larks/ha), while the crested wheatgrass-shrub phase promoted the lowest vesper sparrow and western meadowlark densities (0.9 vesper sparrows/ha; 1.1 western meadowlarks/ha). Finally, the diverse shrubland state supported the greatest richness for common (6.7 species) and shrub-obligate species (4.0 species), while the crested wheatgrass-grassland phase supported the lowest richness for common (4.2 species) and shrub-obligate species (1.5 species; Table 2.4).

Discussion

We quantified fine-scaled habitat relationships for several avifauna species in Northwest Colorado and incorporated these relationships into a recently developed STM. The predicted avifauna densities per state or community phase reflect these relationships. As expected, we predicted greater densities for sagebrush-associated species and lower densities for grassland-

associated songbirds in the states or community phase dominated by sagebrush cover (Table 2.4). For example, Brewer's sparrow densities were highest for the diverse and needle-and-thread shrubland states and the crested wheatgrass-shrubland phase (3.1-3.3 birds/ha), which had more shrub cover. In our study, Brewer's sparrows responded positively to shrub cover, shrub and grass height, and moderate herbaceous cover. However, this species is usually the most prevalent songbird in sagebrush rangelands (Wiens and Rotenberry 1981, Aldridge et al. 2011), which is likely why there was not a large difference in predicted densities among the shrub-dominated states and community phase.

We predicted the highest green-tailed towhee density for the diverse shrubland state, as this species responded positively to greater shrub and ground cover and taller shrubs (Fig. 2.4). The diverse shrubland state had the highest shrub cover on average (33%), as well as taller shrubs on average (Fig. 2.2). Within sagebrush rangelands, towhees may be more common in mountain big sagebrush-montane shrub ecotones or areas interspersed with pinyon-juniper (Knopf et al. 1990, Aldridge et al. 2011). They nest in a diversity of taller shrubs with a greater proportion of living branches (Knopf et al. 1990, Jehle et al. 2006). Because green-tailed towhees are often found in higher elevation, montane shrub communities, ground cover is usually greater and provides ample foraging opportunities for seeds and insects under thick cover (Aldridge et al. 2011, Dobbs et al. 2012). In our study, the diverse shrubland plots typically occurred at higher elevations and contained the least bare ground of the shrub-dominated states and phase (Fig. 2.2).

Sagebrush sparrow densities peaked for moderate shrub cover and less ground cover (Fig. 2.5). Therefore, sagebrush sparrow predicted densities were highest for the needle-and-thread shrubland state and crested wheatgrass-shrubland community phase, which were comprised of

less average shrub cover than the diverse shrubland state (21-22% versus 33%) and more bare ground (9-15% versus 7%; Fig. 2.2). In the Wyoming Basin, sagebrush sparrow abundance was greater for sagebrush landscapes containing less sagebrush cover (Aldridge et al. 2011).

Sagebrush sparrows also tend to use areas with more bare ground during the breeding season (Wiens et al. 1990), probably because they forage on the ground and walk between nesting and foraging sites (Martin and Carlson 1999). However, all of our predicted sagebrush sparrow densities were low within the STM for East Moffat (Table 2.4). For unknown reasons, sagebrush sparrows were not abundant in East Moffat compared to West Moffat, as other survey efforts have found (Boyle and Reeder 2005, Bird Conservancy of the Rockies 2016).

Sage thrasher densities also peaked for moderate shrub cover, although they preferred a higher amount than sagebrush sparrows (Fig. 2.6). They also responded positively to more litter. We predicted similar, low thrasher densities across the shrub-dominated states and phase (Table 2.4), although litter was the highest in the needle-and-thread shrubland state (72%; Fig 2.2). Sage thrashers are typically associated with large sagebrush landscapes (Knick and Rotenberry 1995, Aldridge et al. 2011), and they may use areas with greater litter, which provide better foraging opportunities for this ground feeder (Reynolds et al. 1999). However, our sage thrasher models explained little variation, which could indicate that we missed an important environmental feature in our modeling efforts. The scale we examined for environmental features (i.e., 50 × 50-m plot) may also have been too small for this songbird, especially considering previous studies have found features at larger extents to be the most influential (e.g., Aldridge et al. 2011).

Predicted sage-grouse single pellet density was highest for the crested wheatgrass-shrubland community phase and roost pile density was highest for this phase and the needle-and-thread shrubland state (Table 2.4). Both single pellet and roost pile models indicated sage-grouse

preferred greater sagebrush cover as expected. Sage-grouse reliance on sagebrush has been documented for all life stages, such as lekking (e.g., Patterson 1952), nesting (e.g., Gregg et al. 1994), brood-rearing (e.g., Sveum et al. 1998), and over winter (e.g., Doherty et al. 2008). Sagebrush cover was only slightly lower in the crested wheatgrass-shrubland phase compared to the diverse shrubland state (21% versus 22%; Fig. 2.12).

Pellet densities were likely higher in the crested wheatgrass-shrubland phase because of the higher proportion of bare ground (15%) compared to the diverse shrubland state (7%). Based on our top models, single pellets peaked for areas containing 20-22% bare ground (Fig. 2.7), while roost piles were associated with less herbaceous cover (Fig. 2.8). Areas containing 20-22% bare ground would still have 78-80% shrub and herbaceous cover. To promote sage-grouse breeding habitat (i.e., lekking, nesting, and brood-rearing), Connelly et al. (2000) recommend maintaining 15-25% sagebrush canopy cover and $\geq 15\%$ herbaceous cover, but the appropriate mixture of shrub and herbaceous cover would likely vary depending on the life stage and the ecological site. For example, lek sites are typically areas with less sagebrush and herbaceous cover (either natural or anthropogenic clearings; Patterson 1952), while nesting habitat includes abundant forbs for pre-nesting hens, higher residual grass cover comprised of taller grasses, and taller sagebrush shrubs with greater canopy cover (Aldridge and Brigham 2002, Holloran et al. 2005, Connelly et al. 2011a). Our top roost models also indicated negative relationships between roost pile density and grass height and forb cover (Fig. 2.8). Average grass height was lowest in the diverse shrubland state compared to the other shrub-dominated state and phase (Fig. 2.2), although forb cover was lowest for the needle-and-thread shrubland state. One explanation for these negative relationships could be that roosting sage-grouse require shrub cover for protection

from predators, but less and shorter ground cover increase visibility of threats and provide easy escape routes for the resting birds (Patterson 1952).

As expected, our non-shrub-obligate species had higher predicted densities in the grassland-dominated state and community phase (Table 2.4). These three species all responded positively to less shrub cover because horned larks, vesper sparrows, and western meadowlarks are considered grassland species (Wiens and Rotenberry 1981). However, given the heterogeneity of sagebrush rangelands and structural diversity, these species can be found in areas with varying shrub and ground cover (Rotenberry and Wiens 1980, Wiens et al. 1987). Predicted horned lark density was highest for the crested wheatgrass-grassland phase, likely reflecting their negative relationship with litter (Fig. 2.9). Average litter cover was higher in the native grassland state, but average bare ground was greater for the crested wheatgrass-grassland phase (Fig. 2.2). Horned larks typically occupy areas with less sagebrush and grass cover (Wiens et al. 1987, Knick and Rotenberry 1995), and they also nest in bare ground spaces, such as two-track ruts and plowed fields (Beason 1995). In contrast, predicted western meadowlark density was highest for the native grassland state (Table 2.4) because this songbird was associated with less bare ground (Fig. 2.11). Indeed, within sagebrush rangelands, western meadowlarks occur where shrub cover is limited and grass cover and litter are greater (Wiens and Rotenberry 1981, Knick and Rotenberry 1995) because they use grass cover to conceal nests (Davis and Lanyon 2008). Predicted vesper sparrow density was similar between the grassland-dominated state and community phase. In our study, they preferred less bare ground but taller grasses (Fig. 2.10), which is reasonable for a species that uses surrounding grass cover to conceal nests (Jones and Cornely 2002). The native grassland state had less bare ground while the crested wheatgrass-grassland phase had taller grasses on average (Fig. 2.2).

Previous studies have shown that vertical and horizontal structure within a site affect avian species diversity, so that as habitat complexity increases, niche partitioning should also increase (MacArthur and MacArthur 1961, Rotenberry and Wiens 1980, Williams et al. 2011). For instance, at small scales, songbirds may partition nest placement within or under shrubs to avoid competition (Rich 1980). Predicted richness for both indices was greatest in the shrub-dominated states and community phase (Table 2.4). Compared to the native grassland state and crested wheatgrass-grassland phase, the shrub-dominated areas contained greater structural diversity. Shrub height varied from 14-66 cm, 0-71 cm, and 34-62 cm for the diverse shrubland state, needle-and-thread shrubland state, and crested wheatgrass-shrubland phase compared to 0 cm in the crested wheatgrass grassland phase and 0-31 cm in the native grassland state (Fig. 2.2). Similarly, species richness and structural diversity for shrub and grass-associated birds were positively correlated in the Great Basin region (Wiens and Rotenberry 1981). In our study, species richness for all common species and shrub-obligate species was associated with moderate shrub cover (approximately 30%; Fig. 2.12), which only occurred in the shrub-dominated states and community phase (Fig. 2.2). Further, the top richness models did not include an understory component, so they are more generalizable for species with different understory preferences, such as sagebrush sparrows and green-tailed towhees. However, given the low variance explained for both richness models, we could also have neglected to consider other environmental features or features at larger scales that may influence richness.

In the STM, our confidence intervals did not overlap for most predicted songbird densities among states or community phases with large structural differences. For example, predicted Brewer's sparrow and western meadowlark densities differed for the shrub-dominated states and phase compared to the grass-dominated state and phase (Table 2.4). This is not

surprising given the structural differences between a shrub-dominated and a grass-dominated landscape for shrubland versus grassland-associated species (Knick and Rotenberry 1995). In contrast, confidence intervals for sage-grouse pellet and roost pile densities overlapped among all states and phases in the STM (Table 2.4). One reason for this is that we simply did not capture the best relationship between pellets and habitat features. Both our roost and general use models had low explanatory power and the general use model also had a high prediction error (Table 2.2). Our predictor variables may have been too fine-scaled for a wide-ranging species (Connelly et al. 2011a), although previous studies have identified similar variables as important for sage-grouse (e.g., Doherty et al. 2011). The study areas in Moffat County may also represent high-quality sage-grouse habitat where grouse are known to occur throughout (Colorado Greater Sage-grouse Steering Committee 2008, Bird Conservancy of the Rockies 2016), and we did not adequately discriminate amongst habitat and non-habitat within the area. It is also possible that the pellets were not a reliable index for sage-grouse relative abundance. However, previous studies have used pellets as a surrogate for habitat use (Dahlgren et al. 2006) and abundance (Hanser et al. 2011) and evaluated pellets with a secondary measure, like bird-dog surveys or lek locations. Therefore, we have confidence in the relationships we found between pellets and habitat features. One way to reduce overlapping confidence intervals in future efforts is to increase sample sizes of vegetation plots for defining states and phases, so there is greater distinction and more certainty of vegetation values per state or phase. In addition, increasing sample sizes of avifauna plots in states or phases that are not high-quality grouse habitat (e.g., cheatgrass-dominated grassland or sagebrush state with pinyon-juniper) should widen the gap in predicted pellet densities among states.

Management Implications

Our integration of avifauna density into a locally relevant STM (Bruegger et al. 2016) is useful for management decisions for a variety of reasons. If local managers or landowners want to manipulate over or understory vegetation, then they can gauge how predicted songbird or pellet densities may change in response (Holmes and Miller 2010). For example, if managers want to increase a sagebrush-obligate species, like Brewer's sparrows, then they should promote the shrub-dominated states and community phase, which supported higher Brewer's sparrow densities (Table 2.4). If a manager wanted to increase the local green-tailed towhee population, then vegetation characteristics associated with the diverse shrubland state, such as greater shrub and herbaceous cover and taller shrubs (Fig. 2.2), should be promoted. Managers can also estimate how avifauna populations might respond to a landscape disturbance, such as fire, in addition to how livestock forage production may change. In our study area, a fire transitioning the needle-and-thread shrubland state to a native grassland state, would reduce Brewer's sparrow density by approximately 2 birds/ha (Table 2.4), but would increase forage by roughly 350 kg/ha (Fig. 2.2) for domestic and wild ungulates.

Our predicted avifauna densities were associated with a range of vegetation values per state or phase, which could further guide management decisions. For example, shrub cover within the native grassland state varied from 0-6% (Fig. 2.2) due to unburned patches. Therefore, a manager could predict Brewer's sparrow density in a burned area based on 0% (0.96 birds/ha) or 6% shrub cover (1.01 birds/ha), depending on fire severity (Fig. 2.13). By predicting bird or pellet densities based on vegetation variability, managers can better understand the effect of under and over story components in determining avifauna habitat. For example, for the three grassland-associated species, their densities would increase if a shrub-dominated state or phase

contained the lower range of shrub cover, but would decrease if the native grassland state contained the maximum shrub cover (Fig. 2.13). Green-tailed towhees preferred areas with greater shrub and ground cover, but their densities may decline if a shrub-dominated state is managed for minimum shrub cover, even if ground cover is higher (Fig. 2.13). Managers can also examine the range of vegetation values, like shrub and herbaceous cover per state and see how it matches with published habitat guidelines (e.g., Connelly et al. 2000 for sage-grouse).

Our demonstration is also useful for illustrating the value of landscape heterogeneity. We predicted the highest green-tailed towhee density for the diverse shrubland state, but sage-grouse single pellet density was highest for the crested wheatgrass-shrubland community phase. Therefore, if managers treat the diverse shrubland state as the reference state and promote it on the landscape above other states (Bestelmeyer et al. 2003), the density of some avifauna species could decline. We also predicted modest sage-grouse pellet and roost pile densities in the native grassland state and crested wheatgrass-grassland phase where fire had occurred. One reason for this is that sage-grouse are a landscape species that occupy large territories and can move large distances between and within seasonal ranges (Connelly et al. 2011*b*). Also, sage-grouse will use burned landscapes, provided they are heterogeneous with some unburned patches (Fischer et al. 1996, Knick et al. 2005). Brood use may even be greater in more open habitat with greater herbaceous cover and surrounding sagebrush cover (Dahlgren et al. 2006). All of our burned areas in East Moffat occurred within mostly intact sagebrush habitat, and in the two smaller burns, unburned patches remained in sandy drainages and on clayey ridge tops. Therefore, even in burned areas, sage-grouse were not far from sagebrush cover. Indeed, we found pellets and flushed groups of birds in the two smaller, patchy burns, but did not document any sage-grouse use in the larger (i.e., >10,000 ha), mostly homogenous burn.

Lastly, our approach has greater utility because it includes a variety of avifauna guilds, so we can more clearly illustrate the range of ecosystem services among all states and communities. Focusing on one species and its habitat needs might ignore the value or services provided in seemingly degraded states (Derner et al. 2009). Thus, managing for landscape heterogeneity within a management unit may increase the total services provided because alternate states could benefit additional species, even native grassland patches within sagebrush rangelands. Given that the main objective of STMs is to display non-linear dynamics (Westoby et al. 1989), it seems more reasonable to identify potential services provided by each state or phase rather than subjectively labelling states and phases as “good” or “bad”. For a wide-ranging species like sage-grouse, the landscape diversity provided by multiple states may also be necessary to support multiple life stages, such as lekking and wintering (Connelly et al. 2011*a*). Our habitat models provide a quantitative approach to directly incorporate avifauna densities and species richness as ecosystem services into STMs.

To our knowledge, ours is the first attempt to incorporate multiple ecosystem services, such as livestock forage and avifauna habitat, into a locally developed STM (Bruegger et al. 2016). This attempt demonstrates the need for data-driven STMs that address local or specific problems and incorporate multiple stakeholders. Local ranchers and managers were interested in the effects of fire and re-seeding on vegetation and the local sage-grouse population (Bruegger et al. 2016). In particular, they were concerned that fire would remove sagebrush long term and diminish sage-grouse habitat, but that seeding native species post-fire could prevent cheatgrass establishment. From field surveys, we learned that sage-grouse were using the smaller burned areas with unburned patches and the burned areas did not contain greater amounts of cheatgrass regardless of post-fire seeding (Tipton 2015). By addressing local concerns and including local

knowledge in the STM, we increased the credibility and accuracy of the model, as well as its relevance to potential users, thus increasing the likelihood of local stakeholders using the model for range or wildlife management (Knapp et al. 2011, Kachergis et al. 2013, Bruegger et al. 2016). In addition, using a generalized STM for several dominant ecological sites, could also improve the usefulness for local management, as landowners may prefer to manage by vegetation type rather than ecological site (Knapp and Fernandez-Gimenez 2009).

Additional Considerations

Given limited time and resources by most land managers, it may be difficult to collect additional metrics to describe wildlife habitat, such as shrub and grass height. However, if STMs are developed in an iterative process as is recommended (Bestelmeyer et al. 2009), then the initial site visits and data collection efforts can help determine the most efficient and effective strategy to define states and appropriate ecosystem services. Previous studies or published STMs for a similar ecological site can inform which indicators are most useful in distinguishing ecological sites or states. Initial data exploration of vegetation indicators should also reveal redundancies and guide which indicators to include or discard from future sampling efforts to increase sampling efficiency. In the model we used, management history (e.g., fire and crested wheatgrass seeding) was a significant separator of states (Tipton 2015), so focusing sampling efforts within and outside disturbed or treated areas is a reasonable starting point for monitoring plant and avifauna communities. To best determine wildlife abundance (or other ecosystem service) per state or community phase, vegetation and soil sampling should precede other sampling efforts to ensure an adequate number of sampling plots are distributed per state for drawing accurate conclusions about services provided (Holmes and Miller 2010). Monitoring efforts should also include indicators known to be significant for priority management

objectives, such as grass height for nesting sage-grouse (Doherty et al. 2014) or forage production for cattle. Indicators to collect, like shrub cover, should also serve multiple purposes for defining states and phases and describing wildlife habitat or other services, as previous studies have shown (see Williams et al. 2011). One extension of our approach to improve management efforts would be to create spatially explicit STMs, in which landscape patterns driving transitions could be identified (Bestelmeyer et al. 2011). These landscape patterns could also describe wildlife habitat, such as connectivity, and visually represent ecosystem services within an area of interest. Managers could then prioritize states for restoration efforts or conservation measures depending on the ecosystem services provided.

Table 2.1. Definitions of fine-scaled predictors used in count-based regression models for greater sage-grouse and sagebrush-associated songbirds in Northwest Colorado, 2013-2015.

Predictor ^a	Predictor Description
sb	absolute sagebrush foliar cover as measured via line-point intercept ^b
shrub	absolute shrub foliar cover as measured via line-point intercept
VO	visual obstruction as measured via a modified Robel pole ^c
shrubHT	height (cm) recorded for the tallest part of a shrub (excluding inflorescence) intercepting the transect line via line-point intercept
grassHT	height (cm) of nearest grass measured while recording VO
grass	absolute grass foliar cover as measured via line-point intercept
bg	absolute bare ground cover as measured via line-point intercept
L	absolute litter and woody litter cover as measured via line-point intercept
herb	total herbaceous foliar cover as measured via line-point intercept
exotic	absolute exotic plant foliar cover as measured via line-point intercept
forb	absolute forb foliar cover as measured via line-point intercept

^a All predictors were collected in 50 × 50 or 20 × 50 plots.

^b Bonham 1989. Absolute cover was obtained based on the proportion of any LPI hits out of the total hits, and total cover was obtained based on the proportion of top hits out of the total hits (Tipton 2015).

^c Robel et al. 1970. See text for further description.

Table 2.2. Count-based regression models for greater sage-grouse pellets and songbirds in Northwest Colorado, 2013-2015. We report log-likelihood (LL), number of parameters (K), Bayesian Information Criterion (BIC), difference in BIC compared to lowest BIC of the model set (Δ BIC), BIC weight (w), pseudo- R^2 value, prediction error from five-fold cross validation, and p-value from likelihood ratio test for models with Δ BIC < 4.

	Model ^a	LL	K	BIC	Δ BIC	w	R^2	Error	p-value
Brewer's sparrow:	shrub + shrubHT	277.19	4	574.26	0.00	0.38	0.06	2.78	<0.001
	shrub + shrubHT + herb + herb ²	272.42	5	574.65	0.39	0.31	0.08	2.78	<0.001
	shrub + grassHT + shrubHT + herb + herb ²	270.63	7	576.06	1.80	0.16	0.09	2.77	<0.001
	shrub + grassHT + shrubHT	276.04	5	576.92	2.66	0.10	0.07	2.78	<0.001
Sage thrasher:	shrub + shrub ²	137.11	4	293.53	0.00	0.38	0.04	1.66	0.01
	intercept only	142.26	2	294.18	0.65	0.28	0.00	1.47	NA ^b
	shrub + shrub ² + L	135.28	5	294.71	1.18	0.21	0.05	1.64	0.003
	shrub + shrub ² + forb	135.78	5	295.71	2.18	0.13	0.05	1.66	0.005
	shrub + shrub ² + forb + L	133.43	6	295.83	2.30	0.09	0.06	1.74	0.001
	shrub + shrub ² + grassHT	135.91	5	295.95	2.42	0.08	0.04	1.65	0.005
	shrub + shrub ² + forb + exotic	133.61	6	296.2	2.67	0.07	0.06	1.69	0.002
Sagebrush sparrow:	shrub + shrub ² + grass + exotic	139.52	6	308.01	0.00	0.32	0.21	2.89	<0.001
	shrub + shrub ² + grass	142.17	5	308.48	0.47	0.25	0.20	2.93	<0.001
	shrub + shrub ² + bg + exotic	140.18	6	309.34	1.33	0.17	0.21	2.95	<0.001
	shrub + shrub ² + L + exotic	140.32	6	309.62	1.61	0.14	0.21	3.05	<0.001
	shrub + shrub ² + bg	142.97	5	310.08	2.07	0.11	0.19	3.01	<0.001
Green-tailed towhee:	shrub + shrubHT + bg	131.83	5	288.51	0.00	0.57	0.19	2.29	<0.001
	shrub + bg	135.61	4	291.09	2.58	0.16	0.16	2.21	<0.001
	shrub + shrubHT + L	133.13	5	291.11	2.60	0.15	0.18	2.28	<0.001
	shrub + L	135.87	4	291.61	3.10	0.12	0.16	2.14	<0.001

Table 2.2. cont.

	Model	LL	K	BIC	Δ BIC	w	R ²	Error	p-value
Roost sites:	sb + herb	190.02	4	399.35	0.00	0.18	0.03	4.62	0.005
	sb + grass	190.07	4	399.45	0.10	0.17	0.03	4.58	0.005
	sb + forb	190.19	4	399.69	0.34	0.16	0.03	4.60	0.006
	Intercept-only	195.27	2	400.21	0.86	0.12	0.00	4.62	NA
	sb	192.96	3	400.40	1.05	0.11	0.01	4.66	0.03
	sb + grassHT + forb	188.13	5	400.40	1.05	0.11	0.04	4.59	0.003
	sb + bg + bg ²	188.34	4	400.80	1.45	0.09	0.04	4.69	0.003
	sb + forb + bg + bg ²	186.31	5	401.59	2.24	0.06	0.05	4.60	0.001
	sagebrush + grassHT	191.20	4	401.71	2.36	0.05	0.02	4.60	0.02
	sagebrush + forb + grass	188.83	5	401.8	2.45	0.04	0.03	4.61	0.005
	sagebrush + exotic	191.64	4	402.59	3.24	0.03	0.02	4.62	0.03
	sagebrush + forb + herb	189.28	5	402.70	3.35	0.03	0.03	4.68	0.007
	sagebrush + L	191.75	4	402.80	3.45	0.03	0.02	4.62	0.03
General Use:	sb + bg + bg ²	281.74	5	587.63	0.00	0.47	0.03	20.66	<0.001
	sb	286.64	3	587.76	0.13	0.44	0.01	20.67	0.005
	sb + grassHT + grassHT ²	283.29	5	590.73	3.10	0.10	0.02	20.69	0.002
	intercept-only	290.55	2	590.75	3.12	0.07	0.00	20.72	NA
	sagebrush + bg + bg ² + exotic	280.997	6	590.96	3.33	0.07	0.03	20.63	<0.001
	sagebrush + forb + forb ²	283.69	5	591.52	3.89	0.05	0.02	20.64	0.003
Horned larks:	shrub + L	239.95	4	499.22	0.00	0.55	0.12	3.22	<0.001
	shrub	242.89	3	500.26	1.04	0.33	0.10	3.21	<0.001
	shrub + L + herb	239.04	5	502.23	3.01	0.12	0.12	3.21	<0.001
	shrub + bg	241.90	4	503.12	3.90	0.07	0.11	3.22	<0.001

Table 2.2. cont.

	Model	LL	K	BIC	Δ BIC	w	R ²	Error	p-value
Vesper	shrub + bg	179.76	4	379.39	0.00	0.57	0.15	2.07	<0.001
sparrows:	shrub + grassHT + bg	177.56	5	379.98	0.58	0.43	0.16	2.11	<0.001
Western	shrub + bg	223.22	4	466.33	0.00	0.88	0.15	2.38	<0.001
meadowlarks:	shrub + grassHT + bg	222.69	5	470.24	3.91	0.12	0.15	2.37	<0.001
Species richness	shrub + shrub ²	278.86	3	572.63	0.00	0.91	0.04	4.33	<0.001
(all species):	shrub + shrub ² + grHT	278.71	4	577.31	4.68	0.09	0.04	4.33	<0.001
Species richness	shrub + shrub ²	236.88	3	488.68	0.00	0.66	0.07	2.32	<0.001
(shrub species	shrub + shrub ² + grHT	235.88	4	491.64	2.96	0.15	0.08	2.32	<0.001
only):	shrub + shrub ² + bg	236.03	4	491.93	3.25	0.13	0.08	2.32	<0.001
	shrub + shrub ² + L	236.70	4	493.28	4.60	0.07	0.07	2.32	<0.001

^a Predictor variables described in Table 2.1.

^b Did not run the likelihood ratio test to compare a null (intercept-only) model against a null model.

Table 2.3. Beta coefficient estimates (β), standard errors (SE), and 95% confidence intervals for variables in the top (i.e., $\Delta\text{BIC} < 2$) count-based regression models for greater sage-grouse pellets and songbirds in Northwest Colorado, 2013-2015.

		Variable	β	SE	95% Lower	95% Upper
Brewer's sparrow:	model 1:	intercept	-0.39	0.18	-0.77	-0.02
		shrub	0.01	0.01	0.002	0.03
		shrubHT	0.02	0.01	0.01	0.03
	model 2:	intercept	-0.65	0.31	-1.28	-0.05
		shrub	0.01	0.01	-0.01	0.02
		shrubHT	0.02	0.01	0.01	0.03
		herb	0.04	0.02	0.01	0.07
		herb ²	<0.001	<0.001	-0.001	-0.0002
	model 3:	intercept	-0.87	0.33	-1.53	-0.23
		shrub	0.01	0.01	-0.01	0.02
		shrubHT	0.04	0.02	-0.001	0.07
		herb	0.02	0.004	0.01	0.03
herb ²		0.03	0.02	0.001	0.07	
		grassHT	<0.001	<0.001	-0.001	-0.0001
Green-tailed towhee:	model 1:	intercept	-2.57	0.51	-3.67	-1.58
		shrub	0.01	0.01	-0.01	0.04
		shrubHT	0.03	0.01	0.01	0.05
		bg	-0.07	0.02	-0.10	-0.04
Sagebrush sparrow:	model 1:	intercept	-2.03	0.87	-3.85	-0.37
		shrub	0.26	0.08	0.11	0.43
		shrub ²	-0.01	0.002	-0.01	-0.003
		grass	-0.03	0.01	-0.05	-0.01
		exotic	-0.03	0.01	-0.06	-0.005
	model 2:	intercept	-2.05	0.90	-3.92	-0.36
		shrub	0.26	0.08	0.10	0.43
		shrub ²	-0.01	0.002	-0.01	-0.003
		grass	-0.04	0.008	-0.06	-0.02
Sage thrasher:	model 1:	intercept	-3.16	0.49	-4.23	-2.26
		shrub	0.11	0.04	0.04	0.20
		shrub ²	-0.002	<0.001	-0.004	-0.001
	model 2:	intercept	-1.81	0.13	-2.08	-1.56
	model 3:	intercept	-4.00	0.66	-5.36	-2.74
		shrub	0.13	0.04	0.05	0.21
		shrub ²	-0.002	0.001	-0.004	-0.001
			L	0.01	0.01	-0.0003

Table 2.3 cont.

		Variable	β	SE	95% Lower	95% Upper
Single pellets:	model 1:	intercept	0.54	0.54	-0.43	1.66
		sb	0.05	0.02	0.01	0.09
		bg	0.13	0.05	0.03	0.23
		bg ²	-0.003	0.001	-0.01	-0.001
Roost piles:	model 1:	intercept	1.12	0.55	-0.08	2.53
		sb	0.04	0.02	-0.005	0.08
		herb	-0.03	0.01	-0.06	-0.01
	model 2:	intercept	0.55	0.39	-0.32	1.52
		sb	0.05	0.02	0.01	0.10
		forb	-0.07	0.03	-0.13	-0.01
	model 3:	intercept	0.66	0.22	0.26	1.11
	model 4:	intercept	-0.07	0.34	-0.76	0.70
		sb	0.05	0.02	0.01	0.09
	model 5:	intercept	1.94	0.65	0.36	3.62
		sb	0.05	0.02	0.01	0.09
		grassHT	-0.13	0.05	-0.25	-0.01
forb		-0.07	0.03	-0.13	-0.02	
Horned lark:	model 1:	intercept	1.78	0.25	1.28	2.28
		shrub	-0.06	0.01	-0.07	-0.04
		L	-0.01	0.004	-0.02	-0.002
	model 2:	intercept	1.23	0.12	1.00	1.47
		shrub	-0.05	0.01	-0.07	-0.04
Vesper sparrow:	model 1:	intercept	1.02	0.20	0.62	1.43
		shrub	-0.04	0.01	-0.05	-0.03
		bg	-0.07	0.01	-0.09	-0.05
	model 2:	intercept	0.28	0.39	-0.49	1.07
		shrub	-0.04	0.01	-0.05	-0.02
		grassHT	0.06	0.03	0.004	0.11
	bg	-0.07	0.01	-0.09	-0.05	
Western meadowlark:	model 1:	intercept	0.65	0.23	0.19	1.14
		shrub	-0.04	0.01	-0.06	-0.03
		bg	-0.08	0.01	-0.10	-0.06
Species richness (common species):	model 1:	intercept	1.42	0.09	1.23	1.60
		shrub	0.03	0.01	0.02	0.05
		shrub ²	-0.001	<0.001	-0.001	-0.0003

Table 2.3 cont.

		Variable	β	SE	95% Lower	95% Upper
Species richness (shrub species only):	model 1:	intercept	0.40	0.15	0.10	0.68
		shrub	0.07	0.01	0.04	0.09
		shrub ²	-0.001	<0.001	-0.002	-0.001

^a Predictor variables described in Table 2.1.

Table 2.4. Predicted densities of songbirds and greater sage-grouse pellets and species richness for states and community phases in Northwest Colorado, 2013-2015, for a locally developed state-and-transition model (Tipton 2015, Appendix I). 95% confidence intervals for each density estimate are in parenthesis.

