To the University of Wyoming:

The members of the Committee approve the Dissertation of Kurt T. Smith presented on 11/29/2016.

Jeffrey L. Beck, Chairperson

Brian A. Mealor, External Department Member

Anna D. Chalfoun

Matthew J. Kauffman

Melanie A. Murphy

APPROVED:

Robert O. Hall, Director, Program in Ecology

Angela L. Hild, Interim Associate Vice President for Graduate Studies

Smith, Kurt, T., Ph.D., Identifying habitat quality and population response of greater sage-grouse to treated Wyoming big sagebrush habitats, Department of Ecosystem Science and Management, December, 2016.

Prioritizing and conserving habitat quality is crucial for maintaining viable wildlife populations, particularly for species of conservation concern such as the greater sage-grouse (*Centrocercus urophasianus*). Sage-grouse have experienced widespread population declines across much of their historic range, necessitating an understanding of how to maintain or improve the quality of remaining habitats that support their populations. Habitat loss and fragmentation is a major factor contributing to sage-grouse population declines and maintaining or improving remaining habitats has been thought to increase the value of important habitats for sage-grouse. The aim of my dissertation was to evaluate the influence of habitat management practices on sage-grouse at the population level and then explore potential mechanisms that may explain how populations are influenced by management to develop an understanding of the overall demographic response of sage-grouse to habitat treatments in big sagebrush (*Artemisia* spp.) communities in Wyoming. My dissertation is presented in four journal-formatted chapters. The objectives of Chapter 2 were to identify how treatments influenced annual growth rates in sage-grouse populations using yearly male sage-grouse lek counts within Sage-Grouse Management Zone II in Wyoming's Core Areas from 1994 to 2012. One of the major findings of Chapter 2 was that mechanical sagebrush restoration treatments within 10 km of leks were negatively associated with annual greater sage-grouse population growth rates. This chapter is formatted for *Restoration Ecology* with co-author Jeffrey L. Beck. The primary objective of Chapter 3 was to evaluate how microhabitat use differed between reproductive states (brood-rearing versus broodless females) and if there were differences in summer survival between these states. Findings suggested that broodless females were roosting and foraging in concealed habitats with greater visual

obstruction but less food forb availability. In contrast, brood-rearing females likely selected riskier microhabitats with less shrub cover and greater herbaceous understory as a tradeoff to predictably maximize foraging opportunities and promote growth and survival of their chicks. Chapter 3 is in revision in *Wildlife Research* with co-authors Jeffrey L. Beck and Christopher P. Kirol. The objective of Chapter 4 was to identify how mowing and tebuthiuron (Spike® 20P, Dow Agrosciences, Indianapolis, IN) treatments intended to reduce sagebrush canopy cover influenced the dietary quality of Wyoming big sagebrush in central Wyoming. Results from this chapter suggested that mowing and tebuthiuron treatments may slightly increase crude protein concentrations directly after treatments without immediate changes in plant secondary metabolites. This chapter is formatted for submission to *Rangeland Ecology and Management*. Chapter 5 evaluated whether diet availability and dietary consumption were predictive of sage-grouse chick body condition and if mowing and tebuthiuron treatments influenced the availability of insect and forb dietary resources for juvenile sage-grouse. Findings from this chapter suggest that females with broods selected habitats with diet resources in proportion to their availability, and dietary consumption by chicks was unrelated to available foods at brood-rearing locations. Chicks that consumed proportionally more plants during their first week of life tended to weigh more and have longer wing chords 5 weeks after hatch. Treated big sagebrush habitats contained forb and insect abundances that did not differ from untreated habitats and were equal to or less than habitats used by brood-rearing females. Chapter 5 is formatted for *Journal of Wildlife Management* with co-authors Jeffrey L. Beck, Aaron C. Pratt, and Jason R. LeVan.