	Diverse Shrubland State	Needle-and-thread Shrubland State	Crested Wheatgrass Shrub-Dominated Phase	Crested Wheatgrass Grass-Dominated Phase	Native Grassland State
Brewer's sparrows/ha	3.3 (2.8-3.9)	3.1 (2.4-3.7)	3.2 (2.2-4.1)	0.9 (0.4-1.4)	1.0 (0.5-1.4)
Green-tailed towhees/ha	1.1 (0.8-1.4)	0.5 (0.4-0.7)	0.6 (0.3-0.8)	0.1 (0.02-0.2)	0.2 (0.1-0.4)
Sagebrush sparrows/ha	0.2 (0.04-0.4)	0.5 (0.2-0.8)	0.5 (0.04-0.9)	0.01 (<0-0.03)	0.1 (<0-0.1)
Sage thrashers/ha	0.9 (0.4-1.3)	0.7 (0.3-1.02)	0.8 (0.5-1.2)	0.3 (<0-0.6)	0.3 (<0-0.6)
Single pellets/ha	350 (150-549)	319 (150-488)	452 (109-795)	128 (8-249)	106 (22-189)
Roost piles/ha	55 (24-86)	66 (20-111)	68 (27-108)	35 (<0-84)	28 (<0-70)
Horned larks/ha	0.9 (0.6-1.2)	1.6 (1.3-2.0)	1.9 (1.5-2.3)	6.2 (4.8-7.7)	5.5 (4.2-6.7)
Vesper sparrows/ha	0.9 (0.7-1.2)	1.2 (0.9-1.4)	0.9 (0.6-1.1)	3.1 (0.8-5.5)	3.0 (2.0-4.1)
Western meadowlarks/ha	1.5 (1.1-1.9)	1.5 (1.2-1.9)	1.1 (0.8-1.4)	3.3 (2.1-4.5)	4.4 (2.8-6.1)
Common species richness	6.7 (6.0-7.3)	6.5 (6.0-7.0)	6.6 (6.0-7.2)	4.2 (3.4-4.9)	4.4 (3.8-5.1)
Shrub-associated species richness	4.0 (3.5-4.6)	3.7 (3.3-4.1)	3.8 (3.4-4.2)	1.5 (1.1-2.0)	1.7 (1.3-2.1)

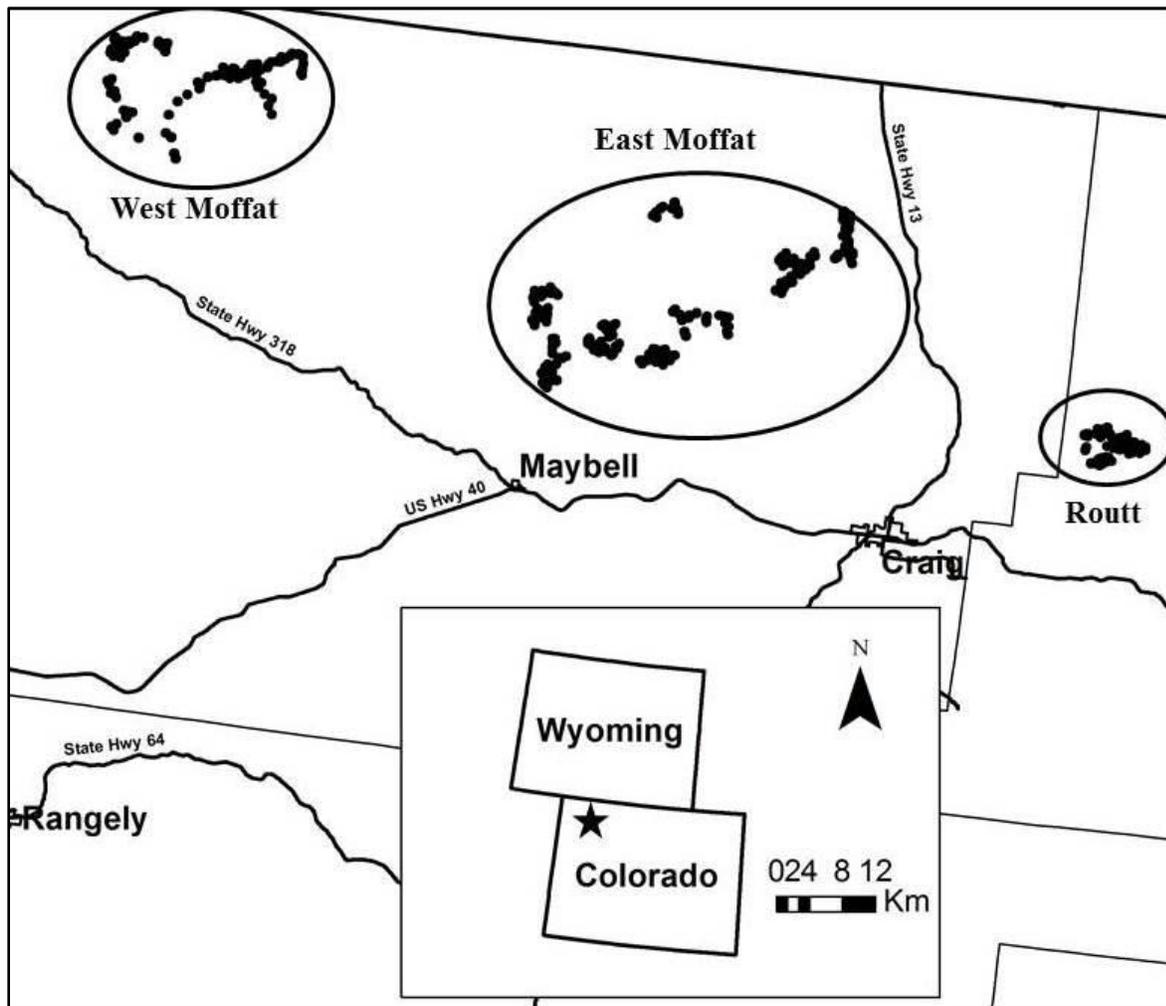


Figure 2.1. Locations of avifauna, vegetation, and soil surveys, 2013-2015, in Northwest Colorado with three study areas outlined and labeled (West Moffat, East Moffat, and Routt). We collected vegetation, soil, and avifauna abundance data at all three areas to quantify avifauna habitat relationships, but predicted avifauna densities in just the East Moffat state-and-transition model.

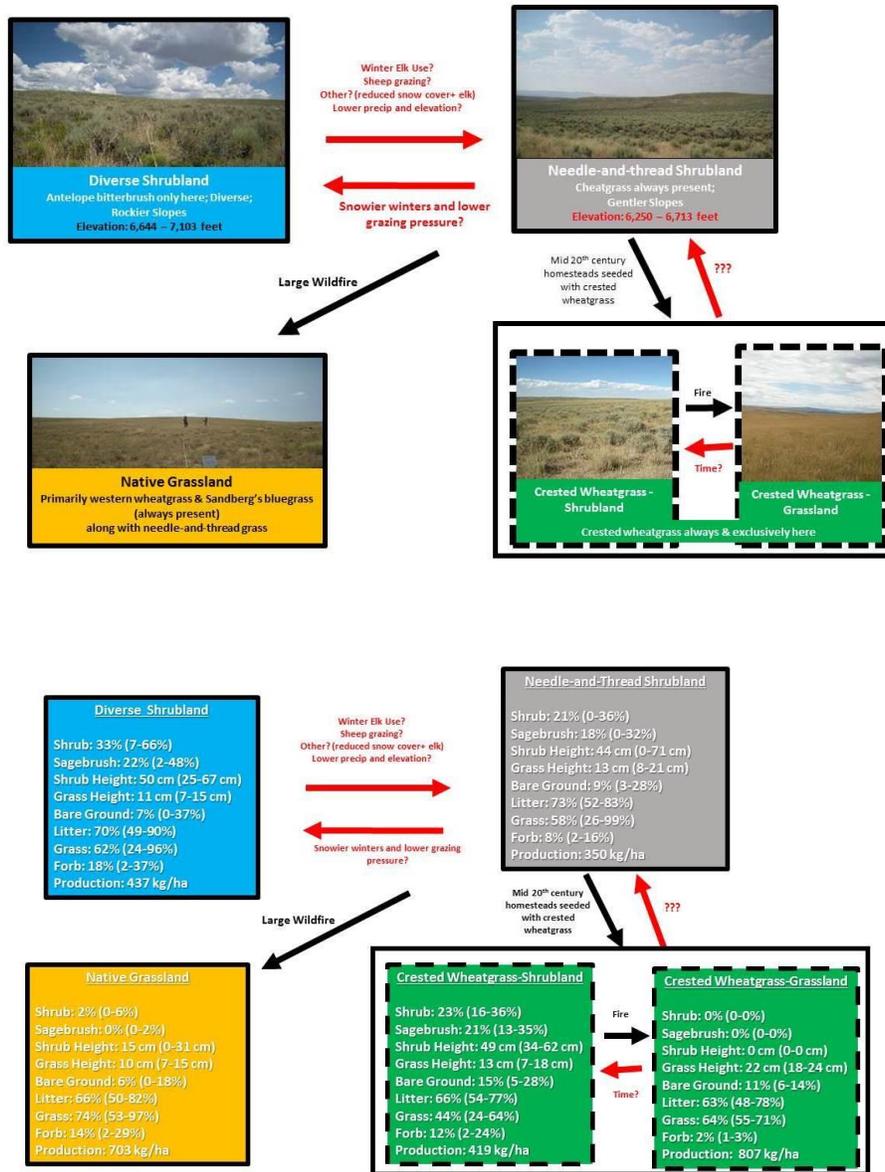


Figure 2.2. Generalized state-and-transition model created for eastern Moffat County on Sandyland, Rolling Loam, Claypan, Deep Loam, and Sandy Foothills ecological sites in Northwest Colorado, 2013-2015 (Tipton 2015) with average and minimum-maximum vegetation values for each state and community phase. Solid lines around boxes indicate states while dotted lines indicate community phases within a state. Production estimates include grasses and forbs. See Tipton (2015) and Appendix I for full description of possible transition drivers and determination of states and phases.

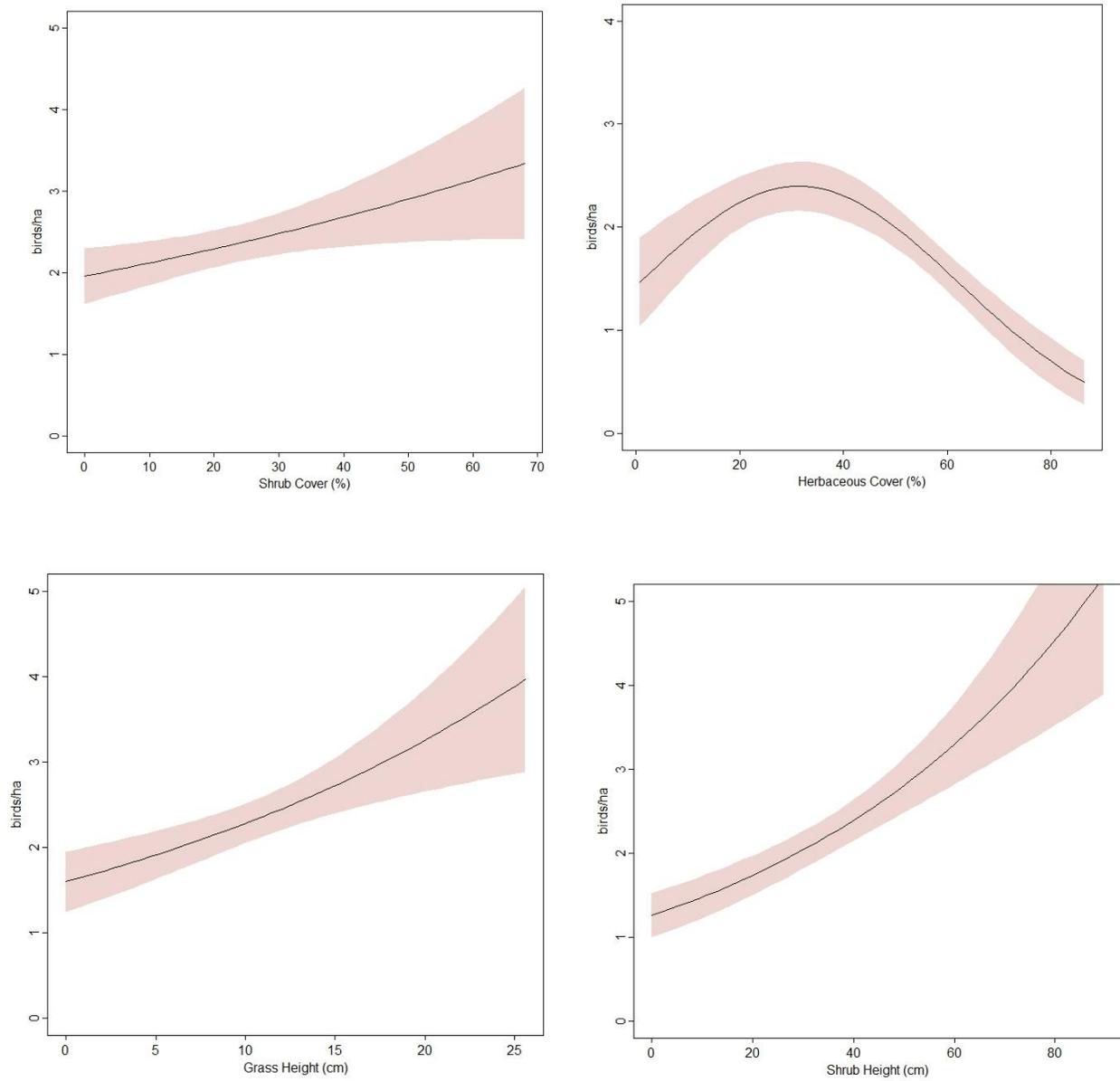


Figure 2.3. Predicted variable relationships and 95% confidence intervals for Brewer's sparrows for the third best negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).

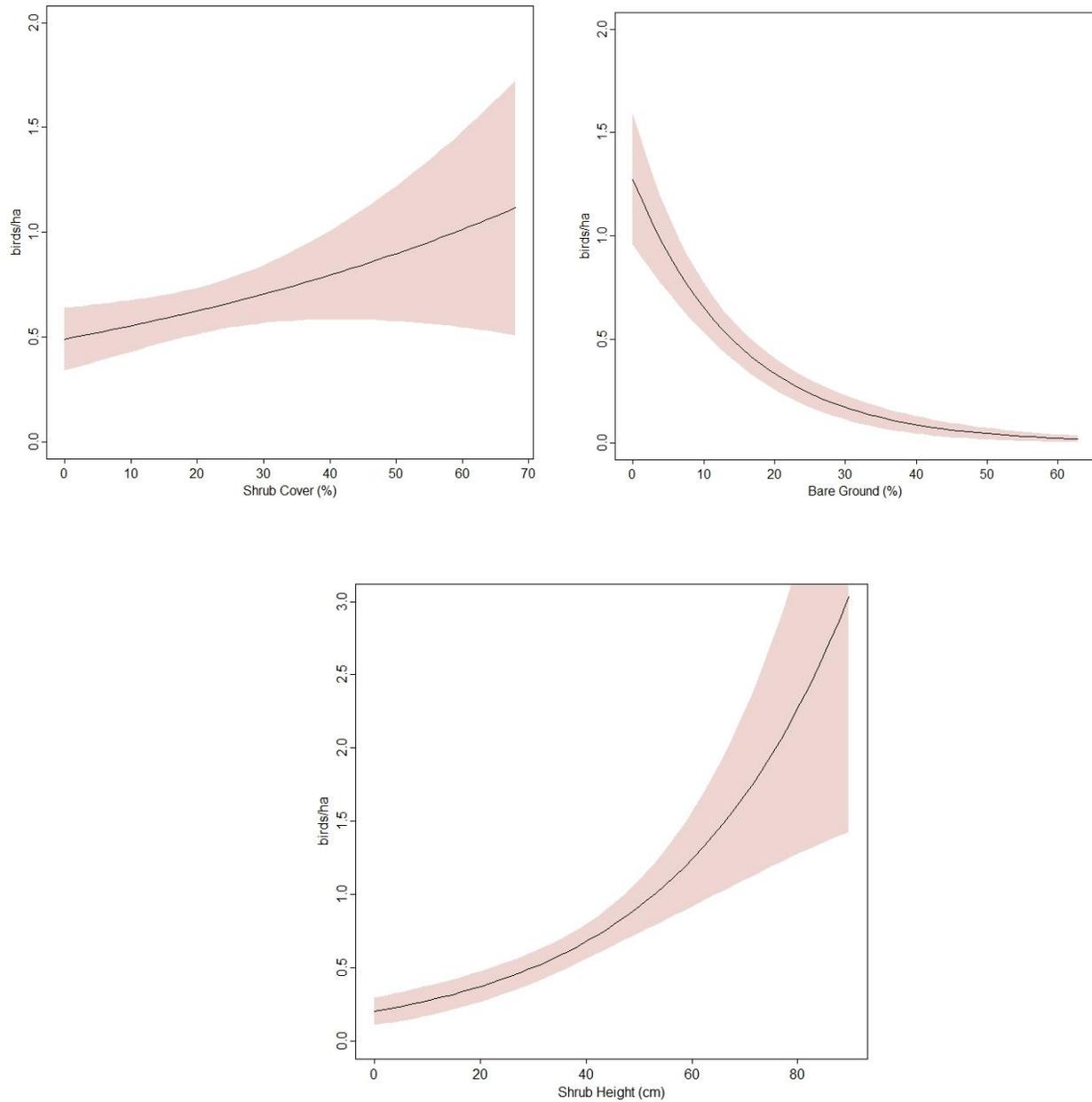


Figure 2.4. Predicted variable relationships and 95% confidence intervals for green-tailed towhees for the top negative binomial model in Northwest Colorado, 2013-2015.

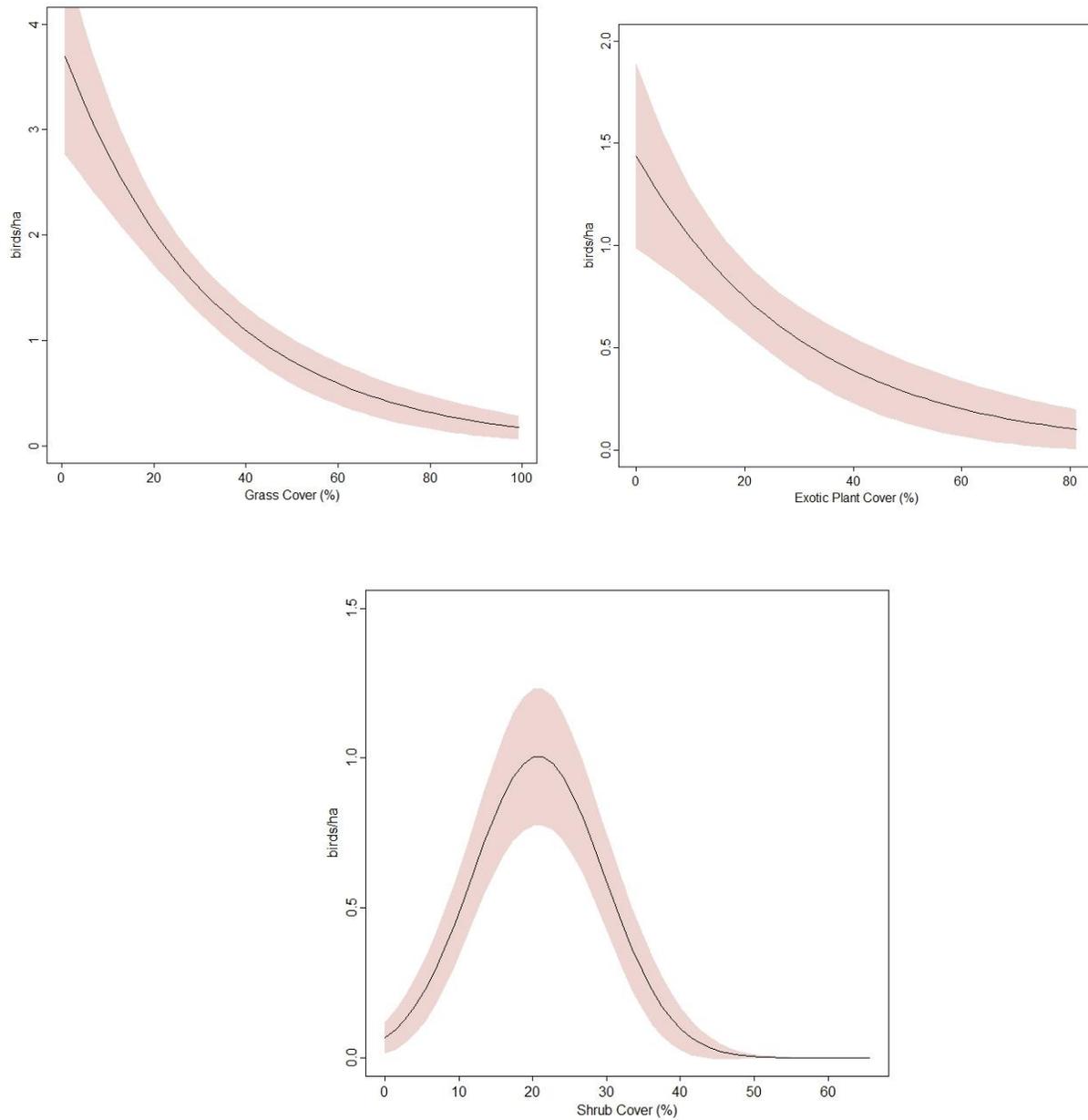


Figure 2.5. Predicted variable relationships and 95% confidence intervals for sagebrush sparrows for the top negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).

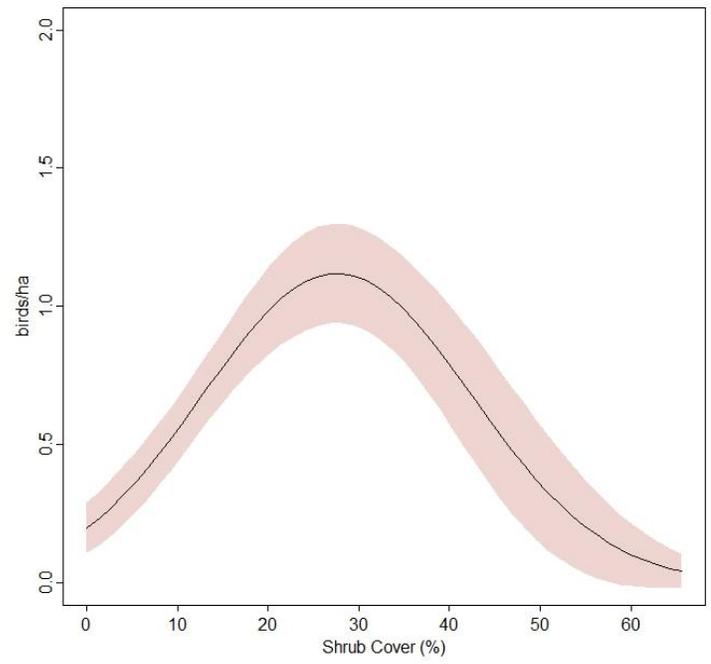
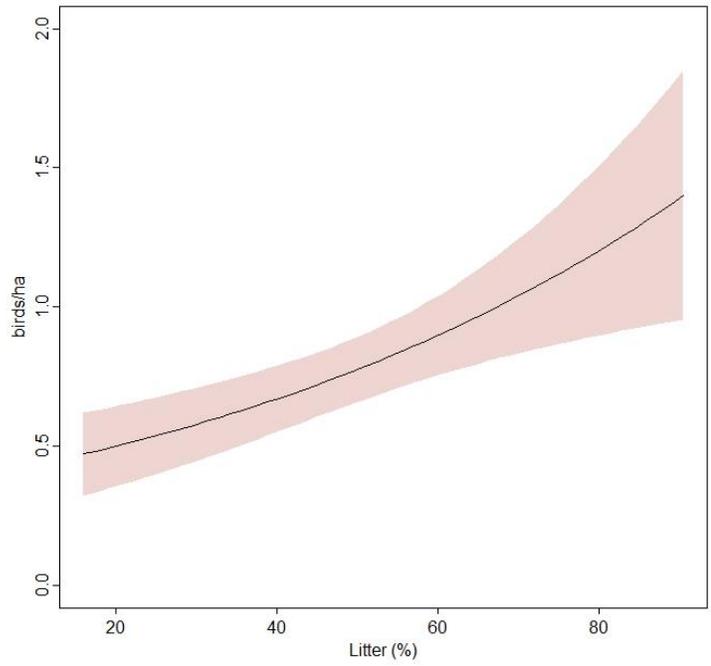


Figure 2.6. Predicted variable relationships and 95% confidence intervals for sage thrashers for the third best negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).

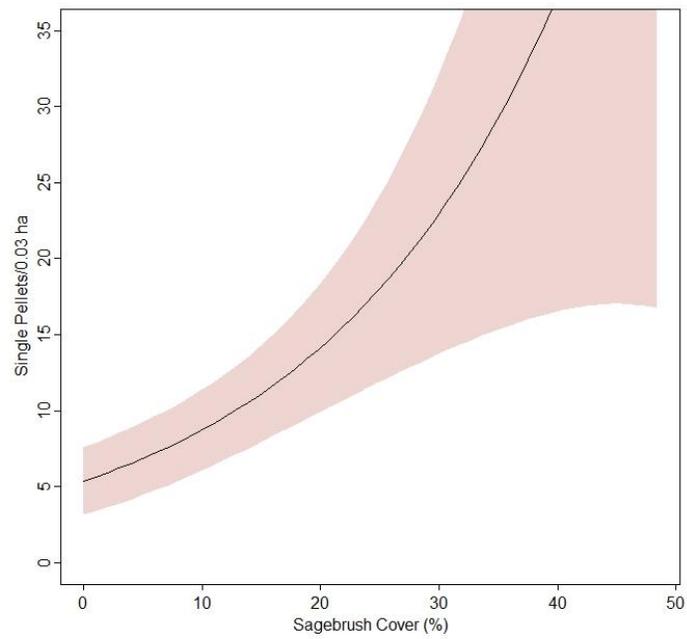
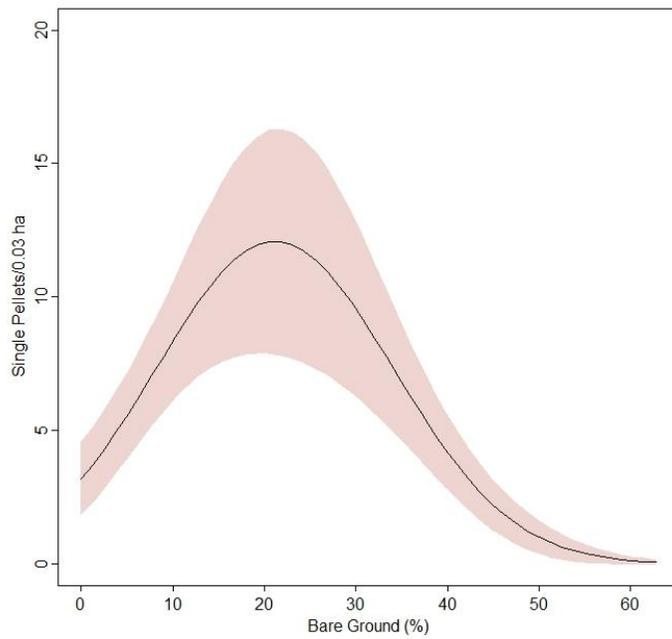


Figure 2.7. Predicted variable relationships and 95% confidence intervals for greater sage-grouse single pellets for the top negative binomial model in Northwest Colorado, 2013-2015.

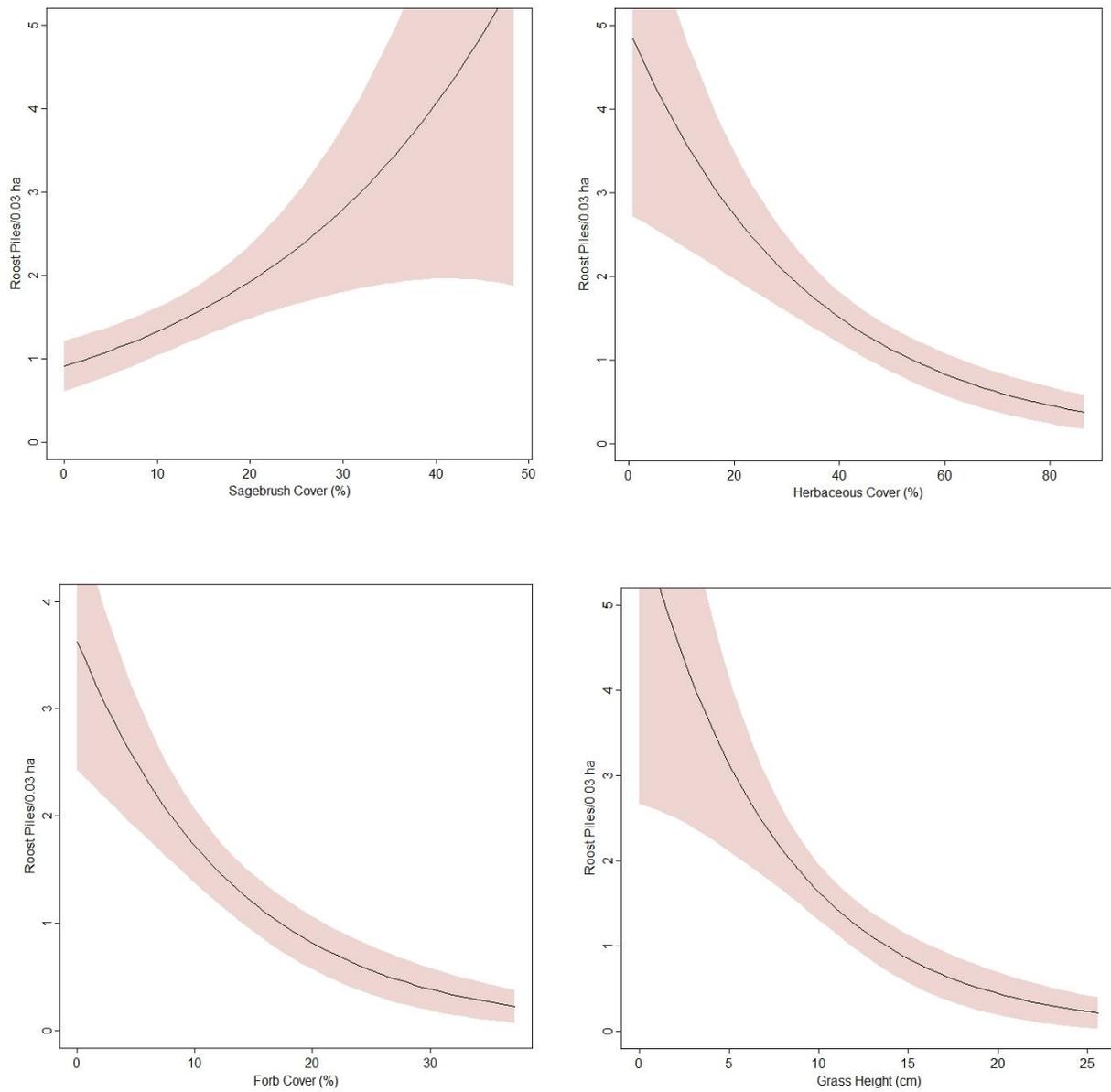


Figure 2.8. Predicted variable relationships and 95% confidence intervals for greater sage-grouse roost piles for the best negative binomial model (sagebrush and herbaceous cover) and the fifth best model (grass height and forb cover) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).

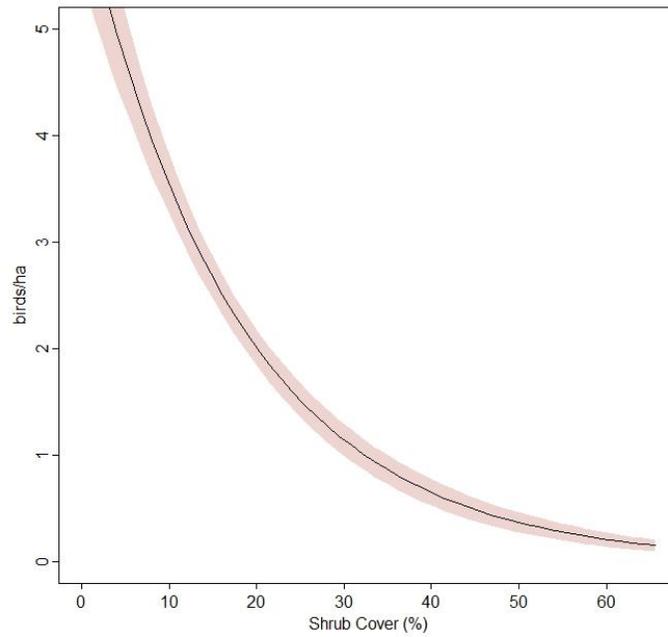
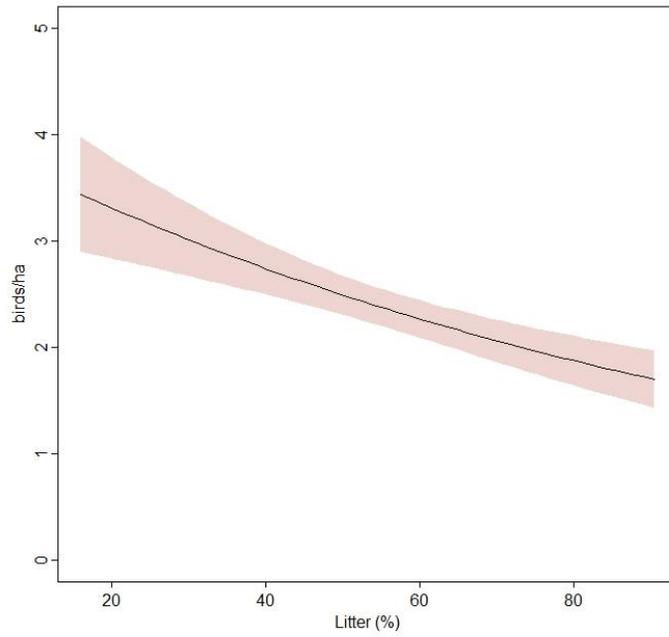


Figure 2.9. Predicted variable relationships and 95% confidence intervals for horned larks for the top negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).