IDENTIFYING HABITAT QUALITY AND POPULATION RESPONSE OF GREATER SAGE-GROUSE TO TREATED WYOMING BIG SAGEBRUSH HABITATS

By

Kurt T. Smith

A dissertation submitted to the Program in Ecology

And the University of Wyoming

In partial fulfillment of the requirements

For the degree of

DOCTORATE OF PHILOSPOPHY

In

ECOLOGY

Laramie, Wyoming

December 2016

COPYRIGHT PAGE

ACKNOWLEDGMENTS

I extend my sincere thanks to my graduate advisor Dr. Jeffrey Beck, for his continued guidance and support throughout my education at the University of Wyoming. Dr. Beck was essential in providing funding, equipment, and collaborations, and has greatly improved my writing abilities through his diligent efforts to improve proposals, reports, and manuscripts. Dr. Beck has given me many opportunities to research a variety of Wyoming's native fauna and our working relationship and friendship has resulted in continued research collaborations. I also thank Drs. Anna Chalfoun, Matthew Kauffman, Brian Mealor, and Melanie Murphy for serving on my graduate committee and providing support in conducting and writing my dissertation research. Their constructive criticisms taught me to think outside of the single species that my dissertation focuses on and greatly expanded my views of applied ecological research. Dr. Jennifer Forbey of Boise State University has been an excellent collaborator on our sagebrush nutritional quality analysis and I thank her along with Chelsea Merriman, Jacqueline Pena, and Naida Rizvic for their assistance with sampling design and sample analysis. Justin Borcherding, Travis Bryan, Luke Driessen, Meghan Karsh, Kierra Kauffman, Clara Laursen, Kirstie Lawson, Jason LeVan, Emily Mitchell, Jacob Pelham, Tyler Saltmer, Rebecca Shartau, Sam Stephens, Leif Wedul, and Meghan White served as valuable field technicians. Current and former graduate students Jason Carlisle, Beth Fitzpatrick, Christopher Kirol, Jason LeVan, Kaitlyn Taylor, and Amarina Wuenschel provided assistance with capturing grouse and aided in many facets of this research. I received a great deal of logistical support from Tom Christiansen, Stan Harter, Brian Parker, and Derrick Lemon from the Wyoming Game and Fish Department along with many others from the Department who assisted with implementing sagebrush treatments. Sue Oberlie and Tim Vosburgh from the Bureau of Land Management-Lander Field Office also served as valuable liaisons for our field project and conducted environmental assessments prior to treatment implementation. I thank Ag Flyers of Torrington, Wyoming for aerial tebuthiuron application and B & A leasing of Greybull, Wyoming for erecting fence exclosures. I also thank Brenna Marsicek, Alison Shaver, Kassandra Thomas, and Cindy Wood; their administrative efforts greatly simplified my graduate career. Many thanks to the students in Dr. Beck’s lab who provided personal and professional guidance throughout my time at the University of Wyoming.

TABLE OF CONTENTS

Contents

COPYRIGHT PAGE…...ii

ACKNOWLEDGMENTS…..iii

TABLE OF CONTENTS….v

LIST OF TABLES….vii

LIST OF FIGURES….x

CHAPTER ONE…..1

Introduction…..1

Literature Cited…6

CHAPTER TWO…...13

Sagebrush Restoration Treatments Depress Annual Population Growth Rates for Greater Sage-grouse…13

Introduction…14

Methods…..18

Results…22

Discussion…..25

Literature Cited…..29

CHAPTER THREE…...48

Reproductive State Leads to Intraspecific Habitat Partitioning and Fitness Tradeoffs in Greater Sage-grouse…...48

Introduction…49

Methods…..53

Results…59

Discussion…..61

Literature Cited…..66

CHAPTER FOUR……………………………………………………………………………..85

Effects of Mowing and Tebuthiuron Treatments on the Nutritional Quality of Sagebrush in Central Wyoming…………………………………………………………………...85

Introduction………………………………………………………………………………86

Methods…………………………………………………………………………………..89

Results……………………………………………………………………………………94

Discussion………………………………………………………………………………..96

Literature Cited…………………………………………………………………………100

CHAPTER FIVE…………………………………………………………………………….111

Reconstructing Greater Sage-grouse Chick Diets: Selection, Body Condition, and Diet Availability at Brood-Rearing and Altered habitats……………………………………111

Introduction……………………………………………………………………………..113

Methods…………………………………………………………………………………117

Results…………………………………………………………………………………..124

Discussion………………………………………………………………………………127

Literature Cited…………………………………………………………………………132

APPENDIX A……………………………………………………………………………..152

LIST OF TABLES

CHAPTER TWO

Table 1. Top and competing models within variable subsets and combined models explaining one-year time lags of sage-grouse annual population growth within Core Areas in Sage-grouse Management Zone II, Wyoming, USA, 1996–2012…………………………………………..43

Table 2. Top and competing models within variable subsets and combined models explaining three-year time lags of sage-grouse annual population growth within Core Areas in Sage-grouse Management Zone II, Wyoming, USA, 1998–2012…………………………………………..44

Table 3. Top and competing models within variable subsets and combined models explaining five-year time lags of sage-grouse annual population growth within Core Areas in Sage-grouse Management Zone II, Wyoming, USA, 2000–2012…………………………………………..45

Table 4. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) for top Generalized Estimating Equation models comparing one-year, three-year, and five-year lag effects of density dependence, precipitation, and habitat treatments on estimated greater sage-grouse annual population growth (r) in Core Areas of Sage-grouse Management Zone II. Models included main effects only……………………………………………………………46

CHAPTER THREE

Table 1. Variables used in model selection evaluating greater sage-grouse microhabitat selection in central Wyoming, USA, 2011–2013. Ground cover and herbaceous canopy cover were estimated from 17 Daubenmire (0.1 m^2) quadrats at each location. ……………………………78

Table 2. Top and competing ($w_i \geq 10\%$ of top model w_i) multinomial logistic regression models best explaining sage-grouse selection for early-brood, late-brood, and broodless female microhabitat in central Wyoming, USA, 2011–2013…………………………………………....79

Table 3. Parameter estimates with 90% confidence intervals (LCL and UCL) from top multinomial logistic regression model comparing sage-grouse early-brood, late-brood, and broodless female microhabitat selection relative to random habitats in central Wyoming, USA, 2011–2013……………………………………………………………………………..80

Table 4. Mean microhabitat characteristics and standard errors (in parenthesis) of sage-grouse early brood, late brood, broodless and random locations in central Wyoming, USA, 2011–2013………………………………………………………………………………………81