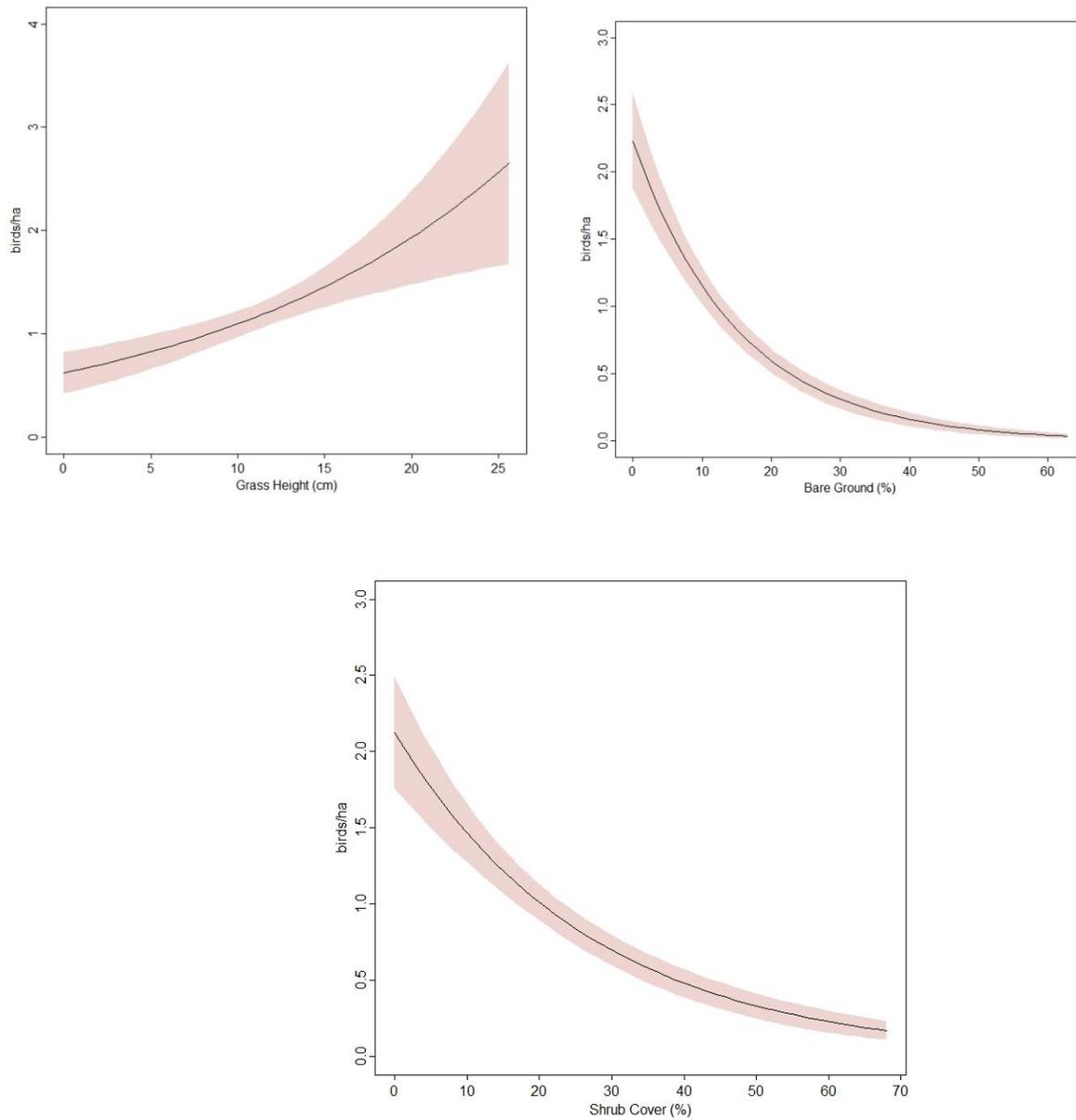


Figure 2.10. Predicted variable relationships and 95% confidence intervals for vesper sparrows for the second best negative binomial model (which contains all the top predictors) in Northwest Colorado, 2013-2015. Variable relationships were similar across all top models (see Table 2.3).

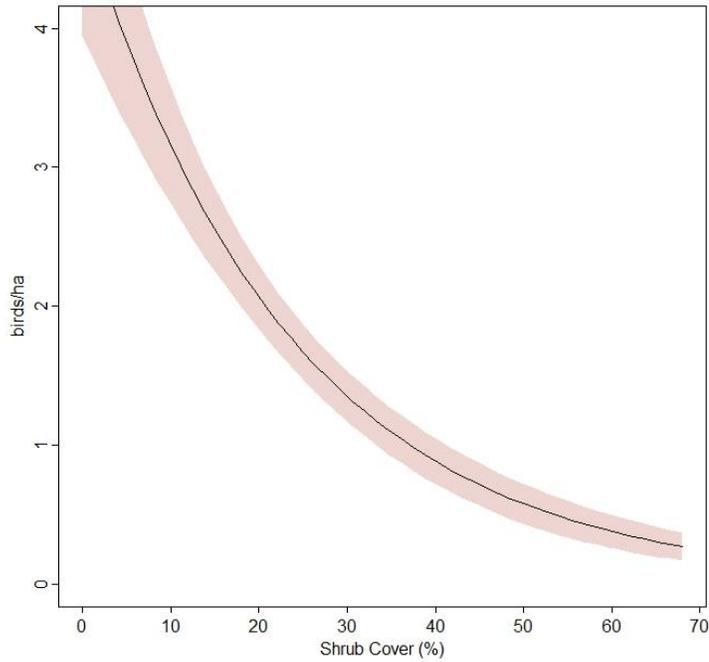
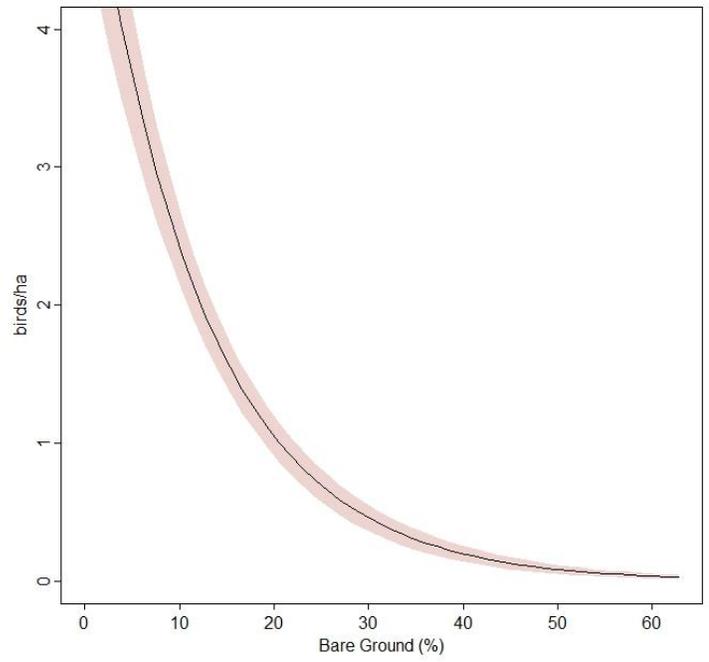


Figure 2.11. Predicted variable relationships and 95% confidence intervals for western meadowlarks for the top negative binomial model in Northwest Colorado, 2013-2015.

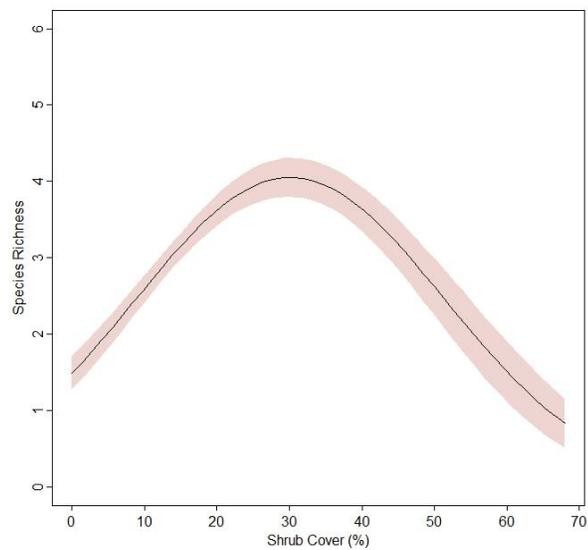
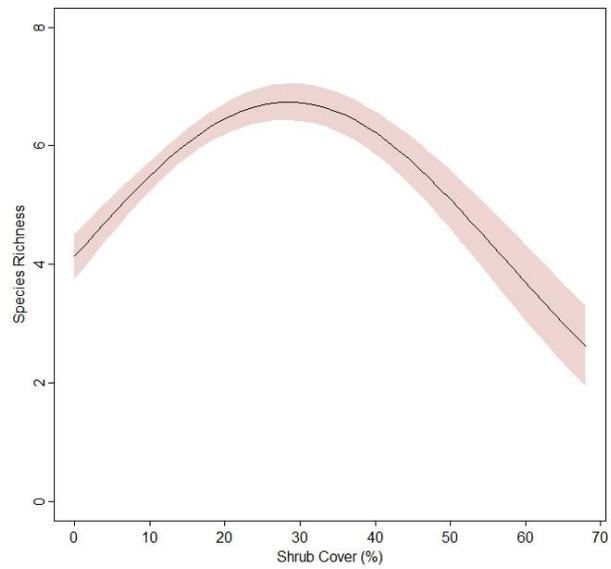


Figure 2.12. Predicted variable relationship and 95% confidence intervals for the top Poisson model for avifauna species richness (all common species in top figure and shrub-obligate species only in bottom figure) in Northwest Colorado, 2013-2015.

LITERATURE CITED

- Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. *Journal of Wildlife Management* 66:433–444.
- Aldridge, C.L., S.E. Hanser, S.E. Nielsen, M. Leu, B.S. Cade, D.J. Saher, and S.T. Knick. 2011. Detectability adjusted count models of songbird abundance. Pp 141-220 in Hanser, S.E., M. Leu, S.T. Knick, and C.L. Aldridge (editors). Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, KS, USA.
- Beason, R. C. 1995. Horned lark (*Eremophila alpestris*), *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/horlar>. DOI: 10.2173/bna.195.
- Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.
- Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, Jr., D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology and Management* 62:1–15.
- Bestelmeyer, B. T., D. P. Goolsby, and S. R. Archer. 2011. Spatial perspectives in state-and-transition models: a missing link to land management? *Journal of Applied Ecology* 48: 746–757.
- Bird Conservancy of the Rockies. 2016. The Rocky Mountain Avian Data Center. [web application]. Brighton, CO, USA. <http://adc.rmbo.org>. (Accessed: 1 November 2016).

- Bonham, C. D. 1989. Measurements for terrestrial vegetation. Wiley-Interscience, New York, New York, USA.
- Boyd, C. S., D. D. Johnson, J. D. Kerby, T. J. Svejcar, and K. W. Davies. 2014. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? *Rangeland Ecology and Management* 67:358-368.
- Boyle, S., and D. R. Reeder. 2005. Colorado sagebrush: a conservation assessment and strategy. Colorado Division of Wildlife, Grand Junction, CO, USA.
- Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. *Wilson Bulletin* 88:165–171.
- Bruegger, R. A., M. E. Fernandez-Gimenez, C. Y. Tipton, J. M. Timmer, and C. L. Aldridge. 2016. Multi-stakeholder development of state-and-transition models: a case study from northwestern Colorado. *Rangelands*. doi: 10.1016/j.rala.2016.10.008.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.
- Buckland, S.T., R.E. Russell, B.G. Dickson, V.A. Saab, D.N. Gorman, and W. M. Block. 2009. Analyzing designed experiments in Distance Sampling. *Journal of Agricultural, Biological, and environmental Statistics* 14:432–442.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag New York Inc., New York, New York, USA.
- Cagney, J. 2009. Grazing influence, management and objective development in Wyoming's greater sage-grouse habitat with emphasis on nesting and early brood rearing. University of Wyoming Cooperative Extension Service. B-1203.

- Colorado Greater Sage-grouse Steering Committee. 2008. Colorado greater sage-grouse conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines for management of sage grouse populations and habitat. *Wildlife Society Bulletin* 28:967–985.
- Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011*a*. Characteristics of greater sage-grouse habitats. Pp 69–83 in S. T. Knick and J. W. Connelly (editors). *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011*b*. Characteristics and dynamics of greater sage-grouse populations. Pp 53–67 in S. T. Knick and J. W. Connelly (editors). *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Dahlgren, D. K., R. Chi, and T. A. Messmer. 2006. Greater sage-grouse response to sagebrush management in Utah. *Wildlife Society Bulletin* 34:975–985.
- Davis, S. K. and W. E. Lanyon. 2008. Western meadowlark (*Sturnella neglecta*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/wesmea>. DOI: 10.2173/bna.104.
- Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. *Rangeland Ecology and Management* 62:111-118.
- Dobbs, R. C., P. R. Martin and T. E. Martin. 2012. Green-tailed towhee (*Pipilo chlorurus*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology.

Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/gnttow>. DOI: 10.2173/bna.368_

- Dobkin, D. S., and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy: distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, OR, USA.
- Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. *Journal of Wildlife Management* 72:187–195.
- Doherty, K. E., D. E. Naugle, J. D. Tack, B. L. Walker, J. M. Graham, J. L. Beck. 2014. Linking conservation actions to demography: grass height explains variation in greater sage-grouse nest survival. *Wildlife Biology* 20:320-325.
- Doherty, K. E., J. L. Beck, and D. E. Naugle. 2011. Comparing ecological site descriptions to habitat characteristics influencing greater sage-grouse nest site occurrence and success. *Rangeland Ecology and Management* 64:344–351.
- Dyksterhuis 1949. Condition and management of range land based on quantitative ecology. *Journal of Range Management* 2:104-115.
- Fischer, R.A., K. P. Reese, and J. W. Connelly. 1996. An investigation on fire effects within xeric sage grouse brood habitat. *Journal of Range Management* 49:194–198.
- Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of Sage Grouse nests in Oregon. *Journal of Wildlife Management* 58:162–166.
- Hanni, D. J., C. M. White, N.J. Van Lanen, J. J. Birek, J.M. Berven, and M.A. McLaren. 2013. Integrated Monitoring of Bird Conservation Regions (IMBCR): Field protocol for spatially-balanced sampling of landbird populations. Unpublished report. Rocky Mountain Bird Observatory, Brighton, Colorado, USA.

- Hanser, S. E., C. L. Aldridge, M. Leu, M. M. Rowland, S. E. Nielson, and S. T. Knick. 2011. Greater sage-grouse: general use and roost site occurrence with pellet counts as a measure of relative abundance. Pp 112-140 in Hanser, S.E., M. Leu, S.T. Knick, and C.L. Aldridge (editors). Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, KS, USA.
- Hastie, T., R. Tibshirani, and J. Friedman. 2009. Model assessment and selection. Pp. 219-259 in Hastie, T., R. Tibshirani, and J. Friedman (editors). The elements of statistical learning: data mining, inference, and prediction. Springer, New York, NY, USA.
- Herrick, J. E., J. W. Van Zee, K. M. Havstad, Burkett L. M., and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland and savanna ecosystems. USDA-Agricultural Research Service, Jornada Experimental Range, Las Cruces, USA.
- Hilbe, J. M. 2011. Negative binomial regression. Cambridge University Press, New York, NY, USA.
- Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater Sage-Grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management* 69:638–649.
- Holmes, A. L., and R. F. Miller. 2010. State-and-transition models for assessing grasshopper sparrow habitat use. *Journal of Wildlife Management* 74:1834–1840.
- Homer, C.G., C.L. Aldridge, D.K. Meyer, and S. Shell. 2012. Implementing a multi-scale remote sensing sagebrush characterization and monitoring framework across Wyoming. *International Journal of Applied Earth Observation and GeoInformation* 14:233-244.
- Hosmer, D. W. and S. Lemeshow. 2000. Applied logistic regression. John Wiley & Sons, Inc., New York, New York, USA.

- Jehle, G., J. A. Savidge, and N. B. Kotliar. 2006. Green-tailed towhee response to prescribed fire in montane shrubland. *Condor* 108:634-646.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Jones, S. L. and J. E. Cornely. 2002. Vesper sparrow (*Pooecetes gramineus*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/vesspa>. DOI: 10.2173/bna.624.
- Kachergis, E. J., C. N. Knapp, M. E. Fernandez-Gimenez, J. P. Ritten, J. G. Pritchett, J. Parsons, W. Hibbs, and R. Roath. 2013. Tools for resilience management: multidisciplinary development of state-and-transition models for northwest Colorado. *Ecology and Society* <http://dx.doi.org/10.5751/ES-05805-180439>.
- Kachergis, E., M. E. Rocca, and M. E. Fernandez-Gimenez. 2011. Indicators of ecosystem function identify alternative states in the sagebrush steppe. *Ecological Applications* 21:2781–2792.
- Knapp, C. N., and M. E. Fernandez-Gimenez. 2009. Understanding change: integrating rancher knowledge into state-and-transition models. *Rangeland Ecology and Management* 62:510-521.
- Knapp, C. N., M. Fernandez-Gimenez, E. Kachergis, and A. Rudeen. 2011. Using participatory workshops to integrate state-and-transition models created with local knowledge and ecological data. *Rangeland Ecology and Management* 64:158-170.
- Knick, S. T., A. L. Holms, and R. F. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. Pages 63–75 in V. A. Saab and H.D.W. Powell, editors.

- Fire and avian ecology in North America. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.
- Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. *Conservation Biology* 9:1059-1071.
- Knopf, F. L., J. A. Sedgwick, and D. B. Inkley. 1990. Regional correspondence among shrubsteppe bird habitats. *Condor* 92:45-53.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.
- Martin, J. W. and B. A. Carlson. 1998. Sagebrush sparrow (*Artemisiospiza nevadensis*). The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/sagspa1>. DOI: 10.2173/bna.326b.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 in S. T. Knicks and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Patterson, R. L. 1952. The Sage Grouse in Wyoming. Sage Books, Denver, CO, USA.

- Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Saur. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105-119.
- Poole, A. (editor). 2005. *The Birds of North America Online*. Cornell Laboratory of Ornithology, Ithaca, New York. <http://bna.birds.cornell.edu/BNA>. Accessed 28 November 2016.
- Pritchett, J., E. Kachergis, J. Parsons, M. Fernandez-Gimenez, J. Ritten. 2012. Home on a transitioning range: a ranch simulation game demonstrating STMs. *Rangelands* 34:53-59.
- R Development Core Team. 2015. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 22 November 2015.
- Reynolds, T. D., T. D. Rich, and D. A. Stephens. 1999. Sage thrasher (*Oreoscoptes montanus*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/sagthr>. DOI: 10.2173/bna.463.
- Rich, T. 1980. Nest placement in sage thrashers, sage sparrows, and Brewer's sparrows. *The Wilson Bulletin* 92:362-368.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.
- Rotenberry, J. T., M. A. Patten, and K. L. Preston. 1999. Brewer's sparrow (*Spizella breweri*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/brespa>. DOI: 10.2173/bna.390.

- Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.
- Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998. Use and selection of brood-rearing habitat by sage grouse in south central Washington. *Great Basin Naturalist* 58:344–351.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5–14.
- Tipton, C. Y. W. 2015. Improving state-and-transition models for management of sagebrush steppe ecosystems. Thesis, Colorado State University 160 p.
- Twidwell, D., B. W. Allred, and S. D. Fuhlendorf. 2013. National-scale assessment of ecological content in the world's largest land management framework. *Ecosphere* 4:1-27.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:265–273.
- Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 51:21–42.
- Wiens, J. A., B. Van Horne, and J. T. Rotenberry. 1990. Comparisons of the behavior of sage and Brewer's sparrows in shrubsteppe habitats. *Condor* 92:264-266.
- Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* 48:132-147.
- Williams, M. I., G. B. Paige, T. L. Thurow, A. L. Hild, and K. G. Gerow. 2011. Songbird relationships to shrub-steppe ecological site characteristics. *Rangeland Ecology and Management* 64:109–118.

Zar, J. H. 1999. Biostatistical analysis. Second edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

CHAPTER III. A SPATIAL APPROACH TO MAP STATES IN A STATE-AND-TRANSITION MODEL FOR SAGEBRUSH RANGELANDS

Summary

A state-and-transition model (STM) is a conceptual model that describes rangeland dynamics and alternate stable states. A STM usually corresponds to one ecological site, which has distinctive soil and hydrologic properties that determine a site's potential plant community. Ecological sites can be represented spatially with soil map units, but STMs are currently criticized for their lack of spatial scale and context. Therefore, we mapped states in a study area on target ecological sites using a previously developed STM for Northwest Colorado. The generalized STM, developed for sagebrush rangelands, included two shrubland states, a native grassland state, and an exotic grass-dominated state. I used multinomial logistic regression with "state" as the response variable and included remotely sensed vegetation components, abiotic data, and disturbance history for predictors. I then predicted the best model(s) to all pixels in the study area on target ecological sites and summarized statistics for each state. Our best model included big sagebrush cover and elevation. Classification accuracy (based on external and internal validation) was 71-74%, and individual component accuracy varied across the four states. Two shrubland states comprised approximately 67% of the study area, while an exotic grassland state comprised the lowest proportion (1%). The shrubland states were also the most contiguous while the exotic grassland state was the least. To our knowledge, ours is the first attempt to map states in a STM for the sagebrush steppe. Predicting and mapping states across a landscape could guide monitoring and restoration efforts, inform ecosystem service values per state, elucidate landscape patterns, and forecast transitions within STMs.

Introduction

State-and-transition models (STM) are conceptual models that describe linear and non-linear range dynamics and are composed of a reference state and alternate states described relative to the reference state (Westoby et al. 1989, Bestelmeyer et al. 2003). Within a state, plant composition can shift among phases, which represent reversible pathways of change among communities in response to natural events (e.g. weather) or management (Bestelmeyer et al. 2003, Stringham et al. 2003). Change between states however, requires crossing of spatial and/or temporal boundaries or thresholds, in which significant ecological processes have been changed. Transitions are the trajectories or drivers of change (Stringham et al. 2003).

Each STM usually corresponds to one ecological site, which has distinctive soil and hydrologic properties that determine a site's potential plant community. Ecological sites can be represented spatially with soil map units by linking tabular data with soil polygons, which are available from the Natural Resource Conservation Service (NRCS) Soil Survey Geographic [SSURGO] Database. The National Cooperative Soil Survey mapped soils over most of the U.S. with field visits and soil sampling, and soil mapping was accomplished by digitizing fine-scaled aerial imagery (USDA-NRCS 2009). Each third order soil map unit may contain multiple soil components or ecological sites due to fine-scale variation that cannot be mapped (Forbis et al. 2007). The map unit is named according to the major soil component or the dominant ecological site within the unit. States within a STM are not typically mapped with their respective ecological site because each ecological site could be represented by multiple states depending on transition drivers (e.g., different locations within one ecological site may be observed in shrubland and grassland states following a fire; Steele et al. 2012).

The NRCS and other land management agencies (i.e., Bureau of Land Management, some state agencies) have integrated ecological sites and STMs into local and regional assessment, monitoring, and management efforts for rangelands (Bestelmeyer et al. 2009). STMs have been successfully developed (e.g., Kachergis et al. 2012) and implemented to address a variety of management concerns for multiple ecosystem services (Cagney 2009, Holmes and Miller 2010). STMs are a useful management tool because they outline the potential vegetation types for a site with natural and anthropogenic drivers of change in a conceptual diagram that is easily communicated to diverse stakeholders (Knapp et al. 2011). In this way, STMs can help land managers and landowners identify the costs and benefits of possible management actions, set appropriate goals relative to land potential, and evaluate the likely outcomes (Bestelmeyer et al. 2003). STMs can also serve as repositories for monitoring data, experimental outcomes, local knowledge, and other sources of information that may influence management decisions.

However, STMs have been criticized for several reasons. First, the probability of thresholds occurring is seldom quantified or supported by rigorous experimental and statistical analyses (Twidwell et al. 2013). Probabilities are usually described by qualitative or observational studies rather than experimental approaches, which can limit their predictive power for management. Second, STMs are often developed based on a small sample of plots that may not capture landscape variability or patterns at multiple scales (Briske et al. 2005, Steele et al. 2012). Third, STMs are frequently developed with expert opinion, literature, and very little ecological data (Knapp et al. 2011). Finally, STMs lack spatially specific information, such as spatial scale, context, and variation in driver histories (Bestelmeyer et al. 2011). Without a spatial approach for applying STMs across a landscape, STMs are greatly limited in their utility for land management because the states merely represent local descriptions and ignore the role of

scale, landscape patterns, and the interaction of processes at multiple scales that influence vegetation dynamics. For example, processes or disturbances at multiple scales could interact to influence transitions between states, which in turn, can influence the surrounding vegetation (Bestelmeyer et al. 2009, 2011). Drivers, such as grazing intensity and precipitation, can vary spatially to influence state transitions and/or phase changes, and spatial nuances in soil properties can also influence transition drivers (Bestelmeyer et al. 2011).

Taken together, limitations of small sample sizes, lack of field data, and non-spatial approaches preclude inference to landscape patterns and processes, especially in heterogeneous environments (Bestelmeyer et al. 2011, Sant et al. 2014). Limitations of STMs as currently developed may also preclude their acceptance by the scientific community and use by managers due to their lack of statistical rigor (Bestelmeyer et al. 2009). Further, conservation and management organizations are adopting ecosystem-based approaches to solve complex problems that often involve large landscapes and require the ability to make spatial inferences across the landscapes from ecological data (Forbis et al. 2007, Boyd et al. 2014).

These hurdles for acceptance and use of STMs may be overcome if states could be extrapolated from a sample of plots and mapped across a larger landscape using a statistically defensible approach. Mapping states on the landscape could create more robust STMs with spatial properties, such as patch size and arrangement, which could improve monitoring and management efforts and increase mechanistic understanding behind transition mechanisms (Bestelmeyer et al. 2011). A spatial representation of states in an area could also illustrate the total value of ecosystem services provided by states, such as livestock forage and wildlife habitat (Troy and Wilson 2006). Further, by mapping states over time, land managers could identify

places of structural change that may indicate functional loss, which could benefit from restoration efforts (Briske et al. 2005).

The approach used to map states on the landscape must be simple and use readily available spatial data in order to make the end product accessible to time- and resource-limited managers. A logical starting point is to develop a STM (see Bestelmeyer et al. 2009) for one ecological site or similar ecological sites. States can be generalized across similar ecological sites because different states should represent differences in structure and ecological processes rather than differences in species composition (Bestelmeyer et al. 2003, Steele et al. 2012). Also, similar ecological sites are often intermingled on a landscape and land owners often manage by vegetation type rather than by ecological site (Knapp and Fernandez-Gimenez 2009). When developing STMs, Bestelmeyer et al. (2011) recommend that managers incorporate three scales (patch, site, and landscape) and three classes of spatial processes that produce spatial heterogeneity: spatial variation in driver histories, spatial dependence in response to drivers, and spatial contagion and feedbacks, such as the spread of transitions to nearby areas.

Because conceptual STMs are easier to understand, communicate, and develop, few attempts have been made to spatially represent STMs (Provenchar et al. 2007). Also, land managers may lack the resources or technical capacity needed to quantify STMs with ecological and spatial data and map states. However, there have been a few attempts to spatially represent states across a landscape. Steele et al. (2012) created a spatial database of ecological sites and states for southern New Mexico using a classification system based on monitoring data, aerial imagery, and field visits. Due to fine-scaled variation in soils, they digitally edited the soil map units to represent multiple ecological sites within a map unit. In southwestern New Mexico, shrub cover classes, including shrub encroachment in regions dominated by native perennial

grasses, were mapped based on relationships between current and previous year precipitation and annual normalized difference vegetation index (NDVI; Williamson et al. 2012).

The approaches used by Steele et al. (2012) and Williamson et al. (2012) were developed and applied in an arid region in the northern Chihuahuan Desert with little ground cover but much variation in soils at fine scales. Both approaches also involved more analytical or spatial processing steps that may not be feasible for a land manager without an extensive statistical or GIS background. Here, we applied a relatively simple approach to map states across a less arid landscape with greater ground cover and coarser variation in soils. We used a previously developed STM for sandy and loamy sites in sagebrush rangelands of Northwest Colorado, which was created using a participatory approach with local knowledge and field data (Tipton 2015, Bruegger et al. 2016). We then evaluated our ability to predict (classify) those defined states using multinomial logistic regression and readily available spatial data, such as remotely sensed vegetation components (Homer et al. 2012), a digital elevation model, and wildland fire perimeter layers (Eidenshink et al. 2007). We then applied the model to the remotely sensed surface within target ecological sites throughout our study area, grouped similar pixels to produce state polygons across the landscape, and determined spatial properties of states, such as average patch size and proportion of state in the sampling region. This approach provides another tool for managers and land owners to improve monitoring and management efforts across broader landscapes, particularly in sagebrush rangelands.

Methods

Study Area

We used a STM developed in Major Land Resource Area 34A (Cool Central Desertic Basins and Plateaus) in eastern Moffat County, Northwest Colorado (Fig. 3.1). Local

stakeholders provided input to create the STM in an iterative, participatory approach (Bruegger et al 2016). Participating stakeholders selected the Sandyland and Rolling Loam ecological sites because these two sites dominate the study area and stakeholders felt vegetation responded similarly to natural and anthropogenic drivers on the two sites. Sampling plots also occurred on Deep Loam, Sandy Foothills, and Claypan ecological sites because they were intermingled with the Sandyland and Rolling Loam sites, and past treatments or disturbances of interest to stakeholders occurred on these sites (Tipton 2015).

Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) communities with either a bunchgrass (e.g., bluebunch wheatgrass [*Pseudoroegneria spicata*]) or western wheatgrass (*Pascopyrum smithii*) understory comprised our study area. In addition, there were two distinct areas that were former homestead properties seeded with crested wheatgrass (*Agropyron cristatum*) in the early 1900's and the exotic grass was still dominant in the understory. A pipeline scar in a separate area had also been seeded with crested wheatgrass prior to our study, which dominated the understory. Three wildfires occurred prior to the study: one in 2010 (3,185 ha), and two in 2008 (10,243 ha and 1,505 ha). Annual precipitation varied between 18–30 cm (Miller et al. 2011) and the common land use activities for this area include cattle and sheep ranching and recreational hunting.

Data Collection

Following the initial workshop, we conducted low intensity traverses (LIT) or reconnaissance throughout the study area (summer 2013) and used digital maps to examine topographic and vegetation variability within focal ecological sites (Bestelmeyer et al. 2009). We also focused our reconnaissance in past shrub treatments and fires to ensure our spatial data correctly characterized treatment or disturbance boundaries. Due to limited time, we only

collected qualitative data on vegetation and site characteristics for the initial traverses. However, the LIT provided us with enough information for further data collection in our study area based on mechanically treated areas, recent fires, and areas with no known disturbances or treatments.

For our high intensity traverses (HIT), we collected detailed vegetation and soils information to further refine our STM with quantitative data. Sampling plots were >400 m apart and >50 m from a fence line, road (two-track or county road), and water source (e.g., stock pond). At each plot, we established 5 parallel 50-m transects with 12.5-m spacing between transects. We dug a soil pit (≥ 50 cm deep) in the center of each plot and described the soil using NRCS standard soil description protocols (Schoeneberger et al. 2012). For each soil pit, we described the soil horizon by recording texture, color, structure, and carbonates in each layer. We recorded slope, aspect, and elevation for each plot, as well as other plot metadata, such as distance to nearest water source and road or two track. To describe the vegetation in each plot, we used the line-point intercept (LPI) method (Bonham 1989) to measure foliar and basal cover by species, litter cover, rock, dung, and bare ground at 1-m intervals on each transect. We also used the dry weight rank method (Jones and Hargreaves 1979) to estimate species composition by weight in 5-15 0.1-m^2 quadrats randomly placed on the transects. For additional details on the HIT and data collection, see Tipton (2015).

After surveying several high intensity plots during the first field season in 2013, we decided to collect quantitative data at additional LIT plots in 2014 in order to increase our sample size for sandy sites. Loamy sites appeared to be over-represented initially and we wanted to make inference about sandy and loamy ecological sites for our STM. At each low intensity plot, we collected metadata (i.e., slope, elevation, aspect, and notes on management history) and dug a soil pit to describe the color, texture, and pedoderm class. We then estimated species

richness for an approximate 50×50 -m area, and used the dry weight rank method to estimate species composition by weight in 15 0.1-m^2 quadrats randomly placed in the sampling plot. For a subset of these LIT plots, we collected high intensity data (e.g., LPI and basal gap) the following field season to further characterize the vegetation in the plot for our STM.

Data Analysis

Tipton (2015) used a variety of multivariate techniques to describe the abiotic gradients in the study area and identify distinct vegetation clusters. The clusters were largely unaffected by abiotic characteristics associated with ecological site, which provided additional support for creating one STM for several ecological sites (Tipton 2015). The resulting STM contained two shrub-dominated states (diverse shrubland and needle-and-thread [*Hesperostipa comata*] shrubland), a native grassland state, and a state dominated by crested wheatgrass (Appendix I). For a more detailed description of each state and potential transition drivers among the states, see Tipton (2015).

To describe statistical relationships at the landscape-scale between the categorical states and spatial predictors, we created multinomial logistic regression models with a logit link (Hilbe 2009). We used the package “nnet” (Ripley and Venables 2016) for the multinomial models and all analyses were performed in program R 3.3.2 (R Development Core Team 2015). We used a remotely sensed, sagebrush mapping product, which included litter, bare ground, herbaceous cover, total shrub cover, all sagebrush cover, and big sagebrush cover within 30×30 -m pixels (Homer et al. 2012). Using multi-scaled spectral imagery, field sampling, and regression tree analysis, Homer et al. (2012) mapped these vegetation components across sagebrush rangelands in Montana, Wyoming, and Colorado. To be consistent with field sampling methods, we summarized the remotely sensed vegetation components within the same area around each

sampling plot. To do this, we buffered each sampling plot by 25 m and used the “feature envelope to polygon” tool to create a 50 × 50-m square buffer around each sampling plot center in ArcMap 10.0 (ESRI 2011). We then calculated zonal statistics for each vegetation component to provide the average pixel value within a 50 × 50-m “plot”.

Because we recorded abiotic metadata at the center of each sampling plot, we simply extracted the value for each subsequent predictor in ArcGIS at the plot center. Our topographical predictors included elevation, aspect, and slope obtained from a digital elevation model (10 × 10-m pixels; U.S. Geological Survey 2014). Our bioclimatic predictors were based on 30-year monthly averaged (1971-2000) temperature and precipitation PRISM data (800 × 800-m pixels) and included annual precipitation, minimum temperature for the coldest month, and maximum temperature for the warmest month (O’Donnell and Ignizio 2012). We used the “nearest” resampling technique when re-projecting the PRISM data and snapped the PRISM raster layers to a vegetation component raster (e.g., all sagebrush cover). To incorporate disturbance events, we downloaded spatial data from the Monitoring Trends in Burn Severity database for the extent of the three wildfires in our study area (<http://mtbs.gov/dataaccess.html>). We then classified sampling plots as “burned” (1) if they occurred within one of the three wildfires in our study area and “not burned” (0) otherwise. We did not include a predictor for management history because mechanically treated areas and homestead properties occurred in small proportions of the study area and represented small proportions of the total sampled plots. Further, when predicting the top model(s) to a larger landscape, we did not have knowledge of all past mechanical treatments and locations seeded with crested wheatgrass in the landscape.

To initially determine which predictors to consider for our multinomial models, we examined boxplots for each descriptor and ran Analysis of Variance tests. If there was little to no

difference in a predictor among the states, it was excluded from further consideration. We also checked correlation among the predictors, so as not to include overly correlated predictors ($R > |0.7|$) in the same model. Prior to running the models, we normalized continuous predictors to a mean of zero and SD of 1, so they were on the same scale and to allow for model convergence (Ripley and Venables 2016). We only included models that contained at least one vegetation component because STMs should convey information about vegetation dynamics (Bestelmeyer et al. 2003), and predicting states on the landscape with some type of vegetation characteristic would help to identify potential management actions; a manager cannot manage elevation.

We used a Bayesian Information Criterion (BIC; Hilbe 2009) to evaluate all possible model combinations and retained models with $\Delta\text{BIC} \leq 2$. We calculated a McFadden's pseudo- R^2 statistic to assess variation captured by a fitted model relative to the null model (Hilbe 2009). We also used the Hosmer-Lemeshow goodness-of-fit (GOF) test to examine each model's fit using the "generalhoslem" package (Jay 2016), and varied the number of groupings ($g = 10, 8, 6, 3$) due to a smaller sample size (Hilbe 2009). The diverse shrubland state was set as the reference level or category for all models, so the predictor relationships must be interpreted relative to this state. Unlike binomial logistic regression and ordered logistic regression, the response variables in multinomial regression are assumed to be unordered and independent of one another (Hilbe 2009). Therefore, the predictor coefficients can be viewed as increasing or decreasing the probability of being in one category or state relative to the reference category. These probabilities are then exponentiated to the relative risk ratios for ease of interpretation (Hilbe 2009). Because continuous predictors were normalized for model convergence, betas are interpreted as a change from the minimum to the maximum value for un-normalized predictors.

Because our main objective was to map the states in the STM by applying the model to relevant point locations within the study area, we tested the classification accuracy of our best model(s) with several methods. First, for internal validation, we predicted the best model(s) to the plots used to build the model to see how many the model correctly classified by state. Second, we used 10-fold cross validation (“caret” R package; Kuhn 2016), as this method may more accurately estimate the classification accuracy for a model relative to other validation methods (Kohavi 1995). Third, we tested the best model with an independent dataset, which represented 20% of the data used for model development (Hilbe 2009). We had 15 LIT plots without HIT data. These plots contained soils, species richness, and DWR data, and from the latter, we could determine species composition for each plot. From these data and the disturbance histories, we could reasonably classify the LIT plots as one of the four states in the STM. We followed a key that included four questions: Is the plot dominated by crested wheatgrass? (if yes, it is most likely a crested wheatgrass state; if no, see next question). Does the plot occur in a burn and contain <5% shrub cover? (if yes to both, it is most likely the native grassland state; if no, see next question). Does the plot contain antelope bitterbrush? (if yes, it is most likely a diverse shrubland state; if no, see last question). Does the plot contain needle-and-thread grass and cheatgrass? (if yes, most likely the needle-and-thread shrubland state).

Once we applied the model(s) to our entire study area, we also compared the model-predicted state for pixels containing our LIT and HIT sampling plots (same as the plots used to evaluate the model independently and develop the model, respectively) to see how many were correctly classified. A final way to informally test the model’s classification accuracy was to see if a similar proportion of pixels within recent fires in our study area were classified as native grassland compared to the proportion of sampling plots within a burn classified as native

grassland (16 of 22 HIT plots). A majority of the pixels within a recent fire should be classified as native grassland because full recovery of Wyoming big sagebrush communities often requires >30 years (Lesica et al. 2007). We also only evaluated pixels within fires occurring from 2008-2010 in our study area in order to match the time period for burned areas in which we sampled.

To map the states across our study area, we restricted our predictions to pixels south and east of the Little Snake River and north of the Yampa River for consistency in land management and vegetation communities where we sampled (Fig. 3.1). We only predicted the top model(s) to pixels within ecological sites that were targeted for the vegetation sampling (i.e., Deep Loam, Rolling Loam, Sandy Land, Sandy Foothills, and Claypan). After extracting each raster predictor layer to the target ESD extent, we read the files into program R using the “raster” package (Hijmans et al. 2016). For continuous predictors, we normalized each raster pixel using the minimum and maximum values from the plot data rather than from the entire study area extent, so that the normalized values would be consistent with the values used to build the model. We then created a raster stack for the top predictors and predicted the best model to all pixels within the study area extent. We model-averaged predictions to the study area extent if there were multiple competitive models. We generated summary statistics for each state from the predicted surfaces, including total area and average patch size, and the proportion of each state within the 2008-2010 fires.

Results

During summer 2013-2015, we collected vegetation and soil data at 73 HIT plots. We also collected species richness, DWR, and soil information for 15 LIT plots during summer 2013. Of the HIT plots, 32 were classified as diverse shrubland according to multivariate techniques, nine were classified as crested wheatgrass, and 16 plots each were classified as

needle-and-thread shrubland and native grassland (Tipton unpublished data). According to our decision key, we classified one LIT plot as diverse shrubland, eight as needle-and-thread shrubland, and six as native grassland.

Slope, aspect, and litter spatial predictors had limited differences among the four states and were uninformative for our models. Several predictors were highly correlated and restricted from occurring in the same model. All sagebrush cover, big sagebrush cover, and total shrub cover were positively correlated ($R > 0.9$), and bare ground was negatively correlated with each of the three shrub predictors ($R > -0.7$). We also discarded minimum temperature for the coldest month due to a positive correlation with annual precipitation ($R = 0.8$), and we discarded maximum temperature for the warmest month due to a negative correlation with elevation ($R = -0.9$).

We had two competitive models: one included big sagebrush cover plus elevation (BIC = 126.46, $w=0.63$) and it explained 53% of the variation (Table 1). Our top model had good model fit based on varied groupings for the Hosmer-Lemeshow GOF test. The second best model included all sagebrush cover plus elevation (BIC = 128.33, $w=0.25$) and explained 52% of the variation. However, this model was essentially the same as the best model due to a high correlation between big and all sagebrush cover ($R=0.9$), so we only considered the top model further. For our best model, relative risk ratios (Table 3.2) suggest that a 20% increase in big sagebrush cover (range 3-23%) decreased the relative risk of being in a native grassland and crested wheatgrass state relative to the diverse shrubland state, but increased the relative risk of being in a needle-and-thread state (Table 3.2). For a 268-m increase in elevation (range 1,903-2,171 m), it was more likely for the state to be diverse shrubland rather than the other three states (Table 3.2).

The classification accuracy for our best model was consistent across methods. The 10-fold cross validation classification accuracy for the top model was 71%. For the classification accuracy of our independent dataset (i.e., LIT plots), we correctly predicted the state for 73% of the plots (11 of 15 plots). Further, our top model correctly classified the state for 71% of the plots used to build the model (52 of 73 plots). When we predicted state to pixels in our entire study area, the model correctly classified the state for 73% of the LIT plots (11 of 15 plots) and 74% of the HIT plots (54 of 73 plots). Individual component accuracies for the model predictions to HIT sampling plots were 94% for diverse shrubland, 81% for needle-and-thread shrubland, and 56% for native grassland, and 0% for crested wheatgrass. Component accuracies for the model predictions to pixels containing HIT plots were the same for diverse shrubland, needle-and-thread shrubland, and crested wheatgrass, but improved to 69% for native grassland. Lastly, of the five fires that occurred in our study area from 2008-2010, the model classified 77% of the total pixels for all burned areas as native grassland (Fig. 3.2), and the model classified 14% as needle-and-thread shrubland, 1% as crested wheatgrass, and 9% as diverse shrubland.

We predicted the model to pixels within the target ecological sites in our study area (total 2,280.14 km²), and the needle-and-thread shrubland state comprised 39% of the area, followed by native grassland at 32%, and diverse shrubland at 28% (Table 3.3, Fig. 3.2). The crested wheatgrass state comprised the lowest proportion in our study area (1%), and also had the patchiest or least contiguous distribution in our study area, with an average patch size of 0.01 km². In contrast, the diverse shrubland state had the largest average contiguous patch size of all states (0.09 km²), followed by the needle-and-thread shrubland state (0.05 km²), and the native grassland state (0.02 km²). The diverse shrubland state also had the largest maximum patch size

at 382.72 km², followed by 100.61 km² and 90.81 km² for the needle-and-thread shrubland and native grassland states, respectively.

Discussion

Our Approach

We used a locally developed, data-driven STM to evaluate landscape predictions of ecological states. We demonstrated that remotely sensed vegetation and abiotic layers could be used to successfully predict ecological states across larger landscapes than we could assess on the ground. Our STM was developed with ecological data and local knowledge using a participatory approach, which should increase relevancy of the product for local land management (Bruegger et al. 2016). This data-driven approach should also improve the quality of the spatial products, providing more accurate and relevant insights into management issues (Steele et al. 2012). To our knowledge, ours is the first attempt to map states within a STM for sagebrush rangelands. Sagebrush rangelands have faced multiple threats over the last century, which have reduced the quality and quantity of sage-grouse habitats, resulting in many wildlife species of conservation concern (Knick et al. 2003). Thus, our spatial approach could have important management implications for local wildlife populations and other ecosystem services by gauging the impact of land-use change on these services (Timmer 2017, Chapter II). Managers could combine the mapped states with values for ecosystem services, such as wildlife habitat, livestock forage, or soil stability to guide management decisions and scenario planning (Troy and Wilson 2006). Our method could also allow managers to identify landscape patterns that may influence transitions between states, such as an exotic grassland-dominated state expanding to surrounding patches (Brisket et al. 2005, Miller et al. 2011), or target areas for restoration efforts.

Our best model included percent cover of big sagebrush, which is an important indicator for management of sagebrush rangelands, especially for managing wildlife habitat (Knick et al. 2003). An increase in big sagebrush cover increased the probability of a plot being a diverse shrubland state, although only the confidence interval for the native grassland state probability did not overlap zero (Table 3.2). “Burn” was not in our top model, but this predictor was negatively correlated with big sagebrush cover ($R = -0.44$). Thus, including it with big sagebrush cover may have been redundant as big sagebrush cover likely accounted for the structural differences between native grassland and diverse shrubland plots. An increase in big sagebrush cover also decreased the probability of a plot being classified as crested wheatgrass relative to diverse shrubland. However, the confidence interval for this probability likely included zero (Table 3.2) because former homestead properties occurred within and outside burned areas in our study area. Therefore, some crested wheatgrass plots contained as much as 17% big sagebrush cover. In contrast, an increase in big sagebrush cover increased the probability of a plot being classified as needle-and-thread shrubland, although the confidence interval for this probability also included zero (Table 3.2). Indeed, total sagebrush cover from LPI data and big sagebrush cover from the remotely sensed product were higher for diverse shrubland plots than for needle-and-thread shrubland plots (22.0% versus 18.3% sagebrush cover from LPI data and 13.7% versus 11.3% remotely sensed big sagebrush cover). However, difference in sagebrush cover from LPI data was not significant between these two states (Tipton unpublished data).

Elevation was the best predictor for differentiating diverse shrubland and needle-and-thread shrubland plots, with diverse plots mostly occurring at higher elevation (i.e., >2,060 m) and needle-and-thread plots occurring mostly at lower elevation. Elevational differences linked to greater precipitation and soil moisture could have driven the differences between the two

shrubland states. The higher elevation sites where most of the diverse shrubland plots occurred received greater annual precipitation (435.7 cm) with a slightly lower maximum temperature for the warmest month (28.4°C) compared to the lower elevation sites where needle-and-thread shrubland plots were more prevalent (406.7 cm and 29.5°C). Antelope bitterbrush was also present at all diverse shrubland plots (Tipton 2015). It occurs over a wider range of elevation than where we sampled and local stakeholders suggested that lack of bitterbrush at lower elevation sites may be a result of grazing history (Tipton 2015). The lower elevation sites experienced increasing elk browsing pressure in the winter over the last several years. In addition, sheep historically grazed the low elevation sites, whereas cattle historically grazed the higher elevation sites. However, because diverse shrubland plots primarily occurred in areas with greater annual precipitation and a lower maximum temperature for the warmest month, our relationships between these two shrubland states and elevation could be attributable to both climate and management history. Not considering local knowledge from multiple stakeholders would have limited our understanding of these relationships between site history and biotic and/or abiotic predictors in STMs (Bruegger et al. 2016), although targeted grazing exclosures over longer time periods would provide greater understanding behind these potential transition drivers.

Our best model classified approximately 77% of the pixels across our study area in all burned areas as native grassland compared to the 73% of our sampled plots classified as native grassland (Tipton unpublished data). These proportions are fairly similar, which gives greater confidence in our model. Further, the model classified 14% of all burned areas as needle-and-thread shrubland, which is the same proportion as our sampled plots (3 of 22 plots). We only classified pixels as “burned” in our study area if the fires occurred during the same time period

as the fires we sampled in (i.e., 2008-2010). However, it is likely that not even partial recovery of Wyoming sagebrush occurred within this short time period (Lesica et al. 2007). Therefore, pixels within earlier burns should probably be classified as native grassland also. Two additional fires occurred in our study area just prior to the included burns, one in 2007 and one in 2006. For the 2007 fire, our model classified most of the pixels as native grassland (96%) and 4% as needle-and-thread shrubland. For the 2006 fire, the model classified 62% of the pixels as native grassland, 36% as diverse shrubland, and <2% as crested wheatgrass and needle-and-thread shrubland. Our model over-estimated pixels classified as diverse shrubland relative to our proportion from burn sampled plots. However, we did not sample burned areas at higher elevations, so it is not surprising that we classified 0 burned plots as diverse shrubland. We also intentionally sampled within a former homestead property in one of our burned areas, so the model under-estimated pixels classified as crested wheatgrass (1%) relative to the proportion from our sampling plots (14%).

In our study area, the needle-and-thread shrubland state comprised the largest proportion of all four states (39%), followed by the native grassland (32%) and diverse shrubland states (28%; Table 3.3). In terms of ecosystem services, over half of the study area (67%) was predicted to be sagebrush communities, and could thus provide habitat for sagebrush-obligate species, many of which are of conservation concern (Knick et al. 2003). The diverse shrubland state also provided the greatest herbaceous biomass for foraging compared to the other shrubland state (Tipton unpublished data). In contrast, approximately one-third of the study area was dominated by native grassland habitat, mostly within burned areas. The native grassland patches may not provide much cover or nesting sites for shrub-obligate wildlife, but they would provide greater foraging opportunities for domestic and wild ungulates compared to the needle-and-

thread shrubland areas. Further, greater sage-grouse will use burned areas if they are heterogeneous with some remaining shrub cover (Fischer et al. 1996, Knick et al. 2005, Timmer 2017, Chapter II), and brood use may be greater in less shrubby habitat if it has surrounding sagebrush cover (Dahlgren et al. 2006). All of the 2008-2010 fires in our study area were predicted to contain a mix of grassland and shrubland habitat with surrounding sagebrush cover (Fig. 3.2), suggesting they could potentially provide sage-grouse habitat.

The diverse and needle-and-thread shrubland states had the largest and second largest average patch size and the largest contiguous patch sizes (Table 3.3). This information could have management implications for ecosystem services. Managers or landowners may want to maintain large patches of the shrubland states for wildlife habitat and habitat connectivity, forage, and ground cover or soil stability. Spatial properties of states could also improve models describing wildlife habitat relationships, such as interspersed patches within a grassland state. Mapping states on the landscape is also useful for identifying undesirable patches and potential triggers that could lead to state transitions (Bestelmeyer et al. 2011, Steele et al. 2012). For example, spatial representation of shrub-dominated states in southwestern New Mexico has directed shrub herbicide applications to areas with specific shrub species and sufficient grass cover (Bestelmeyer et al. 2009, Steele et al. 2012).

The crested wheatgrass state differed from the other states by dominance of an exotic grass species, but Tipton (2015) separated it based on management history (i.e., former homestead properties from the mid 1900's). The crested wheatgrass plots occurred at both the high and low elevation sites, within and outside burned areas, and only represented 9 of 73 sampling plots. We also did not include a specific predictor to discriminate the crested wheatgrass plots because this information was not available throughout the study area. Thus, our

individual component accuracy for these plots was lowest of all the states (0%). Based on our top model, we predicted the crested wheatgrass state comprised 1% of our study area. This estimate seems low for the area (H. Seim, pers. comm.), and is likely unrealistic given the low classification accuracy for the state. However, it is predicted to occur in small pockets distributed throughout the study area (Fig. 3.2), which is realistic given the limited and sporadic distribution of homestead properties and pipeline scars in the area. To improve classification accuracy for a spatially limited state such as this one, increased sampling efforts could increase the power and likelihood of other predictors discriminating each state, such as bare ground or percent sagebrush cover. Local knowledge of an area can also improve sampling efforts for these sparsely distributed states.

Other Approaches

Our approach to map states from a recently developed STM should be applicable to other sagebrush rangelands. However, other approaches to map states may be necessary given variation in soils and vegetation types or different management objectives. In our study area, ground cover was more continuous and soil variation occurred at coarser scales, so soil map units could be classified according to the dominant ecological site (Bestelmeyer et al. 2009). The methods used by Steele et al. (2012) are more complicated than our approach because they edited soil map units to preserve spatial variation at fine scales (i.e., ecological sites within a soil map unit), which entailed delineating spatial features with aerial imagery. Their study area also contained prominent land features, like coppice dunes, that facilitated spatial delineation from imagery. Further, Steele et al. (2012) manually classified states across the landscape with existing monitoring data, aerial imagery, or field visits, which may not be feasible for time-constrained managers over a large landscape. However, the approach used by Steele et al. (2012)

resulted in a spatial database (linked to the SSURGO database) of ecological sites with associated generalized states for southern New Mexico, and the database has already been used to improve range management. For example, the BLM used the mapped states to target shrub control efforts, organize rangeland health assessments, and determine locations for solar energy installations to minimize impact.

Another method that holds promise for improved rangeland monitoring across larger scales is the use of image analysis whereby managers take vertical photos of field plots, and then use software programs to estimate percent cover and bare ground from the images (Booth and Tueller 2003). Ground-based imagery reduces field sampling time, so managers can acquire more field samples and increase statistical power (Booth and Tueller 2003, Cagney et al. 2011). These images also serve as a permanent record of range condition and thus, allow for temporal comparison of sites over time (Cagney et al. 2011, Sant et al. 2014). When combined with remotely sensed data, ground images can be extrapolated across larger spatial and temporal scales to assess patterns and change over time (Sant et al. 2014). Remotely sensed products used in this study have recently been coupled with historical precipitation data to forecast changes in rangeland vegetation components, which could also be used to monitor change over time (Homer et al. 2015). However, one limitation with ground or satellite imagery is a lack of more detailed information to inform specific management objectives, such as grass height for sage-grouse nesting habitat (Doherty et al. 2014) or soil properties to link with ecological sites. Further, imagery of biotic components may need to be combined with other information, such as management history and abiotic predictors, to accurately predict states within a landscape, as we illustrate in our study. Simply predicting vegetation cover to a region without linking it to a STM precludes an understanding of ecosystem services associated with each state and the mechanisms

behind state transitions, which may guide management decisions and restoration efforts (Bestelmeyer et al. 2003).

Considerations and Extensions for our Approach

If our approach were used to map states in other sagebrush regions, managers should include multiple types of predictors in modeling efforts because remotely sensed vegetation components alone may not adequately distinguish states (Steele et al. 2012). States may not have large structural differences and without variation in management history or abiotic features, states may need to be distinguished based on species composition. However, management history predictors can only be included if someone has knowledge of their occurrence throughout the entire area of inference. Managers should also include predictors that span a gradient through the study area, like cover of bare ground, to increase the model's ability to discriminate pixels within the area. Shrub cover may seem like an easier indicator to manage and more relevant to include for sagebrush rangelands, but structural differences in other regions may not be as stark as “burned” and “not burned”, so that shrub cover varies little among states. Bare ground has important implications for soil infiltration and stability and is a useful indicator of rangeland health (Booth and Tueller 2003, Pellant et al. 2005). Further, bare ground is consistently a more accurate indicator (Booth and Tueller 2003, Homer et al. 2012, Sant et al. 2014), and increased bare ground may also be associated with dense, undisturbed sagebrush states (Cagney 2009, Kachergis et al. 2012). When developing the STM, field sampling should similarly include variability across the landscape, such as disturbed and undisturbed areas and diversity in slope and aspect, to provide evidence for or against alternate states (Bestelmeyer et al. 2009).

Managers may also need to prioritize which states are included in the STM for mapping. For example, if multivariate analyses identify a state as a distinct cluster, but it only occurs within a small portion of the study area or is represented by only a few sampling plots (e.g., our crested wheatgrass state), it may be best to combine the state with another which has similar structural and/or functional attributes to improve model classification accuracy. If a state occurs in very small proportions of a study area, it may even be best to not sample those patches and introduce additional variability. However, if the state is of management concern (e.g., critical habitat for a wildlife species), then it should be included in the model, but with greater sampling effort to describe it.

Although it represented only a few plots, we included the crested wheatgrass as a separate state in our STM for demonstration purposes and because it was a distinct cluster in analyses conducted by Tipton (2015). However, to see if classification accuracy for the model improved, we re-assigned the crested wheatgrass plots to one of the other three states based on our LIT classification key. We re-ran analyses post-hoc and the top model's classification accuracy improved slightly for the LOOCV score (71% to 73%) and when predicting the model to HIT plots (from 71% to 74%), but confidence intervals for the parameters for each state did not overlap zero. The mapped STM excluding the crested wheatgrass state was similar to our original map, likely because only a small proportion of sampling plots were classified as crested wheatgrass. This is a useful illustration that the quality of the spatially explicit STM will reflect the quality of the conceptual or data-driven STM (Steele et al. 2012). If the model is developed with probabilistic sampling and large sample sizes to capture landscape variability in the sampling region, then the classification accuracy throughout the study area should be higher.

Managers also need to consider the spatial and temporal resolution of spatial predictors relative to resolution of spatial variation in the study area. For instance, a data layer of vegetation cover types (e.g., The National Land Cover Dataset) may not adequately predict states in a sagebrush system as well as a data layer of vegetation components (e.g., LANDFIRE). The states could be separated by amount of bare ground rather than functional group (e.g., Cagney 2009), and a data layer containing vegetation cover types may be too coarse to discriminate states in the study area. There have been recent improvements to remotely sensed methods and data are becoming increasingly available at regional scales (Homer et al. 2012, 2015) and finer resolutions (e.g., Sant et al. 2014). Thus, this approach could potentially be used to map community phases differentiated by species composition or states with less drastic structural differences (e.g., grasslands). However, it is probably impractical to map ephemeral plant phases on a landscape because they would likely shift in response to precipitation or grazing pressure changes (Bestelmeyer et al. 2003, Steele et al. 2012). Another consideration is relevance of spatial data to the time period of sampling. It may not be possible to conduct field sampling within the same time period as satellite imagery is collected (but see Homer et al. 2012), but the spatial data should still capture relevant landscape variability. For example, fires of interest in our study area occurred from 2008-2010, so we used vegetation cover data that were compiled after the fires occurred. Otherwise, we would not have accurately discriminated native grassland pixels in the study area.

We predicted states to target ecological sites within our study area. However, spatial information for ecological sites may be lacking in certain regions or it may be outdated and inaccurate. In this situation, a manager could use a digital elevation model or satellite imagery to identify different landform features in a region, which are likely different ecological sites

(Bestelmeyer et al. 2009). There are also recent quantitative approaches to create digital soil maps for a region (McBratney et al. 2003, Levi 2012), which could then be paired with a STM to map states. Object-oriented image analysis may also offer an alternative to map ecological sites in a region using image segmentation from remotely sensed imagery and additional spatial information with a classification algorithm (Laliberte et al. 2007, Steele et al. 2012). However, it would be a more cumbersome process for land managers to map ecological sites and states within the sites, and it may be more practical and preferable to simply map at the scale of ecological sites in the region. Ecological sites would still provide useful information on potential plant communities and may be fine-scaled enough depending on management objectives (Bestelmeyer et al. 2009).

Management Implications

Spatial representations of STMs have a variety of useful applications that could greatly improve land assessment, monitoring, and management at landscape scales. They could increase our understanding of vegetation patterns and change at larger scales rather than within small sampling plots (Briske et al. 2005). Managers could use them to design assessment and monitoring programs in a probabilistic, hierarchical fashion or target areas for experiments to test and quantify transition probabilities, and thus, increase statistical rigor (Briske et al. 2005, Bestelmeyer et al. 2009). Spatially represented STMs could also be used for planning purposes to ensure adequate sample sizes across states if managers wish to draw conclusions about ecosystem services provided by states (e.g., Holmes and Miller 2010). Managers could ground truth particular areas, like exotic grassland-dominated states, to target for control or restoration efforts. As a prioritization tool for land managers, mapped states could inform management or

conservation actions, such as promoting larger or more contiguous states that provide valuable ecosystem services.

Landscape diversity may also be a management objective for promoting multiple ecosystem services provided by multiple states. Mountain plovers (*Charadrius montanus*) require a mostly bare ground, heavily grazed or burned state for their nesting habitat, whereas upland sandpiper (*Bartramia longicauda*) nesting habitat is comprised of taller grasses with little grazing (Derner et al. 2009, Augustine and Derner 2012). If combined with simulated state-and-transition modeling (Daniel and Frid 2011), land managers could more accurately forecast potential state outcomes for various management actions or disturbances within a region (Provenchar et al. 2007). This could guide iterative hypothesis-testing, model improvement, and decision-making within an adaptive management framework to solve complex ecosystem problems (Holling et al. 1978), such as pinyon-juniper (*Pinus* spp.-*Juniperus* spp) encroachment in sagebrush rangelands (Boyd et al. 2014). Spatially explicit STMs could ultimately inform conceptual or data-driven STMs by describing landscape patterns that lead to transitions and linking structural changes to ecological function (Briske et al. 2005, Bestelmeyer et al. 2011). Taken together, these should increase the rigor of STMs and potentially promote their acceptance and use by the range and scientific communities.

Table 3.1. Top multinomial logistic regression models considered for predicting states identified from a state-and-transition model in Northwest Colorado, 2013-2015 (Tipton 2015). For each model, we report log-likelihood (LL), number of parameters (K), Bayesian Information Criterion (BIC), difference in BIC compared to lowest BIC of the model set (ΔBIC), and BIC weight (w) for all models $< 7 \Delta BIC$.

Model ^a	LL	K	BIC	ΔBIC	w
bs ^b + elev ^c	43.92	9	126.46	0.00	0.63
as + elev	45.11	9	128.33	1.87	0.25
shrub + elev	46.08	9	130.78	4.32	0.07
as + herb + elev	40.65	12	132.78	6.32	0.03
bs + herb + elev	40.84	12	133.17	6.71	0.02

^a All continuous predictors were normalized on a 0,1 scale.

^b Vegetation predictors include big sagebrush cover (bs), all sagebrush cover (as), total shrub cover (shrub), and herbaceous cover (herb) within 30×30-m pixels (Homer et al. 2012).

^c Elevation in meters.

Table 3.2. Model statistics from the top multinomial logistic regression model for predicting states identified from a state-and-transition model in Northwest Colorado, 2013-2015 (Tipton 2015). Statistics are presented relative to the diverse shrubland state and include parameter probabilities, 95% confidence intervals in parentheses, and relative risk ratios (RRR).

Probabilities:	Intercept	bs ^{a,b}	elev ^c
Crested wheatgrass	13.27 (5.43, 21.11)	-4.13 (-9.24, 0.99)	18.78 (-29.63, -7.97)
Native grassland	14.81 (6.99, 22.62)	-7.37 (-12.65, -2.09)	19.00 (-29.65, -8.36)
Needle-and-thread shrubland	14.99 (7.13, 22.83)	3.86 (-3.01, 10.72)	29.32 (-41.75, -6.88)

RRR:	Intercept	bs	elev
Crested wheatgrass	580354.4	0.02	<0.001
Native grassland	2697262.3	<0.001	<0.001
Needle-and-thread shrubland	3223331.4	47.26	<0.001

^a All continuous predictors were normalized on a 0,1 scale.

^b Vegetation predictor includes big sagebrush cover (bs) within 30×30-m pixels (Homer et al. 2012).

^c Elevation in meters.

Table 3.3 Landscape metrics for spatially explicit states identified from a state-and-transition model in Northwest Colorado, 2013-2015 (Tipton 2015) and predicted with multinomial logistic regression.