Table 5. Parameter estimates, risk ratios, and 90% confidence intervals (LCL and UCL) for variables that were used to assess adult female survival to 95 days in central Wyoming, 2011–2013………………………………………………………………………………………82

CHAPTER FIVE

Table 1. Top and competing models best explaining dietary resources at brood-rearing female sage-grouse locations in the Bighorn Basin and Jeffrey City study areas, Wyoming 2013–2015…..143

Table 2. Top and competing mixed-effects models evaluating the relationship between dietary consumption, estimated from feather $\partial^{15}N$, and dietary abundance at selected brood-rearing locations in the Bighorn Basin and Jeffrey City study areas, Wyoming 2013–2015…………..144

Table 3. Top and competing mixed-effects models evaluating the relationship between diet and age-corrected mass of greater sage-grouse chicks captured in Bighorn Basin and Jeffrey City study areas during 2013–2015, Wyoming, USA…………………………………………….145

Table 4. Top and competing mixed-effects models evaluating the relationship between diet and age-corrected wing chord length of greater sage-grouse chicks captured in Bighorn Basin and Jeffrey City study areas during 2013–2015, Wyoming……………………………………...146

Table 5. Mean (SE) forb and insect abundance (g DM/4 m^2) at treated (mow and tebuthiuron) and un-treated locations collected during 2014 and 2015 (Jeffrey City), and brood-rearing locations collected during 2013–2015 (Bighorn Basin and Jeffrey City), Wyoming, USA……147

LIST OF FIGURES

CHAPTER TWO

Figure 1. Map of the study area depicting vegetation treatments occurring from 1994–2012 in Wyoming's Core Areas within Sage-Grouse Management Zone II, Wyoming, USA…………..47

CHAPTER THREE

Figure 1. Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of big sagebrush density (A), variability in shrub cover (B), visual obstruction (C), forb species richness (D), and non-food forb cover (E) in central Wyoming, USA, 2011–2013……………………………………………………………………………...83

Figure 2. Hazard rates for the most supported model that included total reproductive effort (weeks) predicting adult female sage-grouse survival in central Wyoming, USA, 2011–2013. Hazard rates were plotted with 90% confidence intervals (hashed lines). ……………………...84

CHAPTER FOUR

Figure 1. Study area location map, Fremont and Natrona counties, Wyoming……..………….107

Figure 2. Example of the configuration of a subset of mowing treatments (grey) and two exclosures (hatched) where sagebrush leaves were sampled, Fremont County, Wyoming, 2013–2015……………………………………………………………………………………..108

Figure 3. Mean (± SE) crude protein (% dry matter), monoterpenes (AUC/mg), coumarins (umol/g), and total phenolics (umol/g) of sagebrush leaves in mowing (2013–2015) and control

(left column), and herbicide (2014–2015) and control (right column) exclosures. Asterisks indicate yearly differences between treatment and control plots ($P < 0.05$)…...........................109

Figure 4. Mean paired differences (± SE) in crude protein (% dry matter), monoterpenes (AUC/mg), coumarins (umol/g), and total phenolics (umol/g) in sagebrush leaves collected at mowing and herbicide treatment exclosures, 2014–2015. Asterisks indicate yearly differences between treatment types ($P < 0.05$)……………………………………………………….110

CHAPTER FIVE

Figure 1. Estimated proportion of plant diet with chick age (weeks 1–4 post hatch) from individual greater sage-grouse chicks captured in A) Bighorn Basin during 2013, and Jeffrey City study areas during B) 2013, C) 2014, and D) 2015. Squares indicate the mean and outer lines the range of values estimated from mixing models……………………………………….148

Figure 2. Relationship between feather ∂^{15}N during week 1 and A) age-corrected mass (g) and B) age-corrected wing chord length (mm) for individual chicks from Bighorn Basin ($n = 45$) and Jeffrey City ($n = 108$) study areas, Wyoming USA, 2013–2015……………………………….149

Figure 3**.** Mean forb and insect abundance (g dry mass; ± SE) at mowing, tebuthiuron, and un-treated locations sampled during 2014 and 2015, Jeffrey City study area, Wyoming, USA. Within each panel, means marked with the same letter are not different (Tukey’s HSD test, $P > 0.05$)……………………………………………………………………………………150

Figure 4. Mean forb and insect abundance (grams dry mass; ± SE) at locations used by brood-rearing females (2013–2015) in Bighorn Basin and Jeffrey City, and habitats treated with

mowing and tebuthiuron (2014–2015) in Jeffrey City (only), Wyoming, USA. Within each panel, means marked with the same letter are not different (Tukey's HSD test, P > 0.05)…………...151

CHAPTER ONE

Introduction

Prioritizing species conservation requires the identification of habitats for critical life stages in an animal’s annual life cycle. Habitats that have disproportionately high use by individuals are particularly important for species conservation. Habitat use alone, therefore, may not accurately reflect the importance of habitats, as species may utilize a range of habitat quality (Donovan and Thompson 2001) and understanding habitat use or occurrence may not accurately depict population fitness (Van Horne 1983, Johnson 2007, Chalfoun and Martin 2007). Therefore, identifying habitat quality requires an understanding of how habitat use relates to individual fitness (Van Horne 1983, Hall et al. 1997). Habitat quality can be conceptualized as the per capita influence of a habitat on population growth (Johnson 2007), providing a conservation framework for maintaining or improving crucial habitats.