State	Total area (km ²)	Proportion in study area	Average patch size (km ²)	Maximum patch size (km ²)
Diverse shrubland:	649.71	0.28	0.09	382.72
Needle-and-thread shrubland:	886.45	0.39	0.05	100.61
Native grassland:	720.89	0.32	0.02	90.81
Crested wheatgrass:	23.09	0.01	0.002	0.17

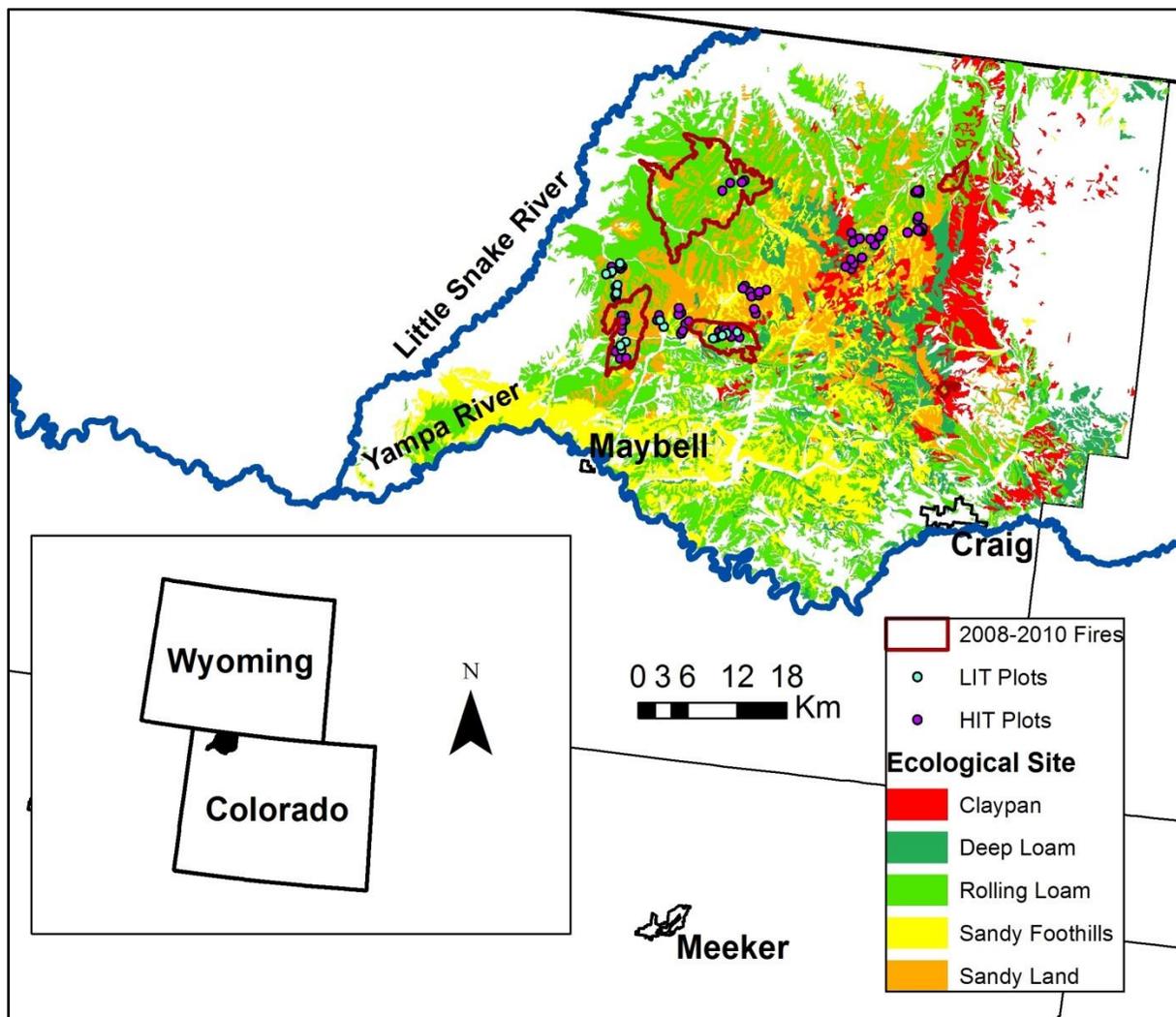


Figure 3.1. Study area extent for making a spatially explicit state-and-transition model in Moffat County, Northwest Colorado (Tipton 2015). Included are focal ecological sites, high intensity traverse (HIT) and low intensity traverse (LIT) sampling plots, recent fires, and past mechanical shrub treatments. Transparent areas within the study area boundaries (i.e., to the north of the Yampa River, to the east of the Little Snake River, and to the eastern Moffat county border) indicate no data.

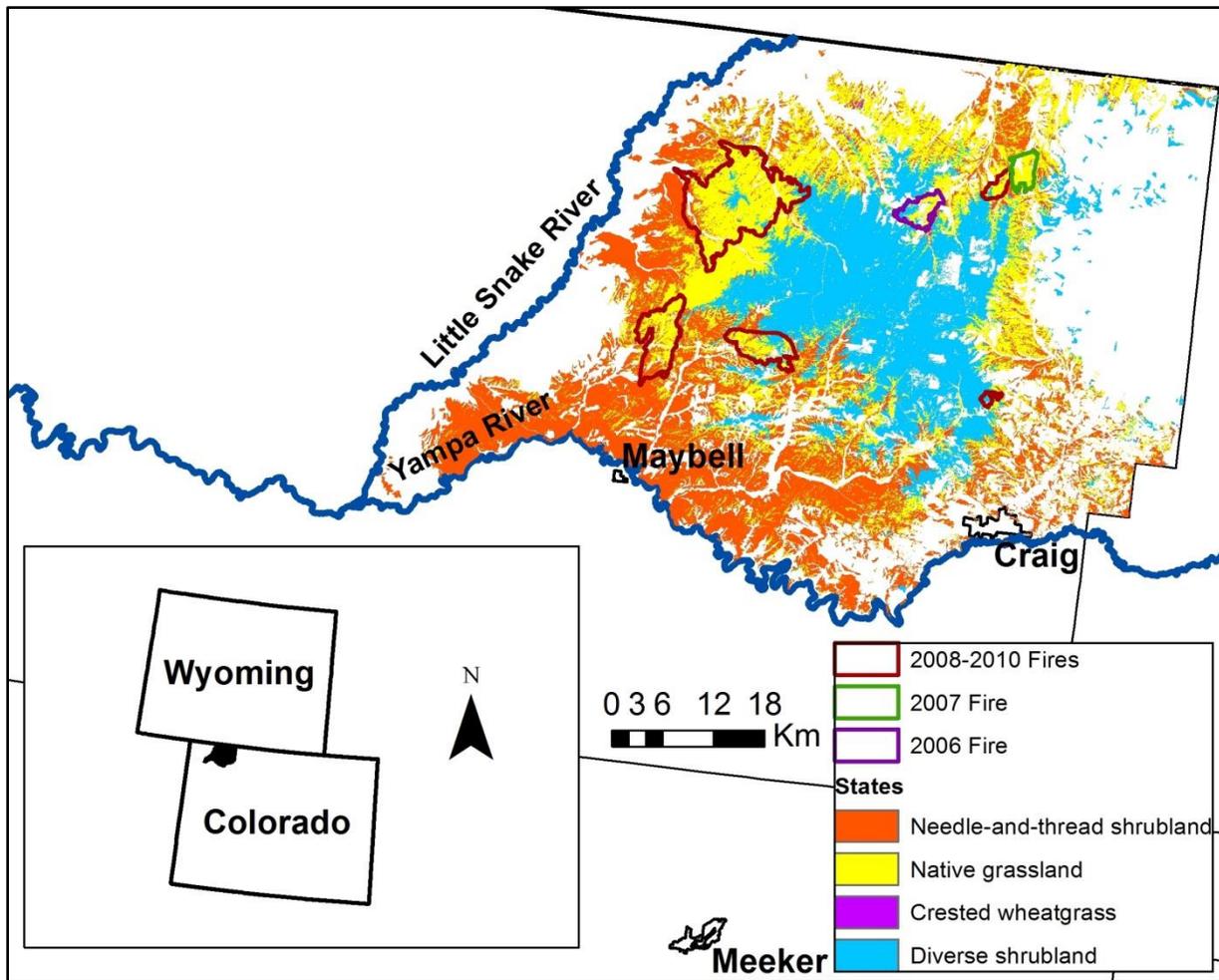


Figure 3.2. Map of multinomial logistic regression model predictions for states in a state-and-transition model in Moffat County, Northwest Colorado (Tipton 2015, Appendix I). Included are four states (native grassland, crested wheatgrass, needle-and-thread shrubland, and diverse shrubland) as predicted by a multinomial logistic regression model. Transparent areas within the outlined study area boundaries (i.e., to the north of the Yampa River, to the east of the Little Snake River, and to the eastern Moffat county border) indicate no data.

LITERATURE CITED

- Augustine, D. J., and J. D. Derner. 2012. Disturbance regimes and mountain plover habitat in shortgrass steppe: large herbivore grazing does not substitute for prairie dog grazing or fire. *Journal of Wildlife Management* 76:721-728.
- Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.
- Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, Jr., D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology and Management* 62:1–15.
- Bestelmeyer, B. T., D. P. Goolsby, and S. R. Archer. 2011. Spatial perspectives in state-and-transition models: a missing link to land management? *Journal of Applied Ecology* 48: 746–757.
- Bonham, C. D. 1989. *Measurements for terrestrial vegetation*. Wiley-Interscience, New York, New York, USA.
- Booth, D. T., and P. T. Tueller. 2003. Rangeland monitoring using remote sensing. *Arid Land Research and Management* 17:455-467.
- Boyd, C. S., D. D. Johnson, J. D. Kerby, T. J. Svejcar, and K. W. Davies. 2014. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? *Rangeland Ecology and Management* 67:358-368.
- Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and-transition models, thresholds,

- and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management* 58:1–10.
- Bruegger, R. A., M. E. Fernandez-Gimenez, C. Y. Tipton, J. M. Timmer, and C. L. Aldridge. 2016. Multi-stakeholder development of state-and-transition models: a case study from northwestern Colorado. *Rangelands*. doi: 10.1016/j.rala.2016.10.008.
- Cagney, J. 2009. Grazing influence, management and objective development in Wyoming's greater sage-grouse habitat with emphasis on nesting and early brood rearing. University of Wyoming Cooperative Extension Service. B-1203.
- Cagney, J., S. E. Cox, and D. T. Booth. 2011. Comparison of point intercept and image analysis for monitoring rangeland transects. *Rangeland Ecology and Management* 64:309-315.
- Clements, F. E. 1936. Nature and structure of the climax. *Journal of Ecology* 24:252-284.
- Dahlgren, D. K., R. Chi, and T. A. Messmer. 2006. Greater sage-grouse response to sagebrush management in Utah. *Wildlife Society Bulletin* 34:975–985.
- Daniel, C. J., and L. Frid. 2011. Predicting landscape vegetation dynamics using state-and-transition simulation models. Pages 5-22 *in* First Landscape State-and-Transition Simulation Modeling Conference.
- Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. *Rangeland Ecology and Management* 62:111-118.
- Doherty, K. E., D. E. Naugle, J. D. Tack, B. L. Walker, J. M. Graham, J. L. Beck. 2014. Linking conservation actions to demography: grass height explains variation in greater sage-grouse nest survival. *Wildlife Biology* 20:320-325.
- Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. *Fire Ecology* 3:3-21.
- ESRI. 2011. ArcGIS Desktop: Release 10.0. Environmental Systems Research Institute, Redlands, CA.

- Fischer, R.A., K. P. Reese, and J. W. Connelly. 1996. An investigation on fire effects within xeric sage grouse brood habitat. *Journal of Range Management* 49:194–198.
- Forbis, T. A., L. Provenchar, L. Turner, G. Medlyn, J. Thompson, and G. Jones. 2007. A method for landscape-scale vegetation assessment: application to Great Basin rangeland ecosystems. *Rangeland Ecology and Management* 60:209-217.
- Herrick, J. E., J. W. Van Zee, K. M. Havstad, Burkett L. M., and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland and savanna ecosystems. USDA-Agricultural Research Service, Jornada Experimental Range, Las Cruces, USA.
- Hijmans, R. J., J. van Etten, J. Cheng, M. Mattiuzzi, M. Sumner, J. A. Greenberg, O. Perpinan Lamigueiro, A. Bevan, E. B. Racine, and A. Shortridge. 2016. Package ‘raster’. Vignette, R Foundation for Statistical Computing. <https://cran.r-project.org/web/packages/raster/raster.pdf>. Accessed 5 May 2017.
- Hilbe, J. M. 2009. Logistic regression models. Taylor & Francis Group, LLC, Boca Raton, FL, USA.
- Holling, C. S. 1978. Adaptive environmental assessment and management. John Wiley and Sons, London, England.
- Holmes, A. L., and R. F. Miller. 2010. State-and-transition models for assessing grasshopper sparrow habitat use. *Journal of Wildlife Management* 74:1834–1840.
- Homer, C.G., C.L. Aldridge, D.K. Meyer, and S. Shell. 2012. Implementing a multi-scale remote sensing sagebrush characterization and monitoring framework across Wyoming. *International Journal of Applied Earth Observation and GeoInformation* 14:233-244.
- Homer, C.G., G. Xian, C.L. Aldridge, D.K. Meyer, T. Loveland, and M. O'Donnell. 2015. Forecasting sagebrush ecosystem components and greater sage-grouse habitat for 2050: capitalizing on 28 years of Landsat satellite imagery and climate data. *Ecological Indicators* 55: 131-145.

- Jay, M. 2016. Package 'generalhoslem'. Vignette, R Foundation for Statistical Computing. <https://cran.r-project.org/web/packages/generalhoslem/generalhoslem.pdf>. Accessed 5 February 2017.
- Jones, R., and J. Hargreaves. 1979. Improvements to the dry-weight-rank method for measuring botanical composition. *Grass and Forage Science* 34:181-189.
- Kachergis, E. J., C. N. Knapp, M. E. Fernandez-Gimenez, J. P. Ritten, J. G. Pritchett, J. Parsons, W. Hibbs, and R. Roath. 2013. Tools for resilience management: multidisciplinary development of state-and-transition models for northwest Colorado. *Ecology and Society* <http://dx.doi.org/10.5751/ES-05805-180439>.
- Kachergis, E., M. E. Fernandez-Gimenez, and M. E. Rocca. 2012. Differences in species composition as evidence of alternative states in the sagebrush steppe. *Rangeland Ecology and Management* 65:486–497.
- Knapp, C. N., and M. E. Fernandez-Gimenez. 2009. Understanding change: integrating rancher knowledge into state-and-transition models. *Rangeland Ecology and Management* 62:510-521.
- Knapp, C. N., M. E. Fernandez-Gimenez, D. D. Briske, B. T. Bestelmeyer, and X. B. Wu. 2011. An assessment of state-and-transition models: perceptions following two decades of development and implementation. *Rangeland Ecology and Management* 64:598-606.
- Knick, S. T., A. L. Holms, and R. F. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. Pages 63–75 in V. A. Saab and H.D.W. Powell, editors. *Fire and avian ecology in North America. Studies in Avian Biology*, University of California-Press, Berkeley, USA.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.

- Kohavi, R. 1995. A study of cross-validation and bootstrap for accuracy estimation and model selection. Proceedings from the International Joint Conference on Artificial Intelligence.
- Kuhn, M. 2016. A short introduction to the caret Package. Vignette, R Foundation for Statistical Computing. <https://cran.r-project.org/web/packages/caret/caret.pdf>. Accessed 9 February 2017.
- Laliberte, A. S., E. L. Fredrickson, and A. Rango. 2007. Combining decision trees with hierarchical object-oriented image analysis for mapping arid rangelands. *Photogrammetric Engineering & Remote Sensing* 73:197-207.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- Lesica, P., S. V. Cooper, and G. Kudray. 2007. Recovery of big sagebrush following fire in southwest Montana. *Rangeland Ecology and Management* 60:261-269.
- Levi, M. R. 2012. Predictive soil mapping in southern Arizona’s basin and range. PhD dissertation, The University of Arizona, Tucson, AZ.
- McBratney, A. B., M. L. Mendonca Santos, and B. Minasny. 2003. On digital soil mapping. *Geoderma* 117:3-52.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 in S. T. Knicks and J.W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- O’Donnell, M. S., and D. A. Ignizio. 2012. Bioclimatic predictors for supporting ecological applications in the Conterminous United States. U.S. Geological Survey Data Series 691, 10 p.
- Pellant, M., P. Shaver, D. A. Pyke, and J. E. Herrick. 2005. Interpreting indicators of rangeland health: version 4. Technical Reference 1734-6. U.S. Department of the Interior,

- Bureau of Land Management, National Science and Technology Center, Denver, Colorado, USA.
- Provencher, L., Forbis, T., Frid, L., and G. Medlyn. 2007. Comparing alternative management strategies of fire, grazing, and weed control using spatial modeling. *Ecological Modelling*. 209: 249–263.
- R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 22 November 2015.
- Ripley, B. and W. Venables. 2016. Package ‘nnet’. Vignette, R Foundation for Statistical Computing. <https://cran.r-project.org/web/packages/nnet/nnet.pdf>. Accessed 1 February 2017.
- Sant, E. D., G. E. Simonds, R. D. Ramsey, and R. T. Larsen. 2014. Assessment of sagebrush cover using remote sensing at multiple spatial and temporal scales. *Ecological Indicators* 43:297-305.
- Schoeneberger, P. J., D. A. Wysocki, E. C. Benham, and Soil Survey Staff. 2012. Field book for describing and sampling soils, version 3.0. Natural Resources Conservation Service, National Soil Survey Center, Lincoln, Nebraska, USA.
- Steele, C. M., B. T. Bestelmeyer, L. M. Burkett, P. L. Smith, and S. Yanoff. 2012. Spatially explicit representation of state-and-transition models. *Rangeland Ecology and Management* 65:213-222.
- Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.
- Tipton, C. Y. W. 2015. Improving state-and-transition models for management of sagebrush steppe ecosystems. Thesis, Colorado State University 160 p.

- Troy, A., and M. A. Wilson. 2006. Mapping ecosystem services: practical challenges and opportunities in linking GIS and value transfer. *Ecological Economics* 60:435-449.
- Twidwell, D., B. W. Allred, and S. D. Fuhlendorf. 2013. National-scale assessment of ecological content in the world's largest land management framework. *Ecosphere* 4:1-27.
- USDA-NRCS. 2009. National soil survey handbook, title 430-VI. Available at: <http://soils.usda.gov/technical/handbook>. Accessed 13 April 2017.
- U.S. Geological Survey. 2014. National elevation data. <https://lta.cr.usgs.gov/NED>. Accessed 4 April 2014.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:265–273.
- Williamson, J. C., B. T. Bestelmeyer, and D. P. C. Peters. 2012. Spatiotemporal patterns of production can be used to detect state change across an arid landscape. *Ecosystems* 15:34-47.

CHAPTER IV. MANAGING FOR MULTIPLE SPECIES: GREATER SAGE-GROUSE AND SAGEBRUSH SONGBIRDS

Summary

Human activity has altered between one-third and one-half of the earth's surface, such as temperate grasslands and sagebrush rangelands, which has resulted in a loss of biodiversity. By promoting habitat for sensitive or wide-ranging species, it is believed that less exigent species will be protected in an umbrella effect. Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) have been proposed as an umbrella species for other sagebrush-obligate species because they have an extensive range that overlaps with many other species, they are sensitive to anthropogenic activity, they require resources over large landscapes, and their habitat needs are well-known. However, the efficacy of this concept is often assumed. Therefore, we surveyed sage-grouse occurrence and sagebrush songbird abundance in Northwest Colorado to determine the amount of habitat overlap between sage-grouse and four sagebrush-associated songbirds (Brewer's sparrow [*Spizella breweri*], sage thrasher [*Oreoscoptes montanus*], sagebrush sparrow [*Artemisiospiza nevadensis*]), and green-tailed towhee [*Pipilo chlorurus*]). During May and June 2013-2015, we conducted standard point count breeding surveys for songbirds and counted sage-grouse pellets within a 10-m radius plot at each songbird point. We then modeled songbird abundance and sage-grouse occurrence with multi-scaled environmental features, such as sagebrush cover and bare ground. To evaluate sage-grouse as an umbrella species, we determined the correlation between apparent sage-grouse occurrence and estimated songbird densities per sampling plot. To incorporate a larger-scaled approach, we mapped model-predicted surfaces for each species across our study area to determine average songbird density in areas likely to contain sage-grouse. Shrub or sagebrush height and a form of sagebrush cover

were important predictors for all species, although the spatial extent varied. Areas likely to contain sage-grouse also contained higher densities for Brewer's sparrows and green-tailed towhees. However, average predicted sagebrush sparrow densities were lower in areas likely to contain sage-grouse. In our study area, sage-grouse may be an effective umbrella for Brewer's sparrows and green-tailed towhees, but sage-grouse habitat does not appear to capture habitat promoting higher sagebrush sparrow densities. A multi-species focus may be the best management and conservation strategy for multiple species of concern.

Introduction

Human activity, such as resource use and extraction, has altered between one-third and one-half of the earth's surface, which has large consequences on regional climates, global carbon fluctuations, hydrological cycles, and biodiversity (Vitousek et al. 1997, Foley et al. 2005). Globally, temperate grasslands are one of the most imperiled biomes and in North America, it is the most converted landscape, with >90% altered, mainly for agriculture (Hoekstra et al. 2005). The sagebrush ecosystem of western North America has also been altered to promote herbaceous forage for livestock, for agriculture, urban development, and energy extraction and now occupies about half its historic distribution (Knick et al. 2003). With the current and projected loss of native habitats in grassland, sagebrush, and other systems, extinction rates for populations and species are unprecedented (Vitousek et al. 1997).

Even though managing for ecosystem health may be more effective to conserve populations and species, as well as to promote other ecosystem services, biologists often monitor and manage with a single-species focus (Vitousek et al. 1997, Boyd et al. 2014). Many biologists manage for single species to generate support and awareness for the conservation of ecosystems that support charismatic species, like Florida panthers (*Puma concolor coryi*). However, some

biologists are mandated via regulation (e.g., the Endangered Species Act) to manage for specific habitats that support protected species, such as old-growth forest and northern spotted owls (*Strix occidentalis caurina*; Simberloff 1998). Protecting habitats for wide-ranging or sensitive species could promote habitat for less exigent species in an umbrella effect and thus, promote biodiversity (Roberge and Angelstam 2004). However, the effectiveness of umbrella species for conservation and management of multiple species is often assumed and rarely tested (Simberloff 1998). Bifulchi and Lodé (2005) tested the umbrella concept with European otters (*Lutra lutra*) and found no difference in species richness for several taxa between paired sites with and without otters. The authors concluded that generalist species may serve as better umbrella species compared to specialists like otters and potential beneficiary species should share similar habitat requirements (Bifulchi and Lodé 2005).

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) have been proposed as an umbrella species for other sagebrush-obligate species (Rowland et al. 2006). Sage-grouse should be an effective umbrella species because they have a large annual range that overlaps with many other species, they are fairly sensitive to anthropogenic activity, their biology is well-known, and many habitat recommendations have been evaluated and published for sage-grouse (Rowland et al. 2006, Hanser and Knick 2011). Sage-grouse populations have declined range-wide due to changing fire intervals (Baker 2011), invasion of exotic plants (Chambers et al. 2007), grazing pressure (Beck and Mitchell 2000), and energy development (Holloran 2005) fragmenting and deteriorating sagebrush rangelands (Garton et al. 2011). Thus, large and small-scale conservation efforts (e.g., Sage Grouse Initiative) are underway to promote sagebrush habitat and prevent further declines in sage-grouse populations (U.S. Fish and Wildlife Service 2015). However, it is unclear how efforts to promote sage-grouse habitat will affect other species, which are

completely or partially dependent on sagebrush. Sagebrush rangelands are not homogenous and features relevant to sage-grouse may not be relevant to species with smaller home ranges (Hanser and Knick 2011). For example, Brewer's sparrow (*Spizella breweri*) and green-tailed towhee (*Pipilo chlorurus*) abundance increased for three years following juniper removal to restore sage-grouse habitat (Sage Grouse Initiative 2015). Mechanical treatments to improve Gunnison sage-grouse (*C. minimus*) habitat reduced occupancy for Brewer's sparrows and green-tailed towhees at plots within treatment areas (Lukacs et al. 2015). Large-scale management for sage-grouse habitat benefitted several shrub-obligate species in Wyoming, but this relationship was not always positive at finer scales (e.g., nest sites; Carlisle 2017).

Given the loss of sagebrush rangelands, many avifauna species dependent on this ecosystem have experienced population declines and are of conservation concern (Braun et al. 1976, Knick et al. 2003). Over the last fifty years, Brewer's sparrow, sagebrush sparrow (*Artemisiospiza nevadensis*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee populations have declined in all or specific regions of the western U.S. according to annual Breeding Bird Survey data (Dobkin and Sauder 2004). Protecting wide-ranging species, such as sage-grouse, could provide protection to numerous species of conservation concern that rely entirely or partially on sagebrush rangelands. However, previous work to identify sage-grouse as an umbrella species used broad patterns at coarse resolutions (Rowland et al. 2006). Further, several studies have shown that sagebrush avifauna respond to habitat characteristics and disturbance at multiple scales (e.g., Wiens et al. 1987, Chalfoun and Martin 2007, Doherty et al. 2008, Carpenter et al. 2010), and have different home range sizes, so umbrella relationships need to be evaluated in a multi-scaled framework (Hanser and Knick 2011).

Given the reduction in sagebrush rangelands and associated avifauna populations across western North America, understanding niche conditions that affect avifauna use and abundance could help inform conservation of this ecosystem and its associated species. These relationships could inform land-use planning and management decisions, which are needed for species of conservation concern, such as sage-grouse and Brewer's sparrows. Further, the decline in sage-grouse populations and the impetus to manage for sage-grouse habitat begs the question of how managing for one species could affect other species with potentially similar habitat requirements but smaller home ranges. To address these concerns, we pursued the following objectives: 1) survey sage-grouse occurrence and sagebrush-associated songbird abundance (i.e., Brewer's and sagebrush sparrows, sage thrashers, and green-tailed towhees) in Northwest Colorado; 2) model sage-grouse occurrence and songbird counts with multi-scaled environmental features using logistic regression and count-based regression models; 3) determine the correlation between apparent sage-grouse occurrence and estimated songbird densities per plot; and 4) determine model-predicted songbird densities and species richness in areas likely to contain sage-grouse.

Methods

Study Area

We conducted sage-grouse pellet surveys and songbird point count surveys on privately- and publicly-owned lands in Moffatt County in Northwest Colorado (Fig. 4.1). The East and West Moffat study sites were characterized as sagebrush steppe and composed primarily of various big sagebrush communities with either a bunchgrass (e.g., bluebunch wheatgrass [*Pseudoroegneria spicata*] or western wheatgrass [*Pascopyrum smithii*]) understory. Wyoming big sagebrush (*A. t. wyomingensis*) communities dominated the East Moffat site and low sagebrush (*A. arbuscula* sp.)-salt shrub (*Atriplex* sp.)-Wyoming big sagebrush communities

dominated the West Moffat site. Annual precipitation varied between 18–30 cm for East Moffat and 20–40 cm for West Moffat (Miller et al. 2011). The East Moffat site was comprised mostly of sandy or loamy soils (Tipton 2015), while West Moffat had greater heterogeneity in soil and topographic features. Three wildfires occurred within the East Moffat study site prior to surveys: a 3,185-h wildfire in 2010, a 10,243-ha wildfire in 2008, and a smaller 1,505 ha fire in 2008. The West Moffat site was grazed by cattle and the East Moffat site was grazed by both cattle and sheep.

Field Surveys

We determined sampling locations based on the objectives of a larger collaborative project to build state-and-transition models in each of three project areas with local input and field data (Bruegger et al. 2016). In East Moffat, we randomly allocated survey points spaced >200 m within past treatments or disturbances and areas with no known treatments or disturbances on target ecological sites (e.g., Rolling Loam and Sandyland; Tipton 2015). In West Moffat, we stratified survey points based on sagebrush cover (Homer et al. 2012) and elevation to capture landscape variability, but allocated greater effort to the strata containing more sagebrush cover. To estimate sage-grouse occurrence, we surveyed a 10-m radius area around each point for sage-grouse pellets. To survey plots, we attached a measuring tape to a piece of rebar in the center of each plot and searched within 2-m increments to reduce observer error. Even though we were mainly interested in presence/absence of sage-grouse, we recorded the number of single pellets, roost piles, and number of pellets per roost pile for other research objectives. We recorded pellets as a roost pile if ≥ 2 pellets were found within a 30-cm diameter area (Hanser et al. 2011). We recorded pellets or roost piles if at least half of the pellet or pile was within the 10-m radius. We also used a simple mark-resight study to estimate naïve pellet

detectability to ensure we were detecting a majority of the pellets within a plot (Pollock et al. 2002).

To estimate songbird abundance, we conducted standard point count surveys at the center of each pellet count plot following distance sampling protocol (Buckland et al. 2001). The protocol included focusing on detections at and surrounding the point, measuring radial distance to the bird with rangefinders or object near the bird to estimate the distance, and recording distance to where a bird was first detected (Buckland et al. 2001). We identified birds both aurally and visually within a six-minute interval at each point and recorded individuals only once. We conducted surveys during the breeding season from sunrise to approximately four hours after sunrise depending on weather. We did not conduct surveys during inclement weather, such as rain or windy conditions when activity or detectability of the birds was hindered. We also conducted surveys beginning at lower elevation sites earlier in the breeding season and moving up in elevation as the season progressed to capture the phenology of the birds' breeding activity (Hanni et al. 2013).

Data Analysis

Detection Probabilities

To estimate songbird abundance, we used program Distance 6.0 (Thomas et al. 2010) and examined several detection model forms (e.g., half-normal). We excluded outlier detections based on visual inspection of detection histograms and binned distances accordingly (Buckland et al. 2001). We compared models with detectability variables using the Multiple Covariate Distance Sampling engine. Variables included start time, Julian date, observer, how the bird was detected (i.e., calling, singing, or visual), temperature, cloud cover (i.e., 0 = 0-15% cloud cover, 1 = 16-50% cloud cover, 2 = 51-75% cloud cover, and 3 = 76-100% cloud cover), and wind

speed (0 = <0 mph, 1 = 1–3 mph, 2 = 4–7 mph, 3 = 8–12 mph, and 4 = 13–18 mph; Hanni et al. 2013). We evaluated models for variables affecting detection probability in three model sets: the weather set included the three weather variables, the time set included start time and Julian date, and the observer set included observer and how the bird was detected. We compared univariable models and models with all combinations of variables for each model set and retained the best model from each set based on Akaike’s Information Criterion (AIC; Burnham and Anderson 1998). We then compared the top detection model from each set along with a null model to see which variables best explained the detection probability for each species and predicted density estimates for each plot using the best detection model.

To determine if we could combine songbird data collected in 2013-2015, we compared songbird density estimates for common species for a subset of plots surveyed in either 2013 and 2014 or 2014 and 2015 with equation 3.102 in Buckland et al. (2001). If density for the common species was similar between years, then we assumed that weather and other factors influencing vegetation and bird density were also similar and we could pool survey data collected in multiple seasons. We used the best detection model for each species to calculate an offset term based on the mean density and survey effort at each point count plot, and included the offset term in subsequent count-based regression models to adjust raw counts for heterogeneity in detection (Buckland et al. 2009).

Predictor Selection

Given limited information on how sagebrush avifauna scale their environment in Northwest Colorado and the importance of a multi-scaled approach to understand habitat relationships, we followed a similar hierarchical exploratory approach as outlined in Leu et al.

(2011). We first summarized landcover predictors in ArcMap 10.0 within three moving window scales: 0.56 km, 1 km, and 5 km of each survey point. Scales were chosen based on previous studies of sage-grouse and sagebrush songbird habitat selection. For instance, previous modeling efforts have shown that the amount of sagebrush habitat within 1 km of a used site best explained sage-grouse site selection (Carpenter et al. 2010, Hanser et al. 2011). Sage-grouse also selected for larger patches within a 0.56-km radius of moderate sagebrush cover for nest and brood habitat in Alberta, Canada (Aldridge and Boyce 2007), and Connelly et al. (2000) suggest protecting suitable habitat within 5 km of a lek for non-migratory sage-grouse populations. In the Wyoming Basin region, the top models explaining Brewer's sparrow, green-tailed towhee, sagebrush sparrow, and sage thrasher abundance included variables at multiple scales (e.g., all big sagebrush cover within a 1-km extent and mountain big sagebrush (*A. t. vaseyana*) cover within a 5-km extent (Aldridge et al. 2011). To incorporate a finer scale of habitat selection, we also included the pixel value for landcover variables at each plot (i.e., 30 × 30-m; Homer et al. 2012).

To summarize multi-scaled landcover predictors, we used a remotely sensed layer developed for sagebrush rangelands across Montana, Wyoming, and northern Colorado (Homer et al. 2012). The biotic predictors included percent cover of all sagebrush (all *Artemisia* spp.), percent cover of big sagebrush, percent cover of tall sagebrush (i.e., sagebrush >29 cm), percent cover of total shrubs, litter, herbaceous understory, and bare ground, shrub height, and sagebrush height (Homer et al. 2012; Table 4.1). We did not explore relationships with anthropogenic features, such as oil or gas wells because few features occurred throughout the study area.

Model Development

We evaluated count-based regression models for songbird counts and logistic regression models for sage-grouse occurrence using the multi-scaled predictors. For songbird models, we excluded songbird counts beyond the truncation distance (as determined by detection histograms) and included an offset term to scale counts for detection heterogeneity across plots (Buckland et al. 2009). If a plot had zero counts, we used the average offset value from plots with a count for each species (Aldridge et al. 2011). For sage-grouse models, we assigned a “1” to plots where we found single pellets, roost piles, or both and a “0” for plots where we did not detect any sage-grouse pellets or roost piles. We only included plots from a study site (East or West Moffat) in each species’ model if we detected songbirds or pellets in that site.

For songbirds, we first identified the appropriate data distribution (i.e., Poisson and negative binomial) for each species using an intercept-only model and comparing Bayesian Information Criterion (BIC) values for the two models. We also used Vuong’s test to determine the appropriate data distribution (Hilbe 2011). We chose not to explore zero-inflated models for two reasons. Firstly, a higher frequency of zero counts can be attributed to a negative binomial distribution with a low mean and this distribution also accounts for overdispersed data, so the more complicated model structure is unnecessary (Warton 2005, Hilbe 2011). Secondly, zero-inflated models assume that excessive zeros are partly due to organisms not occurring in the area (Warton 2005). This was not valid for our study area or focal species, especially because we restricted analyses to portions of the study area where species were detected. For sage-grouse and songbirds, we examined scatterplots of every variable at each scale and raw counts and histograms of counts or occurrence ≥ 1 to check for non-linear relationships, outliers, and variables with limited variation across part or all of the study area. If plots showed evidence for

non-linearity, we evaluated a linear and a quadratic model to assess fit of the functional form of the covariate using BIC (Hilbe 2011) to determine which model structure to retain. We then determined the best spatial extent for each variable in the sage-grouse and songbird analyses by evaluating univariable regression models and retaining the scale of each variable with the greatest explanatory power (i.e., lowest BIC score; Leu et al. 2011). We used Pearson's correlation coefficient to determine if any of the variables in each analysis were overly correlated (i.e., $R \geq |0.7|$; Zar 2010). We performed all analyses in Program R 3.1.3 (R Development Core Team 2015).

We developed candidate models from combinations of the top predictor variables (excluding overly correlated variables) and ranked the models according to BIC to determine the best model(s) explaining sage-grouse occurrence and songbird abundance. We determined competitive models as a model with $\Delta\text{BIC} \leq 4$, similar to recommendations for using AIC (Burnham and Anderson 1998). To avoid over-fitting models, we did not include more than one variable per 10% of plots with ≥ 1 songbird or pellet detection in any model (Hosmer and Lemeshow 2000). We also excluded models when coefficients for any variable were unstable and switched direction of influence across models (Arnold 2010).

Model Assessment and Evaluation

To assess the fit of models over an intercept-only (null) model, we calculated a McFadden's pseudo- R^2 value for all models (Zar 2010). We also used a chi-square likelihood ratio test with the `lrtest` function in package "lmtest" to determine goodness-of-fit for the top model over an intercept-only model. Because we did not have independent datasets to evaluate the predictive capability of our top models for songbirds and sage-grouse, we evaluated predictive success using five-fold cross validation (Hastie et al. 2009) with the `cvFit` function (in

package “cvTools”; Alfons 2015). We also evaluated the area under the curve for a receiver operating characteristic (ROC) to determine the predictive performance of our sage-grouse occurrence models (Hosmer and Lemeshow 2000).

Umbrella Concept

To determine the effectiveness of sage-grouse as an umbrella species for songbirds in our study area, we looked at two scales. We first examined the Pearson’s correlation coefficient between estimated songbird densities (derived in program Distance) and apparent sage-grouse occurrence (raw pellet detections) per plot (i.e., 1-ha for songbirds and 0.03-ha for sage-grouse) in our study area. We hypothesized that sage-grouse should be an effective umbrella species if $R > 0.5$, with greater correlation indicating increasing overlap between species. We then mapped model-predicted songbird densities within the estimated sage-grouse range in Moffat County (Colorado Parks and Wildlife 2011) and restricted predictions to north of the Yampa River (Fig. 4.1) for greater consistency to where we sampled. We model-averaged predicted songbird densities and probabilities of sage-grouse occurrence if there were multiple competitive models (i.e., $\Delta BIC \leq 4$; Burnham and Anderson 1998). We classified the predicted probability of occurrence for sage-grouse as “0” or “1” based on the sensitivity-specificity equality threshold (Liu et al. 2005) and used the “OptimalCutpoints” package in R to determine the optimal threshold (López-Ratón et al. 2014). We then overlaid areas where sage-grouse were predicted to occur on the predicted songbird densities to determine if densities were greatest in these areas. We also calculated a richness index for the four songbird species by classifying the predicted densities as a “1” following Aldridge et al. (2011) and using the minimum density to support a songbird territory. We based the largest territory size on what was recorded for each species in the Birds of North America species’ accounts (Poole 2005) or Colorado Parks and Wildlife

species' accounts (Boyle and Reeder 2005). We could then determine the average richness index for areas predicted to contain sage-grouse.

Results

Field Surveys

We surveyed a total of 300 plots for sage-grouse pellets and songbirds mid-May to late June 2013-2015. We detected a total of 854 Brewer's sparrows (on 233 plots), 158 green-tailed towhees (on 76 plots), 216 sagebrush sparrows (on 77 plots), 263 sage thrashers (on 133 plots), 5,404 single pellets (on 131 plots; mean of 15 pellets per plot), and 782 roost piles (on 111 plots; mean of 2 piles per plot). We surveyed 198 plots in East Moffat County and 102 plots in West Moffat County. Of the 151 plots on which we detected sage-grouse pellets, we detected Brewer's sparrows on 132 of those plots, green-tailed towhees on 53 plots, sage thrashers on 84 plots, and sagebrush sparrows on 31 plots. We detected few sagebrush sparrows in the East Moffat plots (8 birds on 6 plots), so we only included count data from West Moffat for subsequent sagebrush sparrow models.

Detection Probabilities

Based on 30 plots surveyed in both 2013 and 2014 and 32 plots surveyed in both 2014 and 2015, density estimates for common songbird species were not different ($p > 0.10$). Therefore, we combined detections across the three field seasons. For Brewer's sparrows, we truncated distances >200 m and binned the data into seven bins. The best detection model was the hazard rate function with simple polynomial adjustments and no detection variables. Average Brewer's sparrow density was 1.92 birds/ha. For green-tailed towhees, sagebrush sparrows, and sage thrashers, we truncated distances $>220-250$ m and binned the data into 6 or 7 bins. The best detection model for green-tailed towhees was a half-normal function with how the bird was

detected, observer, temperature, and cloud cover. Average green-tailed towhee density was 0.16 birds/ha. The best detection model for sagebrush sparrows was the half-normal function with how the bird was detected and start time. Average sagebrush sparrow density was 0.25 birds/ha. The best detection model for sage thrashers was a half-normal function with no adjustments and how the bird was detected and cloud cover. Average sage thrasher density was 0.15 birds/ha. Sage-grouse pellet detectability was high (i.e., >0.8), and thus, not considered an issue in subsequent modeling efforts.

Model Development

Based on Vuong's test and BIC, the negative binomial distribution was the best model structure for Brewer's sparrows, green-tailed towhees, and sage thrashers. For sagebrush sparrows, Vuong's test indicated a negative binomial model was best; however the result was not significant ($p = 0.1$) and the data were not over-dispersed (mean = 2.01, variance = 2.58). Including a shrub or sagebrush cover variable resulted in a lower BIC value for the Poisson model and a lack of convergence in the negative binomial model, so we used a Poisson distribution for subsequent sagebrush sparrow models.

Of the eight multi-scaled variables included, big sagebrush cover, all sagebrush cover, tall sagebrush cover, and total shrub cover were highly correlated at all scales, so only the best shrub structure variable was retained for each species. Further, we could not include tall sagebrush cover in sagebrush sparrow models due to a limited variability of this predictor in West Moffat County.

For Brewer's sparrow, the best scale for predictors was tall sagebrush cover within 1 km, sagebrush and shrub height within 30 m, herbaceous cover within 5 km, litter within 564 m, and

bare ground within 30 m. All relationships between predictors and Brewer's sparrow counts were linear. For green-tailed towhees, the best scale for predictors with a quadratic relationship was tall sagebrush cover within 1 km, and shrub and sagebrush height within 564 m. The best scale for linear predictors was bare ground and litter within 30 m, and herbaceous cover within 5 km. For sagebrush sparrows, the best scale for quadratic predictors was all sagebrush cover within 1 km and shrub height within 564 m. The best scale for linear predictors was bare ground within 1 km, and sagebrush height, herbaceous cover, and litter within 5 km. For sage thrashers, the best scale for a quadratic predictor was tall sagebrush cover within 564 m, and the best scale for linear predictors was herbaceous cover within 5 km, litter within 564 m, and shrub height, sagebrush height, and bare ground within 30 m. All predictors demonstrated a linear relationship with sage-grouse occurrence and the best scale for each variable was all sagebrush cover, bare ground, litter, and shrub height within 30 m, herbaceous cover within 5 km, and sagebrush height within 564 m.

The best Brewer's sparrow model included tall sagebrush cover within 1 km (BIC = 1259.51; Table 4.2), followed by a model including tall sagebrush cover and herbaceous cover within 5 km (BIC = 1260.54), and a third model with herbaceous cover and sagebrush height within 30 m (BIC = 1262.33). Brewer's sparrow counts increased with greater sagebrush and herbaceous cover and taller sagebrush shrubs (Fig. 4.2; Table 4.3). The best green-tailed towhee model included tall sagebrush cover within 1 km (plus a quadratic term) and herbaceous cover within 5 km (BIC = 493.55; Table 4.2). Towhee counts peaked at approximately 13% tall sagebrush cover and with greater herbaceous cover (Fig. 4.3; Table 4.3). The best sagebrush sparrow model included shrub height within 564 m (plus a quadratic term; BIC = 322.94), followed by a model including shrub height and herbaceous cover within 5 km (BIC = 326.76;

Table 4.2). Sagebrush sparrow counts peaked for shrubs approximately 15 cm tall and with less herbaceous cover (Fig.4.4: Table 4.3). The best sage thrasher model included no predictors (null model; BIC = 728.05), followed by a model including tall sagebrush cover within 564 m (plus a quadratic term; BIC = 731.20), and a third best model including sagebrush height within 30 m (BIC = 731.74; Table 4.2). Sage thrasher counts peaked at approximately 10% tall sagebrush cover and for taller sagebrush shrubs (Fig. 4.5; Table 4.3). The best sage-grouse model included litter within 30 m (BIC = 404.05; Table 2), followed by all sagebrush cover within 30 m (BIC = 404.09), shrub height within 30 m (BIC = 406.05), all sagebrush cover plus herbaceous cover within 5 km (BIC = 406.44), and shrub height plus herbaceous cover (BIC = 407.01). There were other competitive univariable models, such as bare ground within 30 m and herbaceous cover within 5 km (Table 4.2). However, these variables were highly correlated with litter ($R \geq |0.7|$) in the best model and were thus, excluded. Similarly, shrub height plus litter was competitive but excluded because of its similarity to the higher-ranked shrub height plus herbaceous cover model. Sage-grouse probability of occurrence increased with an increase in litter, herbaceous cover, all sagebrush cover, and shrub height (Table 4.3). For model assessment metrics, see Table 4.2.

Umbrella Concept

For the estimated songbird densities (Distance-adjusted) and apparent sage-grouse occurrence per plot, the correlation was positively weak for all species. The correlation between estimated Brewer's sparrow densities and apparent sage-grouse occurrence was 0.28, for green-tailed towhee densities it was 0.19, and for sage thrasher densities it was 0.18 (all correlations were significant [$p < 0.05$]). The correlation was 0.15 for sagebrush sparrows and sage-grouse occurrence in West Moffat only ($p = 0.14$).

Based on our sage-grouse models, sage-grouse are likely to occur in 41% of the overall sage-grouse range north of the Yampa River with probability >0.52 (Fig. 4.6). In 56% of the areas where sage-grouse are likely to occur, species richness was two species (Fig. 4.6). In 42% of areas likely to be occupied by sage-grouse, richness was three species, and all four species were predicted to occur in just 1.5% of areas likely to be occupied by sage-grouse (Fig. 4.6). In areas likely to be occupied by sage-grouse, average Brewer's sparrow density was 3.43 birds/ha (Fig. 4.7), average green-tailed towhee density was 1.04 birds/ha (Fig. 4.8), average sagebrush sparrow density was 0.03 birds/ha (Fig. 4.9), and average sage thrasher density was 0.75 birds/ha (Fig. 4.10). In comparison, average songbird density for the entire study area irrespective of where sage-grouse are likely to occur was 2.74 Brewer's sparrows/ha, 0.55 green-tailed towhees/ha, 0.54 sagebrush sparrows/ha, and 0.72 sage thrashers/ha. Based on our hypothesis, sage-grouse could be an effective umbrella species for Brewer's sparrows and green-tailed towhees in our study area, but not for sagebrush sparrows, and results are inconclusive for sage thrashers.

Discussion

Knowing where sage-grouse or songbirds occur and where their fitness is greatest should help biologists prioritize habitats for management and conservation efforts for those species (Aldridge and Boyce 2007). Further, understanding the environmental features and scales that species select in these areas should guide efforts to manage for resources to sustain or enhance populations, especially for species of conservation concern. Although greater sage-grouse did not receive federal protection in 2015 (U.S. Fish and Wildlife Service 2015), their populations continue to decline throughout their range (Garton et al. 2011) and they are a species of concern in Colorado due to local population declines (Colorado Greater Sage Grouse Steering Committee

2008). In Colorado, all four songbird species included in our modeling effort are also species of conservation concern due to habitat loss from energy extraction, urban development, agricultural conversion, and pinyon-juniper encroachment (*Pinus* spp.-*Juniperus* spp.; Boyle and Reeder 2005). Therefore, our study in Northwest Colorado elucidated important relationships between sagebrush avifauna and their environment and between the avifauna species themselves.

Given different species' needs and home range sizes, such as sage-grouse and songbirds (Knick and Rotenberry 2002), environmental information needs to encompass large areas and incorporate multiple scales of habitat selection (Johnson 1980). This is particularly important when defining a species as an umbrella because the species should have a large home range that encompasses species with smaller home ranges and nuanced habitat requirements (Hanser and Knick 2011). For example, Capercaillie (*Tetrao urogallus*) could be useful as an umbrella for other subalpine forest avian species in the Swiss Prealps with smaller home ranges but similar habitat requirements (Suter et al. 2002). Previous studies have reached different conclusions concerning greater sage-grouse as an umbrella species. Rowland et al. (2006) found only moderate overlap between Brewer's sparrows and sage-grouse habitat for broad landcover associations within the species' ranges in the Great Basin. Brewer's sparrows, sage thrashers, sagebrush sparrows, and green-tailed towhees had greater overlap with sage-grouse along a multi-scaled environmental gradient spanning Wyoming/basin big sagebrush (*A. t. tridentata*) to grass cover (Hanser and Knick 2011). They recommended a multi-scaled approach to assess the effectiveness of sage-grouse as an umbrella species because the strength and direction of association between sage-grouse and passerine species varied across scales (Hanser and Knick 2011). Finally, Brewer's and sagebrush sparrow and sage thrasher abundance throughout the western U.S. was greater for landscapes containing active sage-grouse leks, which was attributed

to greater sagebrush cover surrounding leks (Donnelly et al. 2016). However, no leks in Colorado were included in the analysis.

In Northwest Colorado, we found that greater sage-grouse could be an effective umbrella for sagebrush or shrub-obligate songbird species, but these relationships were scale-dependent. When comparing apparent sage-grouse occurrence and estimated songbird densities at the plot level, we found a moderately positive correlation between sage-grouse and Brewer's sparrows, green-tailed towhees, and sage thrashers ($R = 0.18-0.29$). Correlation was also slightly positive between sage-grouse and sagebrush sparrows ($R = 0.15$), but only when comparing plots in the West Moffat site where sagebrush sparrows were more prevalent. The lack of a stronger positive correlation between sage-grouse and the songbirds could be a mismatch of scales when comparing a wide-ranging species to species with much smaller territory sizes. The plot area for sage-grouse pellets (0.03 ha) was smaller than the plot area for songbird densities (1 ha). A larger survey plot for pellets could have increased the overlap between sage-grouse occurrence and songbird densities, especially given the much larger home range sizes for sage-grouse (Connelly et al. 2000). In addition, previous studies have shown that songbird habitat relationships change depending on the scale of inference (Wiens and Rotenberry 1981, Wiens et al. 1987). For example, sage thrashers respond positively to shrub cover at a biogeographic scale, but may prefer less shrub cover at smaller scales within sagebrush rangelands (Wiens et al. 1987). Therefore, one should expect the correlation between sage-grouse and songbird habitat selection to vary depending on scale.

When evaluating model-predicted songbird densities across the study area, we illustrated higher Brewer's sparrow and green-tailed towhee densities within areas likely to contain sage-grouse. Sage-grouse were more likely to be an effective umbrella for Brewer's sparrows and

green-tailed towhees because these three species selected for similar features at similar scales (Table 4.3). Sage-grouse, Brewer's sparrows, and green-tailed towhees all selected for greater herbaceous cover at the largest scale. In addition, sage-grouse and Brewer's sparrows both selected for taller sagebrush shrubs at the smallest scale and greater sagebrush cover. It was not surprising that correlation was greatest between sage-grouse and Brewer's sparrows because this songbird is typically the most common species detected in sagebrush rangelands (Wiens and Rotenberry 1981, Aldridge et al. 2011), and we also detected Brewer's sparrows at a majority of the plots where sage-grouse were detected. Within sagebrush rangelands, green-tailed towhees often breed in structurally diverse habitats comprised of various shrub species from mountain big sagebrush to pinyon-juniper (Wiens and Rotenberry 1981, Aldridge et al. 2011), so they are not as dependent on sagebrush as sage-grouse. For both Brewer's sparrows and green-tailed towhees, a majority of higher predicted densities were captured within areas likely to be occupied by sage-grouse (Fig. 4.7 and 4.8).

In contrast, we found the opposite pattern for sagebrush sparrows: lower densities were generally captured within areas likely to be occupied by sage-grouse (Fig. 4.9). Sagebrush sparrows were associated with shorter shrubs and less herbaceous cover in contrast to sage-grouse, which selected for taller sagebrush shrubs and greater herbaceous cover. Sage-grouse also preferred areas with greater sagebrush cover, whereas sagebrush sparrows were only prevalent in our study area with less shrub cover. In a nearby study site in Northwest Colorado, sagebrush sparrows were associated with the ecological site that had larger gaps between shrubs and a greater density of shorter shrubs compared to other ecological sites (Williams et al. 2011). Sagebrush sparrow abundance in the Wyoming Basin was similarly greater for sagebrush landscapes containing lower sagebrush cover (Aldridge et al. 2011). The birds may prefer more

open areas with less shrub and herbaceous cover because they walk between nests and forage on the ground (Martin and Carlson 1998).

Even though other studies have determined that sage-grouse could be an effective umbrella for sagebrush sparrows at regional scales (Hanser and Kick 2011), sagebrush sparrows do not occur throughout sagebrush rangelands in Colorado, but are restricted to a few sub-regions where shrub and ground cover are less (Boyle and Reeder 2005, Bird Conservancy of the Rockies 2016). Therefore, overlap between sagebrush sparrow and sage-grouse habitat may undoubtedly be less in our study area. Further, if we had examined overlap between sagebrush sparrow densities and sage-grouse occurrence at larger scales, such as multi-state regions, we may have found a positive relationship similar to previous studies (Hanser and Knick 2011, Donnelly et al. 2016). At larger scales, differences in shrub height or herbaceous cover may not matter as much as simply occurring within sagebrush rangelands. In central Wyoming, the relationship between sagebrush sparrow abundance and sage-grouse pellet counts at a small scale was also negative (Carlisle 2017).

We found almost no relationship between probability of sage-grouse occurrence and predicted sage thrasher densities, as average sage thrasher density was only slightly higher in areas likely to contain sage-grouse (0.75 birds/ha) compared to the total study area (0.72 birds/ha). However, we detected sage thrashers at a majority of the plots where we detected sage-grouse pellets, so sage thrashers were using areas used by sage-grouse. Further, both sage thrashers and sage-grouse preferred areas with taller sagebrush shrubs at the smallest scale (Table 4.3), although sage thrashers preferred moderate amounts of sagebrush cover (10%) rather than increasing sagebrush cover as sage-grouse preferred. The lack of a stronger relationship between predicted sage-grouse occurrence and sage thrasher density is in contrast to previous

studies, which examined overlap in sage-grouse and sage thrasher habitat at large scales (e.g., Hanser and Knick 2011). However, a recent study examining the relationship between sage-grouse pellet counts and songbird abundance also found no relationship between pellet and thrasher abundance (Carlisle 2017).

Because our best sage thrasher models included no predictors or explained little variation, we may have missed important features for sage thrasher habitat in our study area and therefore, underestimated the strength of the relationship between sage-grouse and sage thrashers. For example, amount of landscape fragmentation was an important predictor for sage thrashers in previous studies (Knick and Rotenberry 1995, Vander Haegen 2007), although our study area had relatively little fragmentation from roads or energy development. Previous studies have also found sage thrashers selecting for environmental features at scales larger than 5-km extents (Aldridge et al. 2011). However, due to the extent of our remotely sensed product, we could not investigate scales >5-km. Our count model for thrashers was also zero inflated with mostly single counts and few plots containing multiple detections. Therefore, we examined logistic regression models post-hoc for no predictors and tall sagebrush cover within 564 m to see if we could better predict sage thrasher occurrence. The logistic regression models had ROC scores of 0.50-0.56 indicating that they were not an improvement over count models (Hilbe 2011).

Because sage-grouse and sagebrush-associated species require sagebrush rangelands year round or during the breeding season, managing for large landscapes of sagebrush should be beneficial for all species (Braun et al. 1976, Knick et al. 2003). Within sagebrush rangelands however, the species respond to different features at different scales and quantities, so sagebrush landscapes must also be managed for heterogeneity (Wiens et al. 1987, Connelly et al. 2011, Hanser and Knick 2011). For example, sagebrush sparrows in our study area selected larger

landscapes with less ground cover in contrast to Brewer's sparrows, green-tailed towhees, and sage-grouse. Therefore, managing for a single species, even a wide-ranging species like greater sage-grouse, may not be the best management strategy. Other approaches may offer a better solution to balance habitat needs for multiple species. An ecosystem approach to managing sagebrush rangelands rather than a single-species focus, as the Endangered Species Act encourages, may be a better alternative (Boyd et al. 2014). Complex management problems, such as exotic grass invasion, cannot be addressed within a regulatory, single-species framework, but require solutions that promote management trajectories towards ecosystem health (Boyd et al. 2014). State-and-transition models (STM) are one tool managers could use to promote various plant communities based on their contribution to ecosystem health and ecosystem services provided (Bestelmeyer et al. 2003, Boyd et al. 2014). Further, STMs could promote management of multiple states that provide greater structural diversity and habitat for sagebrush-associated species that have conflicting preferences for bare ground, shrub cover, or shrub height (Derner et al. 2009).

Another management approach that extends umbrella species management is a multi-species strategy, whereby a set of focal species dictate management and conservation efforts (Roberge and Angelstam 2004). A multi-species focus would be ideal when an ecosystem contains several species of conservation concern because there could be conflicting needs for ≥ 2 focal species that must be balanced within the overall ecosystem (Simberloff 1998). All focal species included in our analysis have experienced population declines either range-wide or within Colorado and could warrant federal protection in the future (Knick et al. 2003). The selected focal species for an ecosystem should span spatial scales in terms of resource requirements and response to disturbances (Roberge and Abgelstam 2004). In our study, this

would include the four songbird species and sage-grouse, which selected various scales of environmental features. We estimated species richness at two species for a majority of the study area; however, management efforts could be more effective if they targeted areas predicted to include three or four songbird species within areas likely to contain sage-grouse. In our study, habitat to the east of Little Snake River in Moffat County appears to support the greatest number of species where sage-grouse are also likely to occur (Fig. 4.6).

In addition, many landscapes, such as sagebrush rangelands, are diverse and should be managed for their natural heterogeneity rather than for narrow guidelines at a small scale (e.g., Connelly et al. 2000). This should promote habitat for multiple species (Hanser and Knick 2011) and possibly benefit the entire ecosystem. Biologists and managers also need to support multiple species and a diversity of habitats within an ecosystem because we lack complete knowledge about requirements for all species at all scales (Roberge and Angelstam 2004, Leu et al. 2011).

Management Recommendations

We described multi-scaled habitat relationships for several avifauna species of concern in Colorado and evaluated the use of greater sage-grouse as an umbrella species. These models could be applied in a multi-species management approach rather than managing for sage-grouse habitat alone. However, fine-scale measures known to be important for sage-grouse and sagebrush-associated species, such as grass height or perennial forb cover, should be also considered in modeling and management efforts. For instance, Hanser and Knick (2011) combined fine-scale measures with multi-scaled remotely sensed layers to gain a better understanding of how species may select and partition their environment. Additionally, our use of sage-grouse pellets to reflect habitat use, as has been demonstrated in other studies (Dahlgren et al. 2006), may still warrant consideration of other methods to determine habitat preferences

(i.e., radio telemetry) and links to fitness consequences across life stages. This could help managers confirm purported benefits of conservation actions, such as removal of conifer trees. Given the loss of sagebrush rangelands across the western U.S. and subsequent decline in sagebrush-associated species, biologists and managers must find the best strategy to conserve multiple species. But the first step must be disentangling resource needs for these species at multiple scales in order to understand potential impacts of management efforts.

Table 4.1. Definitions of multi-scaled predictors used in logistic and count-based regression models for greater sage-grouse and sagebrush-associated songbirds in Northwest Colorado, 2013-2015.

Predictor ^a	Predictor Description
bs_30m	percentage of big sagebrush cover within a 30 × 30-m pixel
bs_564m	percentage of big sagebrush cover within a 564-m moving window
bs_1km	percentage of big sagebrush cover within a 1-km moving window
bs_5km	percentage of big sagebrush cover within a 5-km moving window
as_30m	percentage of all sagebrush cover within a 30 × 30-m pixel
as_564m	percentage of all sagebrush cover within a 564-m moving window
as_1km	percentage of all sagebrush cover within a 1-km moving window
as_5km	percentage of all sagebrush cover within a 5-km moving window
shrub_30m	percentage of total shrub cover within a 30 × 30-m pixel
shrub_564m	percentage of total shrub cover within a 564-m moving window
shrub_1km	percentage of total shrub cover within a 1-km moving window
shrub_5km	percentage of total shrub cover within a 5-km moving window
tallSage_30m ^b	percentage of all sagebrush cover within a 30 × 30-m pixel
tallSage_564m	percentage of all sagebrush cover within a 564-m moving window
tallSage_1km	percentage of all sagebrush cover within a 1-km moving window
tallSage_5km	percentage of all sagebrush cover within a 5-km moving window
herb_30m	percentage of herbaceous understory within a 30 × 30-m pixel
herb_564m	percentage of herbaceous understory within a 564-m moving window
herb_1km	percentage of herbaceous understory within a 1-km moving window
herb_5km	percentage of herbaceous understory within a 5-km moving window
litter_30m	percentage of litter within a 30 × 30-m pixel
litter_564m	percentage of litter within a 564-m moving window
litter_1km	percentage of litter within a 1-km moving window
litter_5km	percentage of litter within a 5-km moving window
bare_30m	percentage of bare ground within a 30 × 30-m pixel
bare_564m	percentage of bare ground within a 564-m moving window
bare_1km	percentage of bare ground within a 1-km moving window
bare_5km	percentage of bare ground within a 5-km moving window
shrubHT_30m	shrub height (cm) within a 30 × 30-m pixel
shrubHT_564m	shrub height (cm) within a 564-m moving window
shrubHT_1km	shrub height (cm) within a 1-km moving window
shrubHT_5km	shrub height (cm) within a 5-km moving window
sageHT_30m	sagebrush height (cm) within a 30 × 30-m pixel
sageHT_564m	sagebrush height (cm) within a 564-m moving window
sageHT_1km	sagebrush height (cm) within a 1-km moving window
sageHT_5km	sagebrush height (cm) within a 5-km moving window

^a All biotic predictors based on Homer et al. 2012.

^b For sagebrush shrubs < 29 cm tall.

Table 4.2. Logistic and count-based regression models for greater sage-grouse use and sagebrush-associated songbird density in Northwest Colorado, 2013-2015. For each model, we report log-likelihood (LL), number of parameters (K), Bayesian Information Criterion (BIC), difference in BIC compared to lowest BIC of the model set (Δ BIC), BIC weight (w), pseudo- R^2 value, prediction error from five-fold cross validation, p-value from likelihood ratio test, and receiver operating characteristic score (ROC) for sage-grouse logistic regression models.

Model ^a		LL	K	BIC	Δ BIC	w	R^2	error	p-value
Brewer's sparrow:	tallsage_1km	621.20	3	1259.51	0.00	0.51	0.03	2.87	<0.001
	tallsage_1km + herb_5km	618.86	4	1260.54	1.03	0.31	0.04	3.07	<0.001
	sageHT_30m + herb_5km	619.76	4	1262.33	2.82	0.12	0.03	3.08	<0.001
	sageHT_30m	623.76	3	1264.64	5.13	0.04	0.03	3.08	<0.001
	shrubHT_30m + herb_5km	622.29	4	1267.39	7.88	0.01	0.03	3.08	<0.001
	herb_5km	625.39	3	1267.90	8.39	0.01	0.03	3.08	<0.001
	sageHT_30m + litter_564m	623.75	4	1270.32	10.81	0.00	0.03	3.09	<0.001
	shrubHT_30m	628.20	3	1273.52	14.01	0.00	0.02	3.09	<0.001
	bare_30m	629.68	3	1276.48	16.97	0.00	0.02	3.09	<0.001
	shrubHT_30m + litter_564m	627.87	4	1278.56	19.05	0.00	0.02	3.09	<0.001
	litter_564m	633.71	3	1284.53	25.02	0.00	0.01	3.10	<0.001
Green-tailed towhee:	tallSage_1km + tallSage_1km ² + herb_5km	232.51	5	493.55	0.00	0.95	0.20	2.76	<0.001
	tallSage_1km + tallSage_1km ²	238.42	4	499.66	6.11	0.04	0.18	2.50	<0.001
	tallSage_1km + tallSage_1km ² + litter_30m	237.61	5	503.73	10.18	0.01	0.18	2.60	<0.001
	bare_30m	248.53	3	514.17	20.62	0.00	0.14	2.54	<0.001
	herb_5km	248.63	3	514.38	20.83	0.00	0.14	2.49	<0.001
	sageHT_564m + sageHT_564m ²	246.07	4	514.96	21.41	0.00	0.15	3.31	<0.001
	litter_30m	259.53	3	536.17	42.62	0.00	0.10	2.29	<0.001
shrubHT_564m + shrubHT_564m ²	257.11	4	537.03	43.48	0.00	0.11	2.58	<0.001	
Sagebrush sparrow:	shrubHT_564m + shrubHT_564m ²	154.53	4	322.94	0.00	0.87	0.19	4.25	<0.001
	shrubHT_564m + shrubHT_564m ² + herb_5km	154.13	5	326.76	3.82	0.13	0.20	3.90	<0.001
	as_1km + as_1km ²	160.21	4	334.30	11.36	0.00	0.16	2.89	<0.001

Table 4.2 cont.