While many studies focus on structural and compositional vegetation characteristics associated with animal habitat use, other features of habitat simultaneously influence selection (Jones 2001, Gaillard et al. 2010) such as individual behavioral strategies, forage quality and availability, predation risk, and competition. Incorporating behavior in studies of resource selection can potentially lead to new conclusions about habitat selection and behaviors associated with the process of selection. For example, behavioral differences leading to habitat partitioning between sexes of the same species is a widespread phenomenon across taxa, signifying the importance of understanding how life-history strategies are shaped to balance reproductive costs with survival (e.g., Blanco-Fontao et al. 2013). Forage quality may be directly linked to habitat preference (e.g., Frye et al. 2013), and may also influence early life development and lifetime reproductive success. The negative influence of nutritional deficiencies during ontogeny on fitness during adulthood has been demonstrated in several avian taxa (Lindstrom 1999, Metcalfe and Monaghen 2001). Both direct and indirect effects of predation can alter the behavior and resource allocation of prey species as they respond to risk stimuli (Laundre et al. 2010, Frid and Dill 2002). The information an animal uses to choose its environment, therefore, depends on its perceived availability to recognize important habitats to maximize their fitness. However, mismatches between perceived habitat preference and fitness appear rather common (Chalfoun and Schmidt 2012).

The influence of natural and anthropogenic disturbance to ecosystems and ecosystem processes has been a topic of interest among ecologists for many decades. Changes in disturbance regimes are one of several ways in which biodiversity and ecosystem dynamics are altered by humans (Yaffee 1999, White and Jentsch 2001). Anthropogenic land use activities have altered a significant portion of the planet's land surface (Foley et al. 2005) and may have lasting effects on ecosystem function. Disturbances can significantly alter the structure, composition, and function of ecosystems and habitats, and thereby influence species number, composition, and distribution (McIntyre and Hobbs 1999). Disturbances are a major driver of landscape spatial heterogeneity (Turner 1989) and may directly or indirectly influence habitat quality. Direct loss of important habitats may lead to reduction of habitat availability or indirectly through avoidance behaviors. Disturbances may also result in mismatching cues that animals use to perceive habitat quality, leading to maladaptive habitat selection (Patten and Kelly 2010). Because alteration of natural disturbance regimes may significantly influence species composition and diversity (Yaffee 1999), management practices that maintain plant community dynamics may be needed to maintain quality habitats for terrestrial fauna.

Wyoming big sagebrush (*A. tridentanta wyomingensis*) is the most widely distributed subspecies of big sagebrush in the sagebrush biome (Beetle 1960, Knick et al. 2003), where it is used as habitat by sagebrush-occurring wildlife (Knick et al. 2003, Larrucea and Brussard 2008). Mismanagement has degraded big sagebrush (*Artemisia tridentata* spp.) communities throughout the western United States, depleting herbaceous understory resources used by wildlife for food and cover (Knick et al. 2003, Davies et al. 2011). Wildfires, for example, have been suppressed across most human dominated landscapes. Fire control can often lead to an increase in the time interval and severity of natural fire events (Minnich and Chou 1997, Baker 2006). At higher elevation, infrequent fires in sagebrush habitats, partially affected by fire suppression, have enabled conifer encroachment, which may outcompete shrub and understory production and may result in declines in species diversity (Miller et al. 2000, Davies et al. 2011). Fine fuels from invasive exotic grass species have increased fire frequency in lower elevation sagebrush, which stimulates exotic annual grass monocultures that promote more frequent fire, impeding sagebrush reestablishment and creating a relatively homogenous landscape dominated by non-native vegetation (Davies et al. 2011). By conserving the natural pattern and successional stages of a community, organisms that have evolved with a similar disturbance interval are potentially able to utilize the structure and composition best suited for their persistence (Hobson and Schieck 1999). Vegetation treatments have been adopted by wildlife managers to improve habitats for various wildlife species (e.g., Hancock et al. 2011; Bergman et al. 2014; Dahlgren et al. 2015, Peters et al. 2015). In big sagebrush communities, treatments have been implemented to transition degraded communities to more desirable states by diversifying the age structure of sagebrush plants and increasing herbaceous production for livestock and wildlife (Davies et al. 2009, Beck et al. 2012). A particular need in evaluating treatments for wildlife is to examine effects of treatments on vital rates and population growth of focal species. Unfortunately, relatively little information exists on how sagebrush occurring wildlife populations respond to habitat treatments in big sagebrush habitats (Knick et al. 2003, Beck et al. 2012).

Greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘sage-grouse’) may serve as an ecological indicator of the health of sagebrush ecosystems because they require large landscapes and a diversity of sagebrush habitats to meet their life history requirements (Rich and Altman 2001, Rowland et al. 2006). Sage-grouse have experienced long-term declines across much of their range (Connelly and Braun 19997), with one estimate suggesting they occur in approximately 56% of their pre-settlement habitats (Schroeder et al. 2004). Declining sage-grouse populations are largely attributed to human-mediated loss and fragmentation of sagebrush habitats through agricultural development, energy development, urban and exurban development, livestock grazing, and fire (Connelly et al. 2004). As a result, sage-grouse have received unprecedented conservation efforts in recent years leading the U.S. Fish and Wildlife Service to determine that greater sage-grouse were not warranted for protection under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 2015). Wyoming’s Core Area policy was implemented to limit habitat loss and fragmentation in crucial breeding habitats across Wyoming (State of Wyoming Executive Order 2011) and Core Areas have potential to reduce long term population declines (Copeland et al. 2013). Mitigation practices that aim to improve habitat quality for sage-grouse are one potential way to prevent further declines (Doherty et al. 2010)

A developing body of research has incorporated both habitat selection and demographic rates (e.g., female survival, nest success, and brood success) to measure relative habitat quality for sage-grouse (Aldridge and Boyce 2007, Smith et al. 2014, Kirol et al. 2015). These studies provide important information about the quality of habitats and population level consequences for sage-grouse across large landscapes. Such studies often require a large investment of time, labor, and funding and are often not conducive to long-term monitoring of wildlife following natural or management directed changes in habitat quality across landscapes. Moreover, previous studies often focus on only cover as functional habitat and this does not always explain changes in habitat selection by wildlife. For example, dietary quality of sagebrush explained habitat selection by sage-grouse in Idaho (Frye et al. 2013). Future sage-grouse populations may experience loss of cover and food (Forbey et al. 2013), which may be influenced by management practices. While the structural response of habitats treated with the intent of benefiting sage-grouse populations are generally well known, there is a general lack of information available to understand how treatments influence the quality of sage-grouse habitats.

The aim of my dissertation research was to evaluate whether habitat treatments in big sagebrush elicited a population level response in sage-grouse, provide insights into how treating habitats for one life stage may have implications for individual sage-grouse across different reproductive states, and if habitat quality, measured through changes in nutritional quality of sagebrush and availability of important dietary components, was influenced by treatments. The objective of Chapter 2 was to identify how treatments influenced annual sage-grouse population growth within the Western Association of Fish and Wildlife Agencies Sage-Grouse Management Zone II in Wyoming's Core Areas from 1994–2012. The Objective of Chapter 3 was to evaluate how microhabitat use differed between reproductive states (brood-rearing and broodless females) and whether survival differences between these reproductive states could be attributed to differences in habitat use. Objectives of Chapter 4 were to identify how mechanical mowing and thinning with tebuthiuron treatments, two methods of sagebrush treatments that are commonly implemented to reduce sagebrush canopy cover, influenced the dietary quality of Wyoming big sagebrush in central Wyoming. The objectives of Chapter 5 were to evaluate whether diet availability and dietary consumption were predictive of sage-grouse chick body condition and if mowing and tebuthiuron treatments influenced diet availability for chick sage-grouse. Thus, it was my aim to evaluate the influence of habitat treatments on sage-grouse at the population level and then explore potential mechanisms that may explain how populations may be influenced by treatments to develop an understanding of the overall demographic response of greater sage-grouse to habitats treatments in big sagebrush communities in Wyoming. Appendix A outlines the approach to identify areas for and implement treatments.

LITERATURE CITED

Aldridge, C.L., and M.S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat based approach for endangered greater sage-grouse. Ecological Applications 17:508-526.

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. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management 65:444-455.

Beetle, A.A. 1960. A study of sagebrush-section Tridentatae of Artemisia: Wyoming Agricultural Experiment Station. Bulletin 368. University of Wyoming, Laramie, Wyoming, USA.

Bergman, E.J., C.J. Bishop, D.J. Freddy, G.C. White, P.F. Doherty, Jr. 2014. Habitat management influences overwinter survival of mule deer fawns in Colorado. Journal of Wildlife Management 78:448-455.

Blanco-Fontao, B., B.K. Sandercock, J.R. Obeso, L.B. McNew, and M. Quevedo. 2013. Effects of sexual dimorphism and landscape composition on the trophic behavior of greater prairie chicken. PLoS ONE 8:e79986.

Chalfoun, A.D., and K.A. Schmidt. 2012. Adaptive breeding=habitat selection: is it for the birds? Auk 129:589-599.

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.

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., S.T. Knick, M.A. Schroeder, and S.J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming.

Copeland, H.E., A. Pocewicz, D.E. Naugle, T. Griffiths, D. Keinath, J. Evans, and J. Platt. 2013. Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. PLoS One 8:e67261

Dahlgren, D.K., R.T. Larsen, R. Danvir, G. Wilson, E.T. Thacker, T.A. Black, D.E. Naugle, J.W. Connelly, and T.A. Messmer. 2015. Greater sage-grouse and range management: insights from a 25 year case study in Utah and Wyoming. Rangeland Ecology and Management 68:375-382.

Davies, K.W., J.D. Bates, D.D. Johnson, and A.M. Nafus. 2009. Influence of mowing *Artemisia tridentata* ssp. *wyomingensis* on winter habitat for wildlife. Environmental Management 44:84–92.