Model		LL	K	BIC	Δ BIC	w	R ²	error	p-value
Sagebrush	sageHT_5km	164.24	3	337.72	14.78	0.00	0.14	2.06	<0.001
sparrow:	as_1km + as_1km ² + herb_5km	160.19	5	338.89	15.95	0.00	0.16	2.92	<0.001
	bare_1km	170.26	3	349.76	26.82	0.00	0.11	2.04	<0.001
	litter_5km	171.29	3	351.83	28.89	0.00	0.11	2.04	<0.001
	herb_5km	182.95	3	375.14	52.20	0.00	0.05	2.06	<0.001
Sage	intercept-only	358.32	2	728.05	0.00	0.57	0.00	1.53	NA ^b
thrasher:	tallSage_564m + tallSage_564m ²	354.19	4	731.20	3.15	0.12	0.01	1.57	NA
	sageHT_30m	357.31	3	731.74	3.69	0.09	0.00	1.55	NA
	herb_5km	357.50	3	732.11	4.06	0.08	0.00	1.52	NA
	shrubHT_30m	357.81	4	732.74	4.69	0.05	0.00	1.53	NA
	bare_30m	358.11	3	733.33	5.28	0.04	0.00	1.52	NA
	litter_564m	358.23	3	733.57	5.52	0.04	0.00	1.53	NA
	sageHT_30m + herb_5km	357.20	4	737.22	9.17	0.01	0.00	1.53	NA
	shrubHT_30m + herb_5km	357.47	4	737.76	9.71	0.00	0.00	1.52	NA
Model		LL	K	BIC	Δ BIC	w	R ²	ROC	p-value
Sage-	litter_30m	196.32	2	404.05	0.00	0.24	0.06	0.65	<0.001
grouse:	as_30m	196.34	2	404.09	0.04	0.24	0.06	0.67	<0.001
	bare_30m	196.79	2	404.98	0.93	0.15	0.05	0.65	<0.001
	shrubHT_30m	197.32	2	406.05	2.00	0.09	0.05	0.66	<0.001
	herb_5km	197.48	2	406.37	2.32	0.08	0.05	0.63	<0.001
	as_30m + herb_5km	194.66	3	406.44	2.39	0.07	0.06	0.67	<0.001
	shrubHT_30m + herb_5km	194.95	3	407.01	2.96	0.05	0.06	0.67	<0.001
	sageHT_564m	198.40	2	408.21	4.16	0.03	0.05	0.66	<0.001

^a Predictors defined in Table 4.1.

^b Did not run the likelihood ratio test to compare a null (intercept-only) model against a null model.

Table 4.3. Beta coefficient estimates (β), standard errors (SE), and 95% confidence intervals for predictors in the top (i.e., $\Delta\text{BIC} < 4$) logistic and count-based regression models for greater sage-grouse use and sagebrush-associated songbird density in Northwest Colorado, 2013-2015.

		Coefficients:	β	SE	95% Lower	95% Upper
Brewer's sparrow:	model 1:	intercept	0.40	0.07	0.25	0.54
		tallsage_1km	0.06	0.01	0.05	0.08
	model 2:	intercept	0.11	0.15	-0.18	0.41
		tallsage_1km	0.05	0.01	0.02	0.07
		herb_5km	0.02	0.01	0.002	0.03
	model 3:	intercept	-0.05	0.15	-0.34	0.23
		sageHT_30m	0.01	0.004	0.01	0.02
herb_5km		0.02	0.01	0.01	0.03	
Green-tailed towhee:	model 1:	intercept	-6.24	0.67	-7.68	-5.00
		tallSage_1km	0.47	0.09	0.30	0.65
		tallSage_1km ²	-0.02	0.004	-0.03	-0.01
		herb_5km	0.09	0.02	0.04	0.14
Sagebrush sparrow:	model 1:	intercept	-1.94	0.92	-3.89	-0.29
		shrubHT_564m	0.30	0.11	0.10	0.54
		shrubHT_564m ²	-0.01	0.003	-0.02	-0.01
	model 2:	intercept	-1.74	0.96	-3.75	0.01
		shrubHT_564m	0.31	0.11	0.11	0.56
		shrubHT_564m ²	-0.01	0.003	-0.02	-0.01
Sage thrasher:	model 1:	intercept	-1.52	0.09	-1.69	-1.34
		model 2:	intercept	-1.84	0.15	-2.14
	model 2:	tallSage_564m	0.14	0.05	0.04	0.23
		tallSage_564m ²	-0.01	0.003	-0.01	-0.002
	model 3:	intercept	-1.72	0.16	-2.05	-1.39
		sageHT_30m	0.01	0.01	-0.003	0.02
Sage-grouse:	model 1:	intercept	-1.29	0.31	-1.91	0.70
		litter_30m	0.06	0.01	-0.03	0.08
	model 2:	intercept	-0.84	0.22	-1.28	-0.42
		as_30m	0.08	0.02	0.05	0.12
	model 3:	intercept	-0.98	0.25	-1.48	-0.49
		shrubHT_30m	0.03	0.01	0.02	0.05
	model 4:	intercept	-1.30	0.34	-1.98	-0.65
		as_30m	0.06	0.02	0.01	0.10
		herb_5km	0.03	0.02	-0.002	0.07

Table 4.3 cont.

					95%	95%
Coefficients:			β	SE	Lower	Upper
Sage-grouse:	model 5:	intercept	-1.45	0.34	-2.13	-0.80
		shrubHT_30m	0.02	0.01	0.002	0.04
		herb_5km	0.04	0.02	0.004	0.07

^a Predictors defined in Tables 4.1.

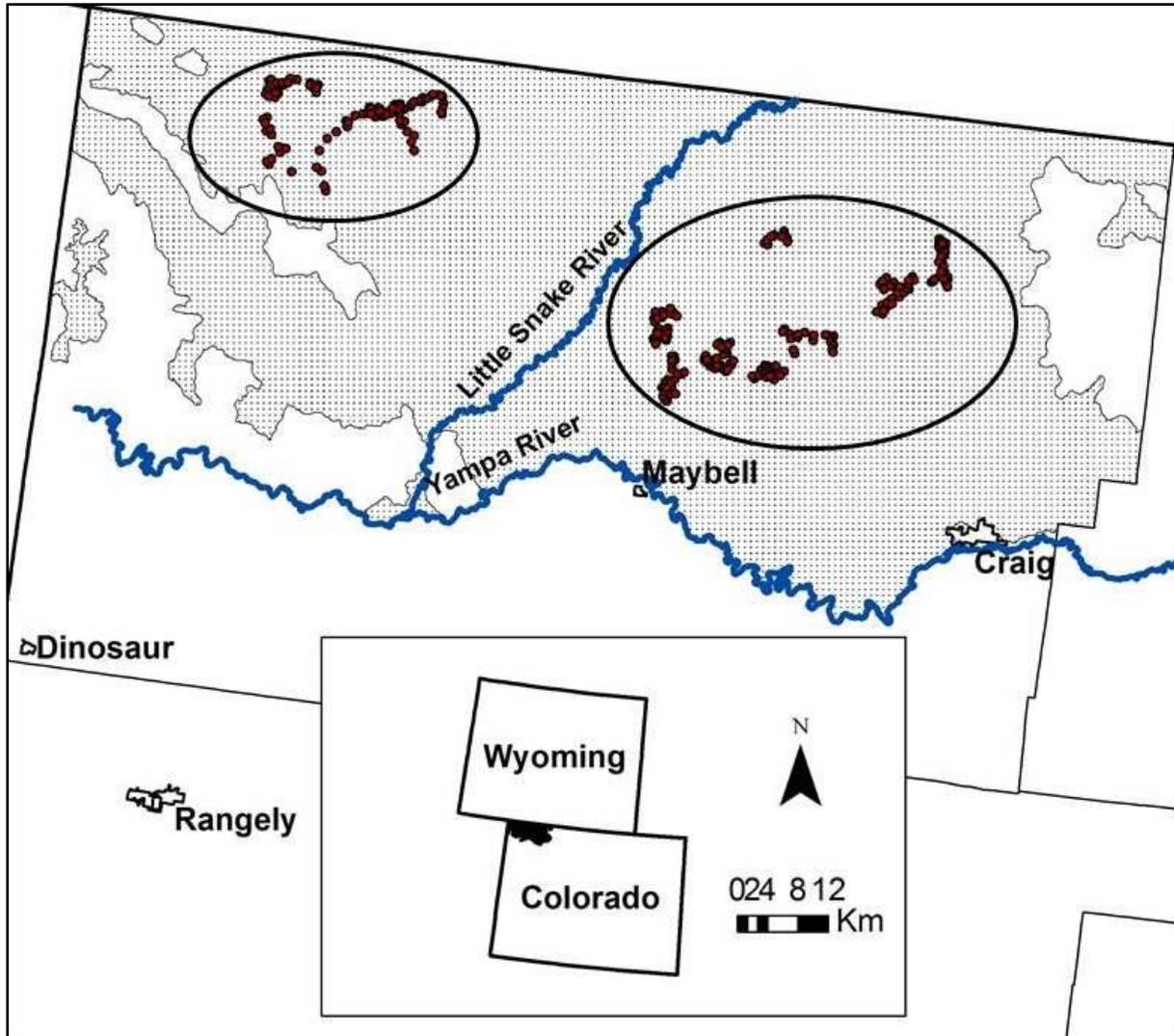


Figure 4.1. Study area for songbird and greater sage-grouse pellet surveys, 2013-2015, with two study sites outlined and labeled (West Moffat on the left and East Moffat to the right) and the overall greater sage-grouse range north of the Yampa River only represented by stippling (Colorado Parks and Wildlife 2011).

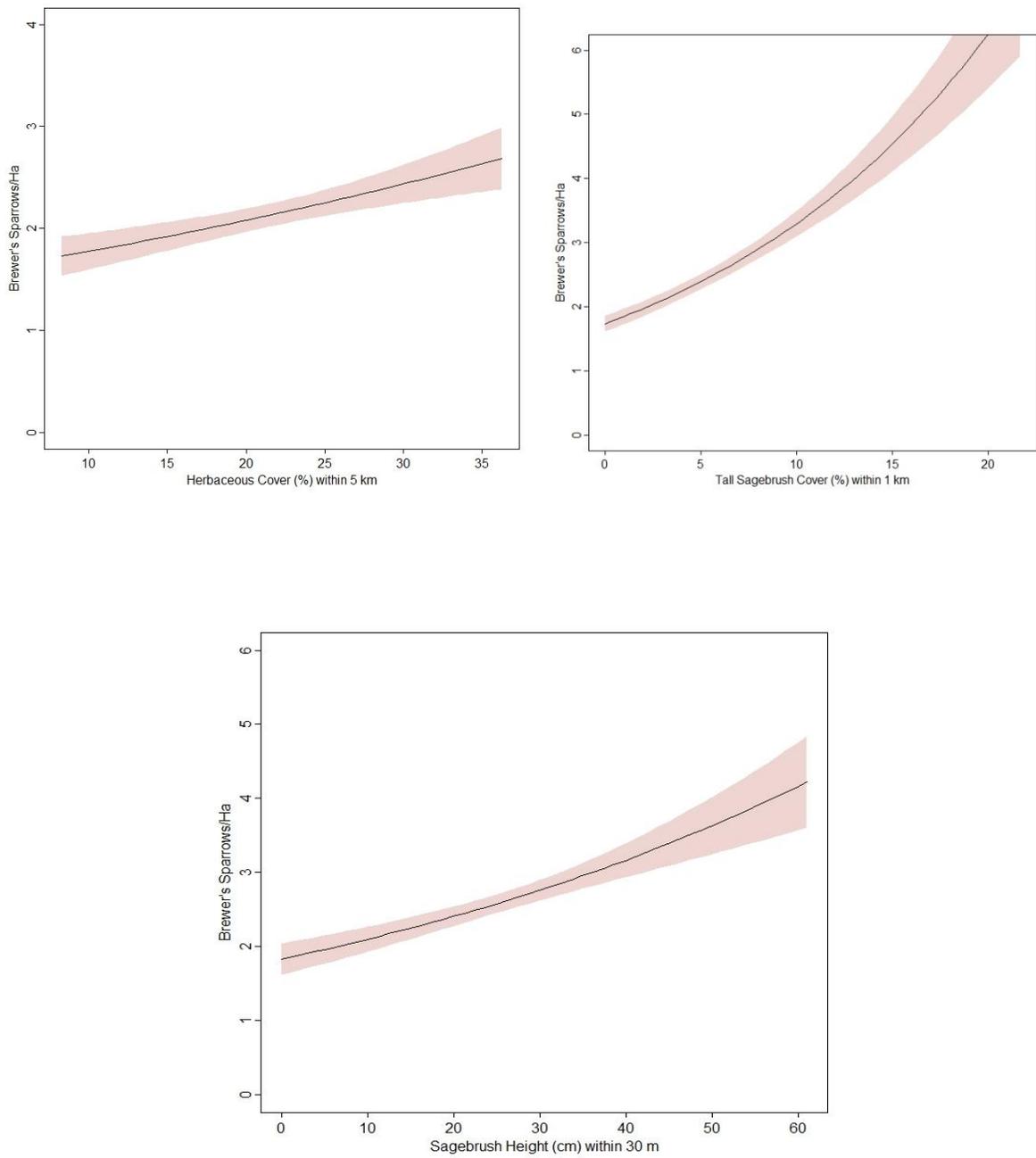


Figure 4.2. Predicted variable relationships and 95% confidence intervals for the top negative binomial models of Brewer's sparrows and multi-scaled predictors in Northwest Colorado, 2013-2015. Variable relationships were similar across top three models (see Table 4.3).

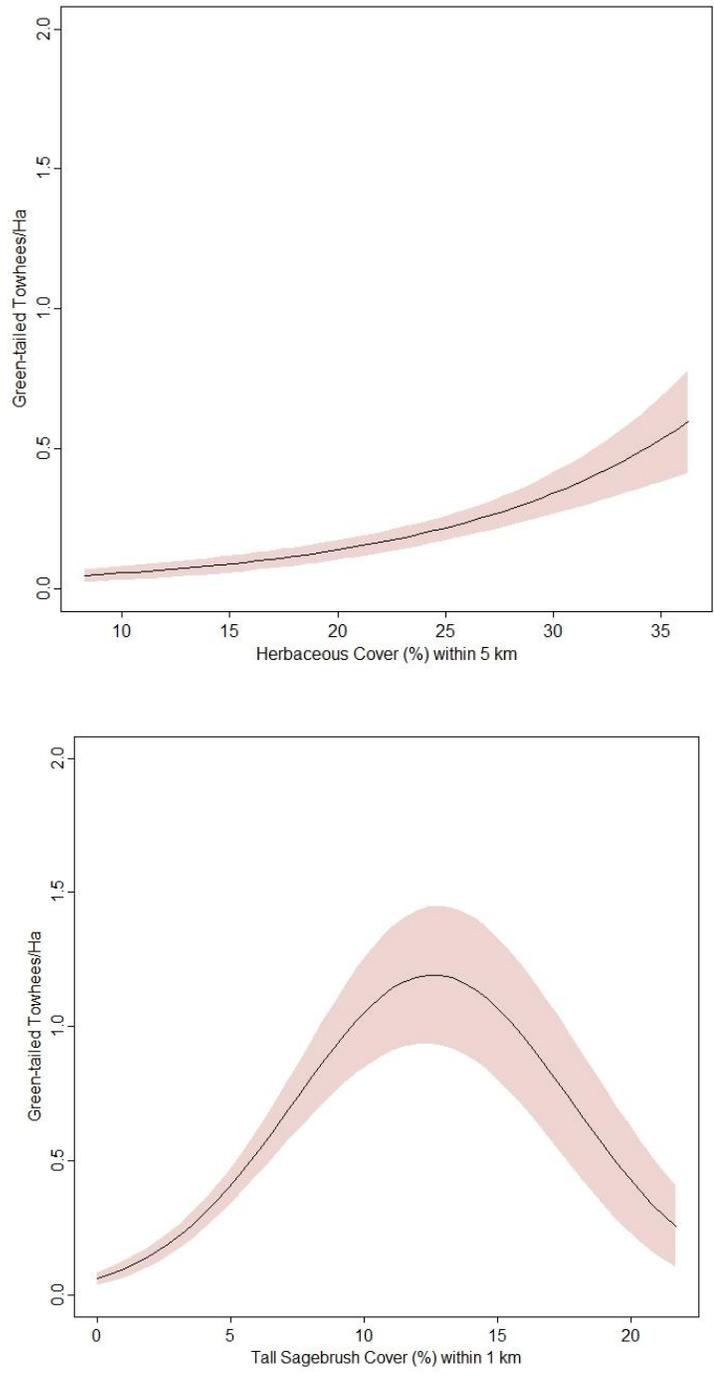


Figure 4.3. Predicted variable relationships and 95% confidence intervals for the top negative binomial model of green-tailed towhees and multi-scaled predictors in Northwest Colorado, 2013-2015.

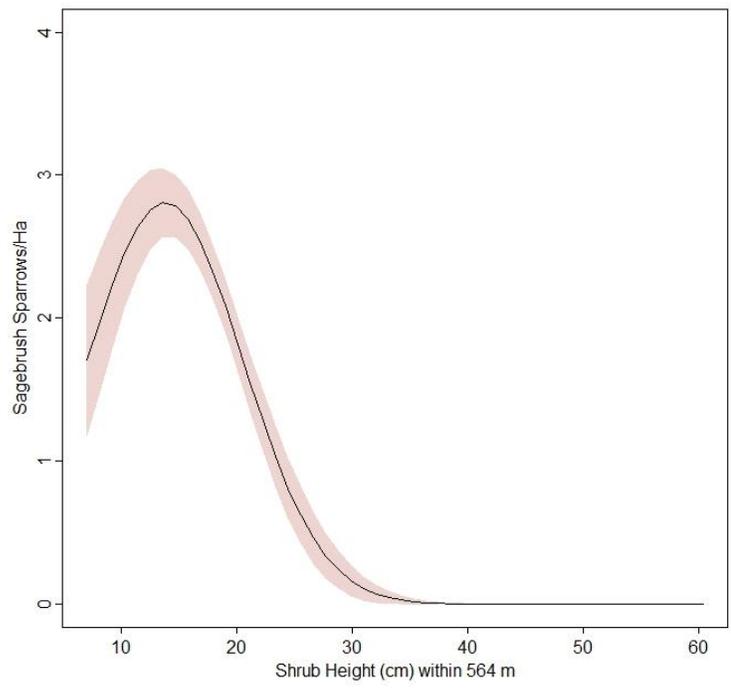
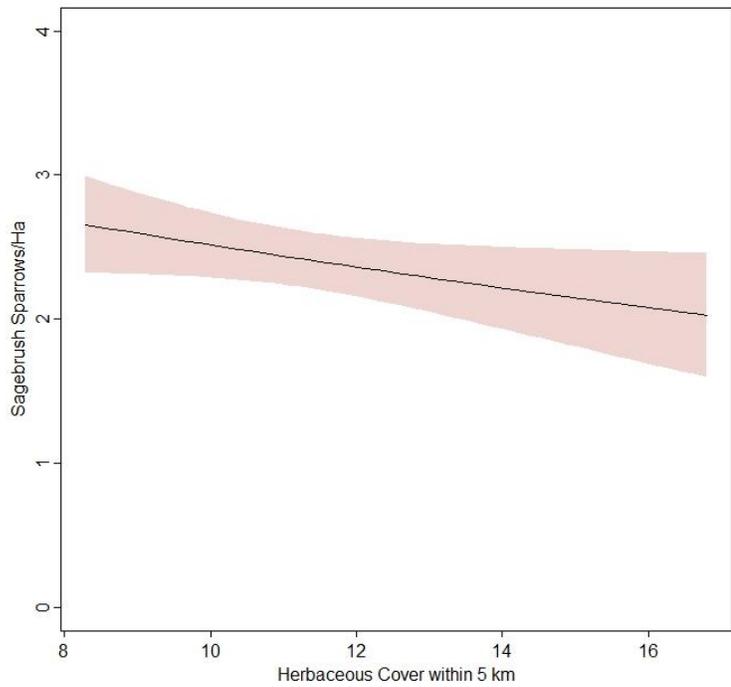


Figure 4.4. Predicted variable relationships and 95% confidence intervals for the top Poisson models of sagebrush sparrows and multi-scaled predictors in Northwest Colorado, 2013-2015.

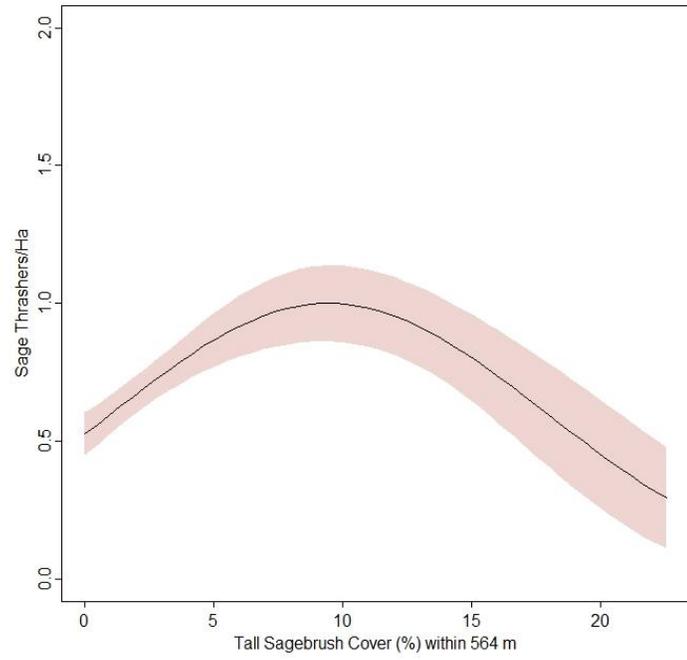
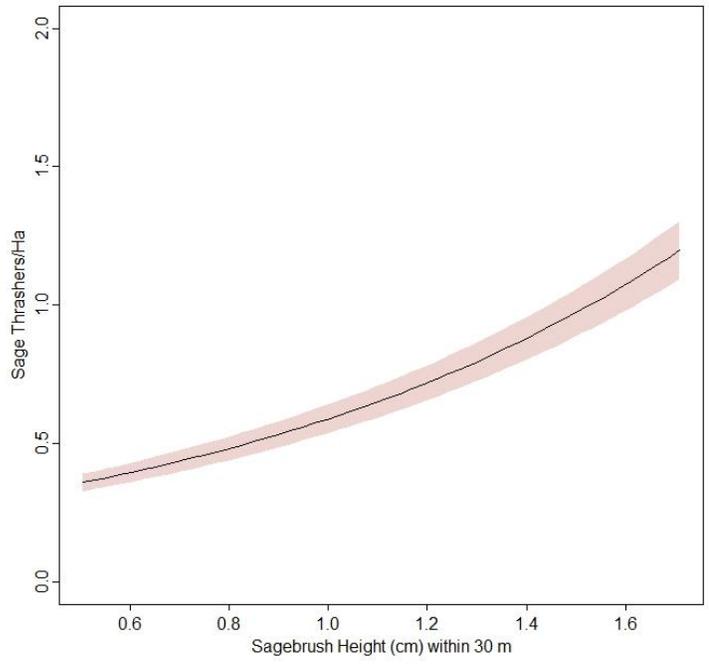


Figure 4.5. Predicted variable relationships and 95% confidence intervals for the top negative binomial models of sage thrashers and multi-scaled predictors in Northwest Colorado, 2013-2015, excluding the intercept-only model.

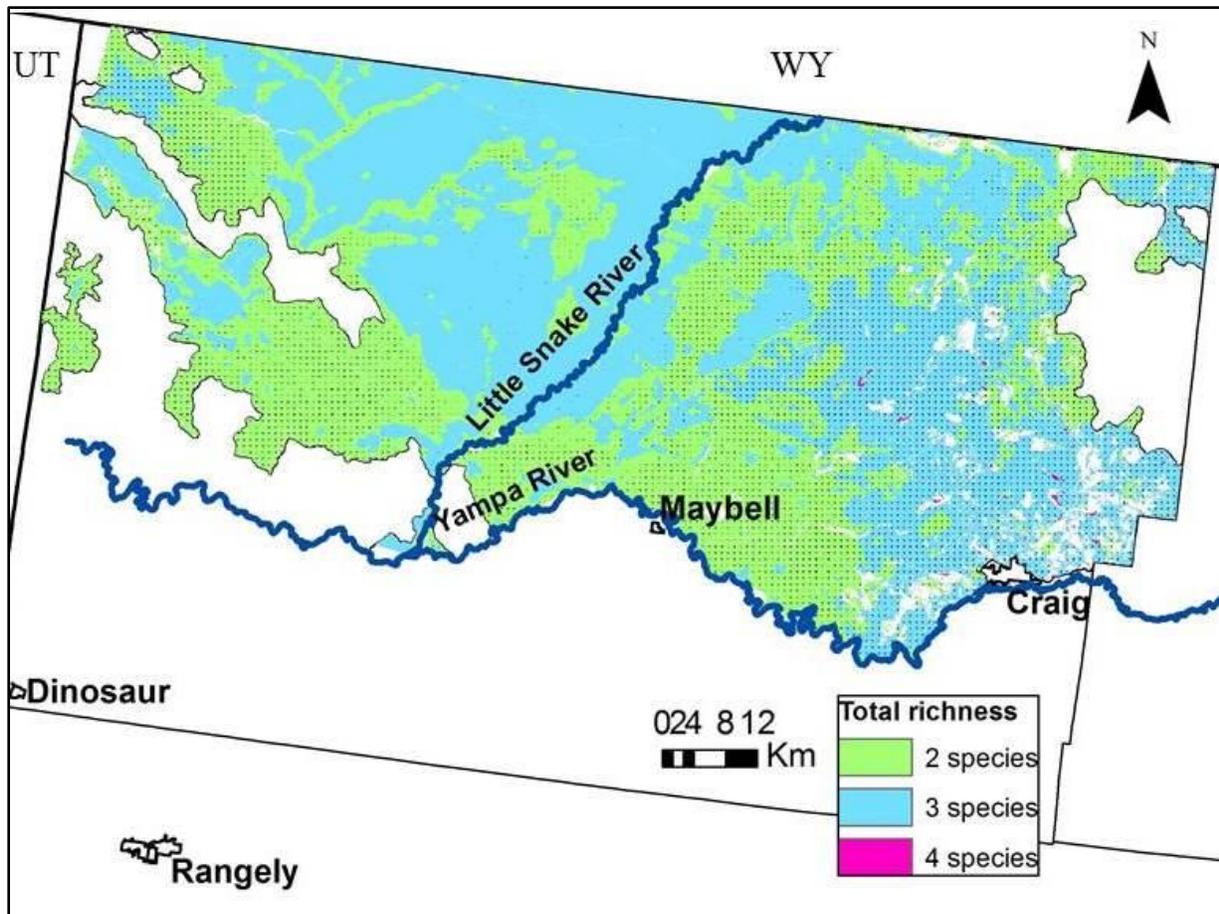


Figure 4.6. Predicted species richness for Brewer's sparrows, green-tailed towhees, sagebrush sparrows, and sage thrashers within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52 and richness was calculated based on a minimum density to support a songbird territory (i.e., 0.42 Brewer's sparrows/ha, 1.11 green-tailed towhees/ha, 0.59 sage thrashers/ha, and 0.14 sagebrush sparrows/ha; Boyle and Reeder 2005, Poole 2005).

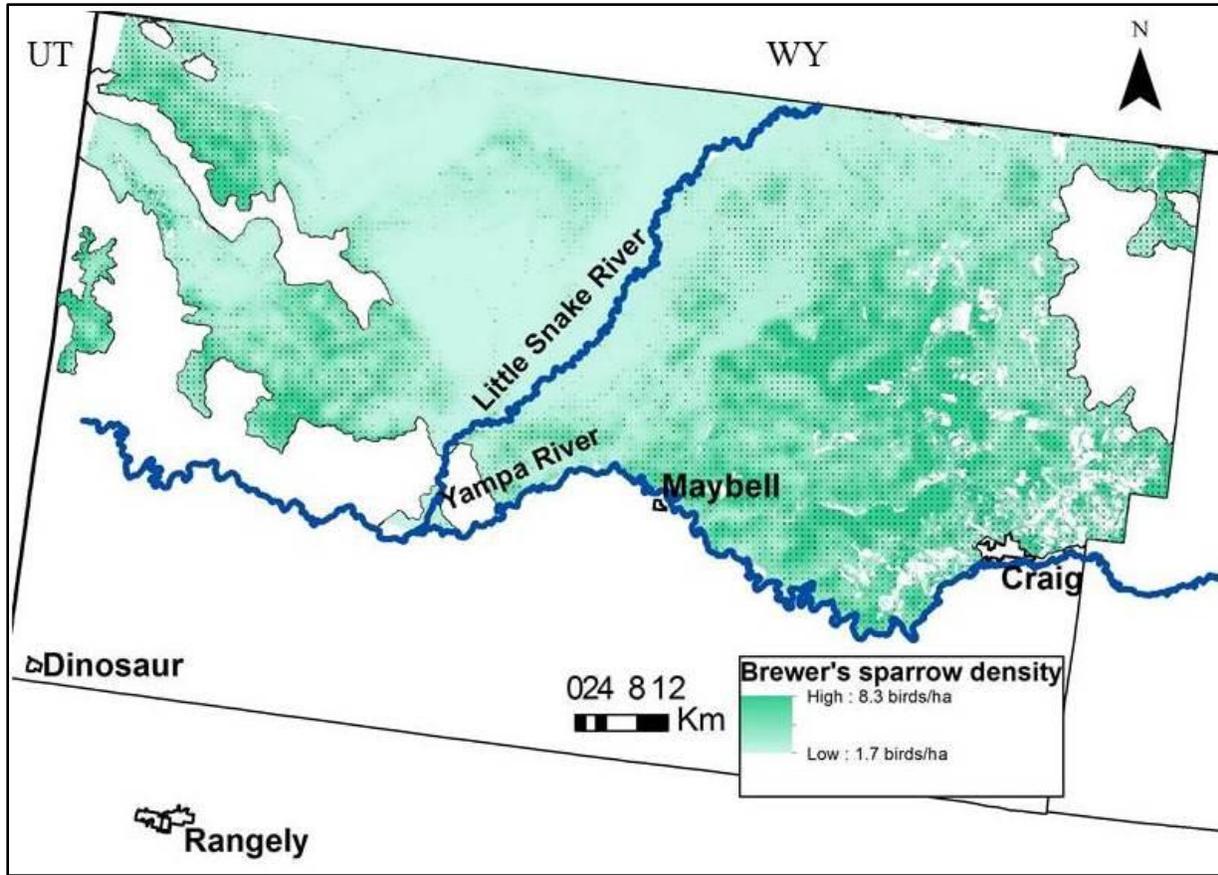


Figure 4.7. Predicted Brewer's sparrow density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52 .

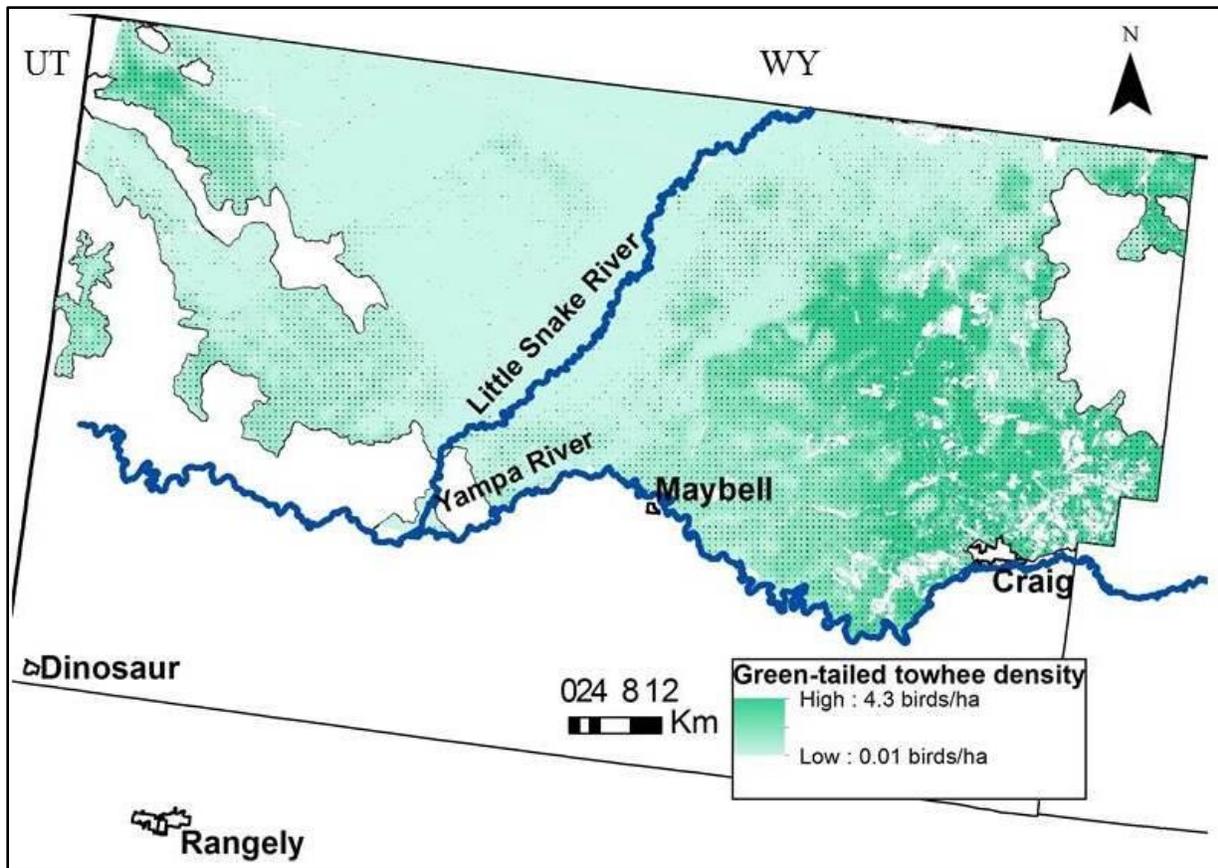


Figure 4.8. Predicted green-tailed towhee density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52 .