Davies, K.W., C.S. Boyd, J.L. Beck, J.D. Bates, T.J. Svejcar, and M.A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573-2584.

Doherty, K.E., D.E. Naugle, and J.S. Evans. 2010. A currency for offsetting energy development impacts: horse-trading sage-grouse on the open market. PLoS ONE 5:e10339.

Donovan, T.M., and F.R. Thompson III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds.

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, P.K. Snyder. 2005. Global consequences of land use. Science 309:570-574.

Forbey, J.S., N.L. Wiggins, G.G. Frye, and J.W. Connelly. 2013. Hungry grouse in a warming world: emerging risks from plant chemical defenses and climate change. Wildlife Biology 19:374-381.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Frye, G.G., J.W. Connelly, D.D. Musil, and J.S. Forbey. 2013. Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology 94:308-314.

Gaillard, J.M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B.V. Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B 365:2255-2265.

Hall, L.S., P.R. Krausman, and M.L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173-182.

Hancock, M.H., A. Amphlett, R. Proctor, D. Dugan, J. Willi, P. Harvey, and R.W. Summers. 2011. Burning and mowing as habitat management for capercaillie *Tetrao urogallus*: an experimental test. Forest Ecology and Management 262:509-521.

Hobson, K.A., and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects of 30 years. Ecological Applications 9:849-863.

Johnson, M.D. 2007. Measuring habitat quality: a review. Condor 109:489-504.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557-562.

Kirol, C.P., J.L. Beck, S.V. Huzurbazar, M.J. Holloran, and S.N. Miller. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:968-990.

Knick, S.T., D.S. Dobkin, J.T. Rotenberry, M.A. Schroeder, W.M. Vander Haegen, and C.V. Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Larrucea, E.S., and P.F. Brussard. 2008. Shift in location of pygmy rabbit (*Brachylagus idahoensis*) habitat in response to changing environments. Journal of Arid Environments 72:1636-1643.

Laundre, J.W., L. Hernandez, and W.J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. The Open Journal of Ecology 3:1-7.

Lindstrom, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology and Evolution 14:342-348

McIntyre, S., and R.J. Hobbs. 1999. A framework for conceptualizing human impacts on landscape and its relevance to management and research. Conservation Biology 13:1282-1292.

Metcalfe, N.B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution 16:254-260

Miller, R.F., T.J. Svejcar, and J.A. Rose. 2000. Impacts of western juniper on plant community composition and structure. Journal of Range Management 53:574-585.

Minnich, R.A., and Y.H. Chou. 1997. Wildland fire patch dynamics in the chaparral of southern California and northern Baja California. International Journal of Wildland Fire. 7:221-248.

Patten, M.A., and J.F. Kelly. 2010. Habitat selection and the perceptual trap. Ecological Applications 20:2148-2156.

Peters, D.C., J.M. Brooke, E.P. Tanner, A.M. Unger, P.D. Keyser, C.A. Harper, J.D. Clark, and J.J. Morgan. 2015. Impact of experimental habitat manipulation on northern bobwhite survival. Journal of Wildlife Management 79:605-617.

Rich, T., and B. Altman. 2001. Under the sage-grouse umbrella. Bird Conservation 14:10.

Rowland, M.M., M.J. Wisdom, L. Suring, and C.W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation 129:323-335.

Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, M.A. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363-376.

Smith, K.T., C.P. Kirol, J.L. Beck, and F.C. Blomquist. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:art15.

State of Wyoming. 2011. Greater sage-grouse core area protection. Office of the Governor, Executive Order Number 2011-5.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171-197.

U.S. Fish and Wildlife Service. 2015. Endangered and threatened wildlife and plants: 12 moth finding on a petition to list greater sage-grouse (*Centrocercus urophasianus*) as an endangered or threatened species. Federal Register 80:59858-59942.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

White, P.S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62:399-450.

Yaffee, S.L. 1999. Three faces of ecosystem management. Conservation Biology 13:713-725.

CHAPTER TWO

Sagebrush Restoration Treatments Depress Annual Population Growth Rates for Greater Sage-grouse

Kurt T. Smith and Jeffrey L. Beck
Department of Ecosystem Science and Management, College of Agriculture and Natural Resources, University of Wyoming, Dept. 3354,1000 E. University Ave., Laramie, Wyoming 82071, USA.

In the format for manuscripts submitted to *Restoration Ecology*

ABSTRACT

Vegetation restoration practices have been applied worldwide to enhance habitats for a variety of wildlife species. Big sagebrush (*Artemisia tridentata* spp.) communities, iconic to western North America, have been treated to restore herbaceous understory through chemical, mechanical, and prescribed burning practices to improve habitat conditions for greater sage-grouse (*Centrocercus urophasianus*) and other species. Although the response of structural attributes of sagebrush communities to treatments is well understood, there is a need to identify how treatments influence wildlife population dynamics. We investigated the influence of vegetation treatments occurring within Sage-Grouse Management Zone II in Wyoming's Core Areas from 1994–2012 on annual sage-grouse population growth using yearly male sage-grouse lek counts. We investigated this response across 1, 3, and 5-year post-treatment lags to evaluate how the amount of treated sagebrush communities and time since treatment influenced population growth, while accounting for climate, wildfire, and anthropogenic factors. We found that mechanical treatments were negatively associated with sage-grouse population growth in 1 and 5-year post-treatment lag models. Our work supports a growing body of research that advocates against treating big sagebrush habitats for sage-grouse, particularly in Wyoming big sagebrush (*A. t. wyomingensis*). Loss and fragmentation of sagebrush habitats has been identified as a significant threat for remaining sage-grouse populations. We recommend practitioners use caution when designing projects to alter remaining sagebrush habitats, especially when management is focused on habitat requirements for one life stage and a single species.