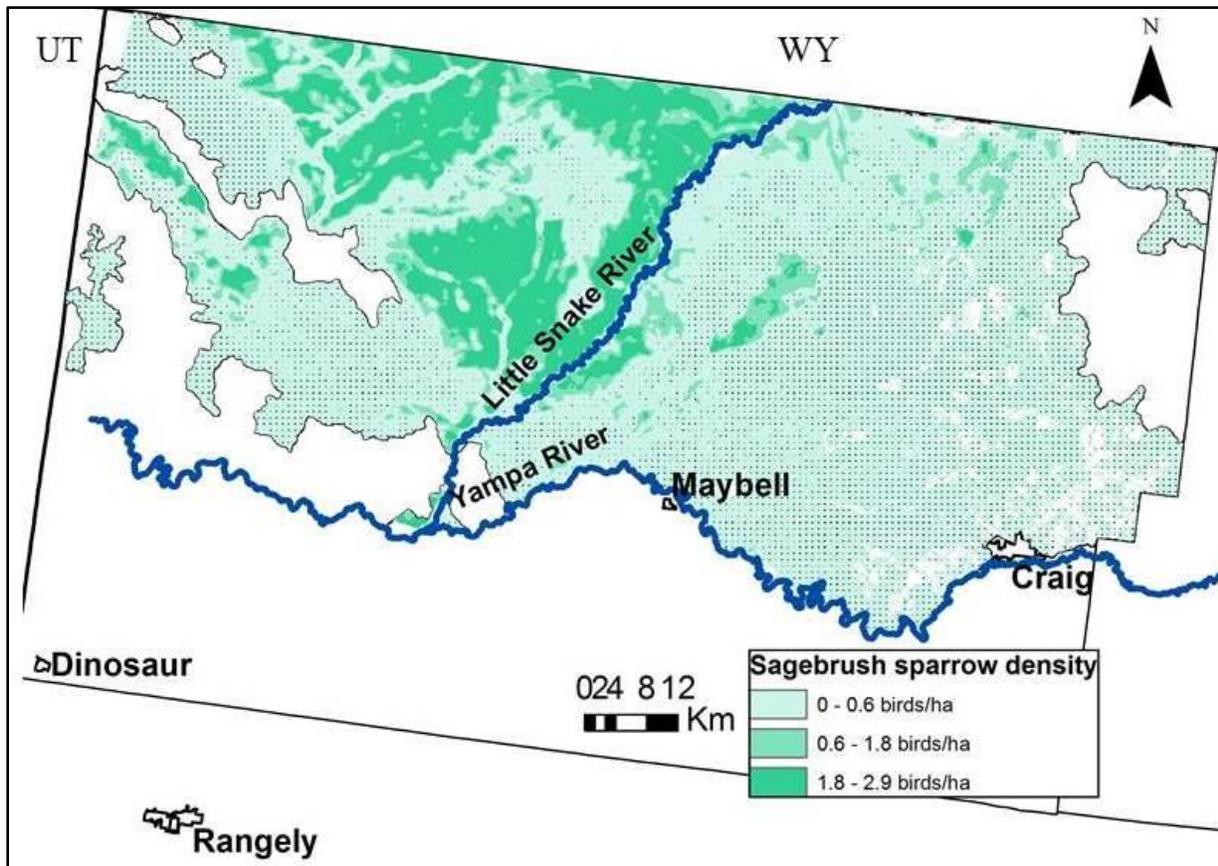


Figure 4.9. Predicted sagebrush sparrow density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52 .

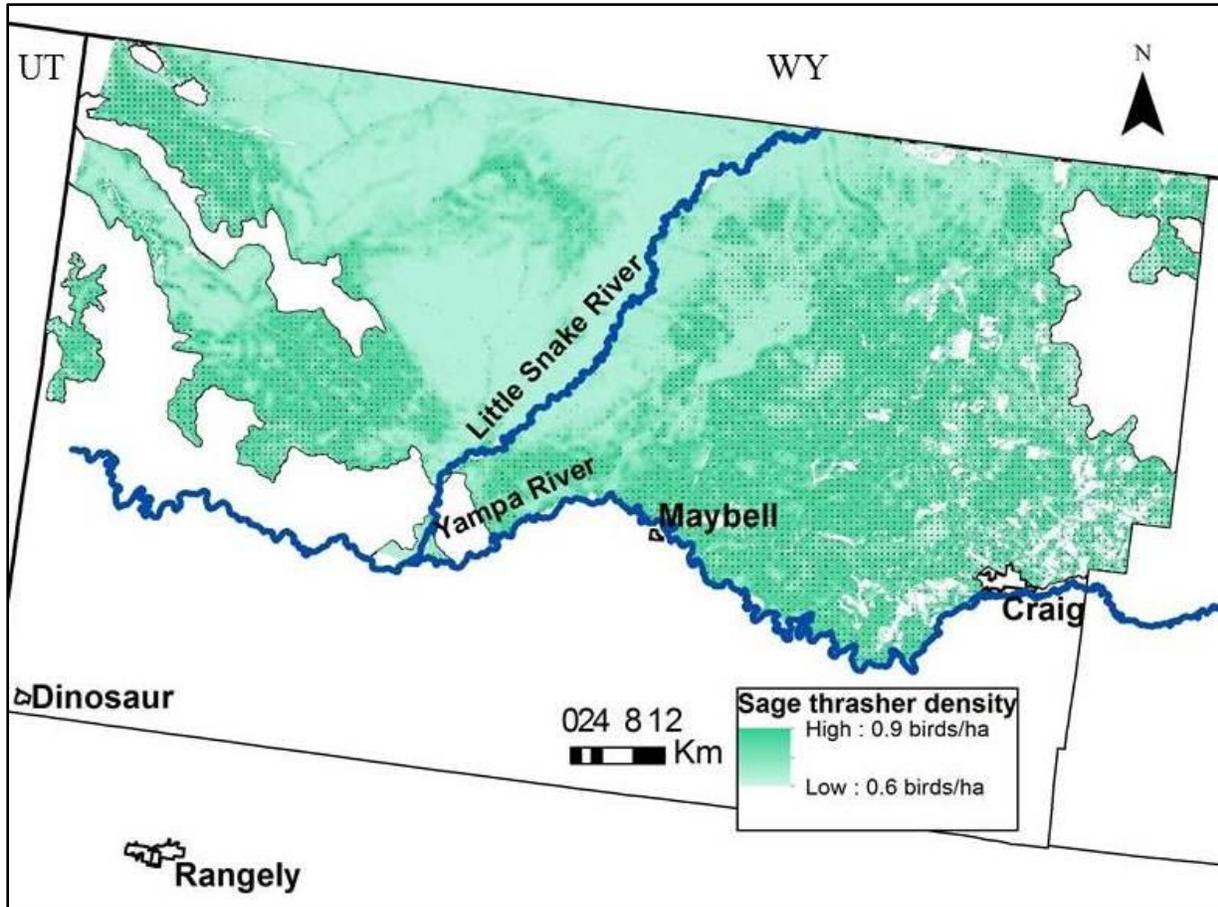


Figure 4.10. Predicted sage thrasher density within the overall greater sage-grouse range (Colorado Parks and Wildlife 2011) in Northwest Colorado. Stippled areas indicate where sage-grouse are likely to occur with probability >0.52.

LITERATURE CITED

- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater sage-grouse. *Ecological Applications* 17:508–526.
- Aldridge, C.L., S.E. Hanser, S.E. Nielsen, M. Leu, B.S. Cade, D.J. Saher, and S.T. Knick. 2011. Detectability adjusted count models of songbird abundance. Pp 141-220 in Hanser, S.E., M. Leu, S.T. Knick, and C.L. Aldridge (editors). *Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins*. Allen Press, Lawrence, KS, USA.
- Alfons, A. 2015. Package ‘cvTools’. Vignette, R Foundation for Statistical Computing. <https://cran.r-project.org/web/packages/cvTools/cvTools.pdf>. Accessed 30 November 2015.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike’s Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Baker, W. L. 2011. Pre-Euro-American and recent fire in sagebrush systems. Pp 185–201 in S. T. Knick and J. W. Connelly (editors). *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. *Wildlife Society Bulletin* 28:993–1002.
- Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.
- Bifulchi, A., and T. Lodé. 2005. Efficiency of conservation shortcuts: an investigation with otters as umbrella species. *Biological Conservation* 126:523-527.
- Bird Conservancy of the Rockies. 2016. The Rocky Mountain Avian Data Center. [web

- application]. Brighton, CO, USA. <http://adc.rmbo.org>. Accessed: 1 November 2016.
- Boyd, C. S., D. D. Johnson, J. D. Kerby, T. J. Svejcar, and K. W. Davies. 2014. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? *Rangeland Ecology and Management* 67:358-368.
- Boyle, S., and D. R. Reeder. 2005. Colorado sagebrush: a conservation assessment and strategy. Colorado Division of Wildlife, Grand Junction, CO, USA.
- Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. *Wilson Bulletin* 88:165–177.
- Bruegger, R. A., M. E. Fernandez-Gimenez, C. Y. Tipton, J. M. Timmer, and C. L. Aldridge. 2016. Multi-stakeholder development of state-and-transition models: a case study from northwestern Colorado. *Rangelands*. doi: 10.1016/j.rala.2016.10.008.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.
- Buckland, S.T., R.E. Russell, B.G. Dickson, V.A. Saab, D.N. Gorman, and W. M. Block. 2009. Analyzing designed experiments in Distance Sampling. *Journal of Agricultural, Biological, and environmental Statistics* 14:432–442.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag New York Inc., New York, New York, USA.
- Carlisle, J. D. 2017. The effect of sage-grouse conservation on wildlife species of concern: implications for the umbrella species concept. Dissertation, University of Wyoming 205 p.
- Carpenter, J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection in winter in Alberta. *Journal of Wildlife Management* 74:1806–1814.
- Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology* 44:983-992.

- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invulnerable by *Bromus tectorum*? Ecological Monographs 7:117–145.
- Colorado Greater Sage-grouse Steering Committee. 2008. Colorado greater sage-grouse conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Colorado Parks and Wildlife. 2011. CPW Greater sage grouse, overall range. <<https://www.arcgis.com/home/item.html?id=75734173c73b485daa1aa90a069e56f2>>. Accessed 2 May 2017.
- Connelly, J. W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines for management of sage grouse populations and habitat. Wildlife Society Bulletin 28:967–985.
- Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011. Characteristics of greater sage-grouse habitats. Pp 69–83 in S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Dahlgren, D. K., R. Chi, and T. A. Messmer. 2006. Greater sage-grouse response to sagebrush management in Utah. Wildlife Society Bulletin 34:975–985.
- Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. Rangeland Ecology and Management 62:111-118.
- Dobbs, R. C., P. R. Martin and T. E. Martin. 2012. Green-tailed towhee (*Pipilo chlorurus*). The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/gnttow>. DOI: 10.2173/bna.368.
- Dobkin, D. S., and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy: distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, OR, USA.
- Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

- Doherty, K. E., D. E. Naugle, J. D. Tack, B. L. Walker, J. M. Graham, J. L. Beck. 2014. Linking conservation actions to demography: grass height explains variation in greater sage-grouse nest survival. *Wildlife Biology* 20:320-325.
- Donnelly, J. P. J. D. Tack, K. E. Doherty, D. E. Naugle, B. W. Alldred, and V. J. Dreitz. 2016. Extending conifer removal and landscape protection strategies from sage-grouse to songbirds, a range-wide assessment. *Rangeland Ecology and Management* <http://dx.doi.org/10.1016/j.rama.2016.10.009>.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, . G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. *Science* 309:570-574.
- Garton, E. O., J. W. Connelly, J. S. Horne, C. S. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pp 293–382 *in* S. T. Knick and J. W. Connelly (editors). *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Hanni, D. J., C. M. White, N.J. Van Lanen, J. J. Birek, J.M. Berven, and M.A. McLaren. 2013. Integrated Monitoring of Bird Conservation Regions (IMBCR): Field protocol for spatially-balanced sampling of landbird populations. Unpublished report. Rocky Mountain Bird Observatory, Brighton, Colorado, USA.
- Hanser, S. E., C. L. Aldridge, M. Leu, M. M. Rowland, S. E. Nielson, and S. T. Knick. 2011. Greater sage-grouse: general use and roost site occurrence with pellet counts as a measure of relative abundance. Pp 112-140 *in* Hanser, S.E., M. Leu, S.T. Knick, and C.L. Aldridge (editors). *Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins*. Allen Press, Lawrence, KS, USA.
- Hanser, S. E., and S. T. Knick. 2011. Greater Sage-Grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. Pp 473–487 *in* S. T. Knick and J. W. Connelly (editors). *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California-Press, Berkeley, USA.

- Hastie, T., R. Tibshirani, and J. Friedman. 2009. Model assessment and selection. Pp. 219-259 in Hastie, T., R. Tibshirani, and J. Friedman (editors). *The elements of statistical learning: data mining, inference, and prediction*. Springer, New York, NY, USA.
- Hilbe, J. M. 2011. *Negative binomial regression*. Cambridge University Press, New York, NY, USA.
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8:23-29.
- Holloran, M. J. 2005. Greater Sage-Grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Ph.D. dissertation, University of Wyoming, Laramie, WY.
- Homer, C.G., C.L. Aldridge, D.K. Meyer, and S. Shell. 2012. Implementing a multi-scale remote sensing sagebrush characterization and monitoring framework across Wyoming. *International Journal of Applied Earth Observation and GeoInformation* 14:233-244.
- Hosmer, D. W. and S. Lemeshow. 2000. *Applied logistic regression*. John Wiley & Sons, Inc., New York, New York, USA.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Knick, S. T., and J. T. Rotenberry. 2002. Effects of habitat fragmentation on passerine birds breeding in intermountain shrubsteppe. *Studies in Avian Biology* 25: 130-140.
- Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. *Conservation Biology* 9:1059-1071.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.
- Leu, M., S. E. Hanser, C. L. Aldridge, S. E. Nielsen, B. S. Cade, and S. T. Knick. 2011. A sampling and analytical approach to develop spatial distribution models for sagebrush-associated species. Pp. 88-111 in S. E. Hanser, M. Leu, S. T. Knick, and C. L. Aldridge (editors). *Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins*. Allen Press, Lawrence, KS, USA.

- Liu, C., P. M. Barry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28:383-393.
- Lòpez-Ratòn, M., M. X. Rodrìguez-Àlvarez, C. Cadarso-Suàrez, and F. Gude-Sampedro. 2014. OptimalCutpoints: An R package for selecting optimal cutpoints in diagnostic tests. *Journal of Statistical Software* 61:1-36.
- Lukacs, P. M., A. Seglund, and S. Boyle. 2015. Effects of Gunnison sage-grouse habitat treatment efforts on associated avifauna and vegetation structure. *Avian Conservation and Ecology* 10(2):7. <http://dx.doi.org/10.5751/ACE-00799-100207>.
- Martin, J. W. and B. A. Carlson. 1998. Sagebrush sparrow (*Artemisiospiza nevadensis*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/sagspa1>. DOI: 10.2173/bna.326b.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 *in* S. T. Knicks and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies in Avian Biology*, University of California-Press, Berkeley, USA.
- Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Saur. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105-119.
- R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roberge, J., and P. Angelstam, P. 2004. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18:76–85.
- Rotenberry, J. T., M. A. Patten, and K. L. Preston. 1999. Brewer's sparrow (*Spizella breweri*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/brespa>. DOI: 10.2173/bna.390.

- Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323-335.
- Sage Grouse Initiative. 2015. Sagebrush songbirds benefit from sage grouse habitat restoration. Science to Solutions Series Number 9. Sage Grouse Initiative. 4pp.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83:247-257.
- Suter, W., R. F. Graf, and R. Hess. 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology* 16:778-788.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5–14.
- Tipton, C. Y. W. 2015. Improving state-and-transition models for management of sagebrush steppe ecosystems. Thesis, Colorado State University 160 p.
- U.S. Fish and Wildlife Service. 2015. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition to List Greater Sage-grouse (*Centrocercus urophasianus*) as an Endangered or Threatened Species. FWS–R6–ES–2015–0146.
- Vander Haegen, W. M. 2007. Fragmentation by agriculture influences reproductive success of birds in a shrubsteppe landscape. *Ecological Applications* 17:934-947.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494-499.
- Warton, D. I. 2005. Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data. *Environmentrics* 16: 275 – 289.
- Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* 48:132-147.
- Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 51:21–42.
- Zar, J. H. 2010. *Biostatistical Analyses*. Fifth edition. Prentice Hall, Upper Saddle River, NJ, USA.

CHAPTER V. CONCLUSION

Given a decline in sage-grouse (*Centrocercus* spp.) and songbird populations and a loss of sagebrush rangelands (Knick et al. 2003), managers need to understand habitat relationships for these species at small and large scales, as well as the impact of managing for a single species. Managers must also have a better understanding of how landscape patterns may influence transitions between habitat types, and how these changes in turn, affect avifauna populations. Further, this information should be gleaned with participation of local stakeholders to elucidate local phenomena and concerns and ensure the information is used for local management of wildlife and rangelands (Kachergis et al. 2013, Bruegger et al. 2016). Taken together, these conditions should foster an ecosystem approach for tackling avifauna population declines and loss of habitat, in which the provision of multiple ecosystem services for multiple stakeholders is paramount (Boyd et al. 2014).

In my second chapter, I incorporated avifauna densities and species richness into a locally developed STM for sagebrush rangelands (Tipton 2015). My purpose was to address multiple ecosystem services within the model and gauge the impact of local management decisions on avifauna populations. I also learned about several avifauna species' habitat relationships for Northwest Colorado. I predicted higher species richness and greater densities for sagebrush-associated species and lower densities for grassland-associated songbirds in the states or community phase dominated by sagebrush cover. However, each species responded to fine-scaled predictors differently, indicating that a "one-size-fits-all" management approach could be detrimental. For example, green-tailed towhees (*Pipilo chlorurus*) preferred the diverse shrubland state with taller shrubs and greater shrub and ground cover, while sagebrush sparrows (*Artemisiospiza nevadensis*) preferred areas with moderate shrub cover and more bare ground.

The native grassland state, which resulted from several wildfires, provided the most herbaceous forage and promoted higher densities for grassland-associated species, such as vesper sparrows (*Pooecetes gramineus*). By incorporating habitat relationships for each species in the states and communities, local managers can predict how avifauna populations will respond to a change in over or under story from drivers, such as wildfire, and determine which state(s) promotes the greatest densities for the most species (Holmes and Miller 2010). This was the first attempt to use a participatory process to build locally relevant STMs with multiple ecosystem services, such as livestock forage and avifauna habitat (Bruegger et al. 2016). In particular, landowners were concerned that wildfires removed greater sage-grouse habitat (*C. urophasianus*), but I predicted higher than expected pellet densities for the native grassland state due to unburned patches of sagebrush and surrounding shrub cover. This approach also illustrated the value of landscape heterogeneity as the management of one state or phase over another could be detrimental to other species.

In the third chapter, I took the same locally developed STM and mapped the states within the study area using a novel approach for sagebrush rangelands. A previous approach employed more steps to manually map states in the Chihuahuan Desert in order to preserve fine scale soil variation (Steele et al. 2012). My approach included multinomial logistic regression with biotic and abiotic predictors (including site history) for extrapolating sampling plots to an entire area of interest. The STM included four states: diverse shrubland, needle-and-thread (*Hesperostipa comata*) shrubland, native grassland, and crested wheatgrass (*Agropyron cristatum*). The top model included big sagebrush (*Artemisia tridentata* spp.) cover and elevation with greater sagebrush cover discriminating diverse shrubland from native grassland pixels and higher elevations discriminating diverse from needle-and-thread shrubland pixels. The two shrubland

states comprised approximately 67% of the study area, while the exotic grassland state comprised the lowest proportion (1%). The shrubland states were also the most contiguous while the exotic grassland state was the least.

Model classification accuracy indicated that the approach was successful, although future endeavors should incorporate greater sample sizes to address variability within the area of interest, such exotic grassland-dominated plots. Managers could combine the spatially represented states with values for ecosystem services, such as wildlife habitat, livestock forage, or soil stability to guide management decisions and scenario planning (Troy and Wilson 2006). This method could also allow managers to identify landscape patterns that may influence undesirable transitions between states, such as the spread of cheatgrass (*Bromus tectorum*)-dominated patches to surrounding sagebrush communities (Miller et al. 2011). By examining these patterns, managers could target the degraded areas for restoration efforts to prevent the transitions. Spatially represented STMs could also increase the rigor of rangeland management if they were used to design assessment and monitoring programs in a probabilistic, hierarchical fashion or to target areas for experiments to test and quantify transition probabilities (Briske et al. 2005, Bestelmeyer et al. 2011).

For the last chapter, I examined the efficacy of greater sage-grouse as an umbrella for several sagebrush-associated songbirds in Northwest Colorado. To determine this, I first modeled songbird abundance and sage-grouse occurrence with multi-scaled predictors, and then examined the overlap in sage-grouse habitat for each songbird at two scales. These results are important because all four species included in the analysis are species of conservation concern in Colorado (Boyle and Reeder 2005) and the use of greater sage-grouse as an umbrella has not been examined in a small region or in northern Colorado (but see Lukacs et al. 2015 for

Gunnison sage-grouse). The best predictors for all species in this study included some form of shrub cover or shrub height, which is not surprising for sagebrush-associated species (Knick et al. 2008). However, the birds responded to these features at different scales, which previous studies have also found (e.g., Wiens et al. 1987, Aldridge et al. 2011). For example, Brewer's sparrows (*Spizella breweri*) preferred greater sagebrush cover within 1-km and taller sagebrush shrubs within the smallest scale (i.e., 30 m), whereas shorter shrubs (approximately 15 cm tall) within 564 m and less herbaceous cover at the largest scale were the best predictors for sagebrush sparrows. Sage-grouse occurrence was positively associated with all sagebrush cover, sagebrush height, and litter at the smallest scale and herbaceous cover at the largest scale, which corresponds with previous studies for the species (e.g., Connelly et al. 2000, Holloran et al. 2005, Kirol et al. 2012).

Based on the model-predicted surfaces in the fourth chapter, I determined that sage-grouse could be an effective umbrella for Brewer's sparrows and green-tailed towhees, but sagebrush sparrow populations could decline if management efforts in the study area promoted sage-grouse habitat. This latter result is contrary to previous studies (Hanser and Knick 2011), but the umbrella concept has not been examined for sage-grouse in Northwest Colorado and sagebrush sparrows do not occur throughout sagebrush habitat in Colorado (Boyle and Reeder 2005). In this study, the best approach for avifauna management would likely be a multi-species strategy, whereby a set of focal species dictate management and conservation efforts (Roberge and Angelstam 2004). This strategy would be ideal when an ecosystem contains several species of conservation concern, which could have conflicting needs and respond to environmental features at different scales (Simberloff 1998, Roberge and Abgelstam 2004). By promoting

habitat for multiple species, managers should prioritize landscape diversity within sagebrush rangelands, which could also benefit the entire ecosystem

Together, these three chapters illustrate the value of locally informed, data-driven STMs and the need to manage for landscape heterogeneity. The STM was improved by insight from local participants on seeding history, and participant concerns, such as sage-grouse use in burned landscapes, helped prioritize field sampling. Further, the resulting STM with multiple ecosystem services and spatially represented states is more likely to be accepted and used by local landowners and managers, who provided input and were informed during all steps of model development (Bruegger et al. 2016). The STM illustrates the services provided by every state and how management for only one state could be detrimental to other services or avifauna species. Local management efforts for sage-grouse populations and habitat should also be improved with a greater understanding of habitat needs for other sagebrush-associated species.

This approach of using a participatory process to build locally relevant STMs with multiple ecosystem services is novel (Bruegger et al. 2016), and as such, I learned several valuable lessons that could facilitate a smoother process for other researchers or managers who wish to undertake similar efforts. First, there must be a balance between the amount of landscape heterogeneity one wishes to include in a model and the resources available to fully capture that variability with adequate sample sizes for making inferences. Although it is recommended to include all sources of landscape variability within an ecological site to disentangle management history, soil-geomorphological properties, and climate (Bestelmeyer et al. 2009), it is not always possible to address this variability with adequate sampling effort. Therefore, one needs to prioritize variability in the area of interest, such as disturbed or re-seeded patches. Also, sampling efforts should be prioritized around stakeholders' main interests or questions in order

to adequately address these main concerns and provide locally relevant results. Otherwise, it is easy to lose focus and get distracted by new questions or lower priority concerns. To best determine wildlife abundance (or other ecosystem service) per state or community, the vegetation and soil sampling should precede other sampling efforts, like bird surveys (see Holmes and Miller 2010). This will help ensure an adequate number of sampling plots are distributed per state or community for drawing accurate conclusions about services provided (Holmes and Miller 2010). Lastly, to increase sampling efficiency and sample size, redundant indicators, such as basal gap and bare ground from line-point intercept (Herrick et al. 2005), should be discarded as soon as correlation between the indicators is suspected.

Future Research Needs

This dissertation represents new or improved approaches for management of sagebrush avifauna species and sagebrush rangelands. However, knowledge is never complete and management efforts can only be improved with further research. One natural extension would be to combine the efforts of chapters two and three and map the spatially explicit states with their predicted avifauna densities. This would illustrate potential densities within the entire study area for songbirds and sage-grouse pellets, the amount of high-quality versus low-quality habitat for each species, and connectivity of high-quality habitat. Managers could then predict how populations may change within the landscape if state transitions occur from fire or other drivers. To better evaluate the umbrella concept and incorporate avifauna habitat in STMs, future research efforts should also include measuring fitness (e.g., nest success) for each species and not just use or abundance. Similarly, rather than using sage-grouse pellets as a surrogate for habitat use, future efforts could radio-mark individual birds to gain a better understanding of habitat relationships and survival or reproductive output.

For the spatially represented states in the STM, local efforts could include ground truthing a random sample of pixels to verify the model's classification accuracy and increasing the sample size of crested wheatgrass plots to improve the accuracy for this particular state in the region. The spatial approach should also be applied in other sagebrush regions to verify its ease and applicability for land managers. Mapped states could further be combined with simulated state-and-transition modeling, so land managers could forecast potential state outcomes for various management actions or disturbances within a region. This exercise could guide iterative hypothesis-testing, model improvement, and decision-making within an adaptive management framework to solve complex ecosystem problems or increase the rigor behind transition probabilities.

LITERATURE CITED

- Aldridge, C.L., S.E. Hanser, S.E. Nielsen, M. Leu, B.S. Cade, D.J. Saher, and S.T. Knick. 2011. Detectability adjusted count models of songbird abundance. Pp 141-220 in Hanser, S.E., M. Leu, S.T. Knick, and C.L. Aldridge (editors). Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, KS, USA.
- Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, Jr., D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology and Management* 62:1–15.
- Bestelmeyer, B. T., D. P. Goolsby, and S. R. Archer. 2011. Spatial perspectives in state-and-transition models: a missing link to land management? *Journal of Applied Ecology* 48: 746–757.
- Boyd, C. S., D. D. Johnson, J. D. Kerby, T. J. Svejcar, and K. W. Davies. 2014. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? *Rangeland Ecology and Management* 67:358-368.
- Boyle, S., and D. R. Reeder. 2005. Colorado sagebrush: a conservation assessment and strategy. Colorado Division of Wildlife, Grand Junction, CO, USA.
- Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management* 58:1–10.
- Bruegger, R. A., M. E. Fernandez-Gimenez, C. Y. Tipton, J. M. Timmer, and C. L. Aldridge. 2016. Multi-stakeholder development of state-and-transition models: a case study from northwestern Colorado. *Rangelands*. doi: 10.1016/j.rala.2016.10.008.

- Connelly, J. W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines for management of sage grouse populations and habitat. *Wildlife Society Bulletin* 28:967–985.
- Herrick, J. E., J. W. Van Zee, K. M. Havstad, Burkett L. M., and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland and savanna ecosystems. USDA-Agricultural Research Service, Jornada Experimental Range, Las Cruces, USA.
- Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management* 69:638–649.
- Holmes, A. L., and R. F. Miller. 2010. State-and-transition models for assessing grasshopper sparrow habitat use. *Journal of Wildlife Management* 74:1834–1840.
- Kachergis, E. J., C. N. Knapp, M. E. Fernandez-Gimenez, J. P. Ritten, J. G. Pritchett, J. Parsons, W. Hibbs, and R. Roath. 2013. Tools for resilience management: multidisciplinary development of state-and-transition models for northwest Colorado. *Ecology and Society* <http://dx.doi.org/10.5751/ES-05805-180439>.
- Kirol, C. P., J. L. Beck, J. B. Dinkins, M. R. Conover. 2012. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. *The Condor* 114:75–89.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.
- Knick, S. T., J. T. Rotenberry, and M. Leu. 2008. Habitat, topographical, and geographical components structuring shrubsteppe bird communities. *Ecography* 31:389–400.
- Lukacs, P. M., A. Seglund, and S. Boyle. 2015. Effects of Gunnison sage-grouse habitat treatment efforts on associated avifauna and vegetation structure. *Avian Conservation and Ecology* 10(2):7. <http://dx.doi.org/10.5751/ACE-00799-100207>.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L.

- Hild, 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 in S. T. Knicks and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California-Press, Berkeley, USA.
- Roberge, J., and P. Angelstam, P. 2004. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18:76–85.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83:247-257.
- Steele, C. M., B. T. Bestelmeyer, L. M. Burkett, P. L. Smith, and S. Yanoff. 2012. Spatially explicit representation of state-and-transition models. *Rangeland Ecology and Management* 65:213-222.
- Tipton, C. Y. W. 2015. Improving state-and-transition models for management of sagebrush steppe ecosystems. Thesis, Colorado State University 160 p.
- Troy, A., and M. A. Wilson. 2006. Mapping ecosystem services: practical challenges and opportunities in linking GIS and value transfer. *Ecological Economics* 60:435-449.
- Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* 48:132-147.

APPENDIX I

Tipton (2015) differentiated two states and two community phases within one state based on multivariate techniques, and the vegetation clusters were most strongly associated with fire and seeding history. A needle-and-thread (*Hesperostipa comata*) shrubland phase contained cheatgrass (*Bromus tectorum*; average 13% cover), needle-and-thread grass (average 30% cover), and 4-36% cover of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). The diverse shrubland phase always contained antelope bitterbrush (*Purshia tridentata*; average 8% cover), Wyoming big sagebrush (average 25% cover), and green rabbitbrush (*Chrysothamnus viscidiflorus*; <5% cover). Tipton (2015) identified these two shrub-dominated clusters as community phases within one state due to low effect sizes between plant functional groups. However, we chose to classify them as states rather than community phases because some structural differences existed, such as taller shrubs on average in the diverse shrubland cluster (Tipton 2015). Further, the two shrubland clusters differed based on elevation, and this separation was potentially linked to management history differences occurring at low and high elevation (Tipton 2015). Antelope bitterbrush was found predominantly at the higher elevation sites. Local stakeholders observed that antelope bitterbrush historically occurred in the lower elevation sites, but declined over the last 50 years and is largely absent now. The higher elevation sites, where the diverse shrubland plots were most prevalent, lacked historic sheep grazing and experienced less elk browsing pressure during the winter. Even after several years without sheep grazing, antelope bitterbrush had not returned to the lower elevation sites, indicating that the needle-and-thread shrubland phase was likely a persistent state. However, it would require more targeted grazing exclosure experiments over long periods of time to thoroughly address these potential transition drivers.

The native grassland state contained western wheatgrass (*Pascopyrum smithii*; average 33% cover) and Sandberg bluegrass (*Poa secunda*; average 13% cover) with <5% shrub cover. The crested wheatgrass (*Agropyron cristatum*) state included plots dominated by the exotic grass (average 41% cover). Due to functional and structural differences, we divided this state into two community phases (Bestelmeyer et al. 2003): a shrub-dominated phase (average 22.5% shrub cover) and a grass-dominated phase (average <1% shrub cover). Both phases were seeded with crested wheatgrass as a homestead property or pipeline scar, but the grass-dominated phase experienced a wildfire in 2010.