KEY WORDS: *Centrocercus urophasianus*, herbicide application, mechanical treatment, population growth, prescribed burning, wildfire

Implications for Practice

- Density dependence, well pad density, and wildfire were consistently predictive of annual sage-grouse population growth across 1, 3, and 5-year time lag models.
- Sagebrush restoration treatments were negatively associated with annual greater sage-grouse population growth rates across space and time.
- Area of mechanical treatments within 10 km of a lek and winter precipitation was negatively associated with population growth in 1-year time lag models. Winter precipitation reduced the negative association with population growth and mechanical treatments.
- Mechanical treatments within 10 km of a lek were negatively and fall precipitation was positively associated with population growth in 5-year lag models, respectively. Increased fall precipitation 1 year prior to lek counts reduced the negative association of mechanical treatments conducted 6 years prior.

Introduction

Habitat management practices that mimic natural disturbances are increasingly applied as conservation strategies to maintain or increase species diversity and abundance (Hunter 1993; Hobson & Schieck 1999; Franklin et al. 2002). Vegetation treatments have been implemented by wildlife managers to restore habitats for an array of wildlife species worldwide in attempts to shift plant communities to conditions thought to increase species abundance (e.g., Hancock et al. 2011; Bergman et al. 2014; Peters et al. 2015). Mismanagement has degraded big sagebrush

(*Artemisia tridentata* spp.) communities throughout the western United States, depleting herbaceous understory resources used by wildlife for food and cover (Knick et al. 2003; Davies et al. 2011). Treatments have been implemented to transition degraded big sagebrush communities to more desirable states by diversifying the age structure of sagebrush plants and increase herbaceous production for livestock and wildlife (Perryman et al. 2002; Dahlgren et al. 2006; Davies et al. 2009, 2011; Beck et al. 2012; Davies et al. 2012a,b). Treatments in Wyoming big sagebrush (*A. t. wyomingensis*) often result in increased total herbaceous cover (Lesica et al. 2007; Payton et al. 2011; Davies et al. 2012a), but perennial forb abundance exhibits little difference between treatments and reference areas 1-to-5 years following treatments (Fischer et al. 1996; Nelle et al. 2000; Davies et al. 2007; Payton et al. 2011; Davies et al. 2012a; Davies & Bates 2014). Forb abundance may increase in mountain big sagebrush (*A. t. vaseyana*) communities following treatment (Dahlgren et al. 2006; Davies et al. 2012b) and desired sagebrush states are more likely to be achieved in these more productive habitats following treatment. State and transition models are often employed to predict how sites in sagebrush will respond to treatments (Pyke 2011; Boyd et al. 2014; Pyke et al. 2015); however, many degraded sagebrush systems may have passed a threshold, where management actions are unlikely to achieve desirable effects (Pyke 2011; Davies et al. 2012a). As such, clear definitions and goals need be applied to restoration practices to identify appropriate indicators of restoration success (Wortley et al. 2013).

Evaluation of restoration success often includes measures such as vegetation change or increased abundance of targeted wildlife species which are often inadequate surrogates for demographic response of wildlife to vegetation treatments (Block et al. 2001; Bergman et al. 2015). A particular need in evaluating treatments for wildlife is to examine effects of treatment on vital rates and population growth of focal species. Unfortunately, relatively little information exists on how sagebrush-occurring wildlife populations respond to habitat treatments in big sagebrush habitats (Knick et al. 2003; Beck et al. 2012; but see Bergman et al. 2014; Dahlgren et al. 2016). Greater sage-grouse (*Centrocercus urophasianus*) have received unprecedented conservation efforts in recent years leading the U.S. Fish and Wildlife Service to determine that greater sage-grouse (hereafter 'sage-grouse') were not warranted for protection under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 2015). In Wyoming, the Core Area policy was implemented in 2008 to limit habitat loss and fragmentation in areas of high sage-grouse population densities in crucial breeding habitats (State of Wyoming Executive Order 2011). Core Areas may reduce projected long term sage-grouse declines (Copeland et al. 2013) and suggest that mitigation practices have potential to prevent further declines (Doherty et al. 2010a). Treating sage-grouse habitats is one form of mitigation thought to improve important food resources for adult and chick sage-grouse during the breeding season, potentially supplementing local populations and offsetting declines in more disturbed habitats.

For treatments to increase sage-grouse populations, habitat conditions must improve survival of females, their nests, and chicks, or a combination of these important vital rates. Female survival is among the most influential vital rates for sage-grouse populations, yet process variation in adult female survival is lower than nesting success or chick survival (Johnson & Braun 2009; Taylor et al. 2012). Vital rates most influential of population change often have lower temporal variability and may not be readily influenced by management actions (Mills et al. 1999; Raithel et al. 2007). Improved foraging resources in treated habitats adjacent to intact nesting cover could potentially improve availability of important nutritional resources for females during the pre-laying period, which may benefit reproduction (Barnett & Crawford 1994; Dunbar et al.

2005; Gregg et al. 2006). During early brood-rearing, brooding females select intermediate sagebrush cover with greater herbaceous understories compared to available habitats (Sveum et al. 1998; Connelly et al. 2000; Bunnell et al. 2004; Hagen et al. 2007; Doherty et al. 2010b). Brood-rearing females may utilize treated areas in close proximity to edges of intact sagebrush habitats (Dahlgren et al. 2006); however, abundance of critical insect and forb foods often does not exhibit positive response following treatments in Wyoming big sagebrush (Fischer et al. 1996; Nelle et al. 2000; Davies et al. 2007; Rhodes et al. 2010; Davies et al. 2012a; Hess & Beck 2012a; Hess & Beck 2014).

Sagebrush communities recover slowly following disturbances (e.g., Beck et al. 2009; Baker 2011; Hess & Beck 2012a), making it difficult to estimate demographic responses in sage-grouse populations without evaluating long-term associations between population trends and habitat conditions. We used a retrospective study to evaluate sage-grouse population response to sagebrush reduction treatments occurring across different spatial and temporal scales in Wyoming. The objective of our study was to determine if treatments intended to improve herbaceous understories in sagebrush influenced annual sage-grouse population growth rates. We thus evaluated annual population growth of male sage-grouse using lek censuses across a range of vegetation treatments occurring in Wyoming from 1994–2012, while accounting for environmental and anthropogenic factors that have been previously shown to influence sage-grouse populations. Sage-grouse congregate at leks (i.e., communal breeding or strutting grounds) in spring, providing opportunities to estimate relative sage-grouse population abundance (Connelly et al. 2004; Johnson & Rowland 2007), which have been used to assess changes in populations across landscapes influenced by factors such as energy development and wildfire (Walker et al. 2007; Harju et al. 2010; Holloran et al. 2010; Blomberg et al. 2012; Gregory & Beck 2014; Coates et al. 2015).

Methods

Study Area

Our study occurred in Sage-Grouse Core Areas within the Wyoming portion of the Western Association of Fish and Wildlife Agencies Wyoming Basins Sage-Grouse Management Zone II; (MZ II; Stiver et al. 2006; Figure 1). This area encompassed all or portions of 25 (~81%) of Wyoming's 31 Core Areas. We restricted our analyses to this area because data collected on treatments were limited to Core Areas (described below), evidence suggests that sage-grouse populations respond differently to energy development (and conceivably other habitat alterations) between Sage-Grouse Management Zones I and II within Wyoming (Doherty et al. 2010a; Gamo and Beck 2017), and treatments are generally not recommended in Sage-Grouse Management Zone I due to limited big sagebrush cover (WGFD 2011). Our study area encompassed 50,957 km^2 and individual Core Areas ranged in size from 41 to 18,567 km^2. The region was dominated by Wyoming big sagebrush communities interspersed with black sagebrush (*A. nova*) and low sagebrush (*A. arbuscula*), with communities of mountain big sagebrush at higher elevations (Rowland & Leu 2011; Knight et al. 2014).

Lek Count Data

We used maximum male lek count data from the Wyoming Game and Fish Department (WGFD) annual sage-grouse lek survey database from 1995 to 2012 to assess population growth in response to treatments occurring from 1994 to 2012. Annual counts of male sage-grouse attending leks are performed range-wide by state and provincial wildlife agencies and provide estimates of relative population abundance when conducted across sufficient spatial and temporal scales (Reese & Bowyer 2007; Fedy & Aldridge 2011; Blomberg et al. 2013). We followed WGFD definitions to classify leks as occupied or unoccupied (WGFD Sage-grouse definitions 2010) and restricted leks to Wyoming's Core Areas within Sage-Grouse MZ II to match the extent of vegetation treatment data. In addition, we removed consecutive annual lek counts of zero to minimize spurious estimates of no population change when zero males were present (*see* Coates et al. 2015). We estimated intrinsic annual rate of change for each lek, with the form:

$$r_{it} = \ln[\mathrm{N}_{it}] - \ln[\mathrm{N}_{it-1}]$$

Where N was the maximum male lek count at lek i, during year t. We added a constant of 0.1 to all lek counts when no males were recorded to avoid zero counts (Coates et al. 2015). We refer to this metric of intrinsic annual rate of change as population growth.

Predictor Variables

We assessed the influence of density dependence on population change with Gompertz methods. Gompertz density dependence estimates population change with logarithmic abundance (Dennis et al. 2006). We evaluated Gompertz density dependence with no time lag ($\ln[\mathrm{N}_t]$) and one-year time lags ($\ln[\mathrm{N}_{t-1}]$) as these have been supported in regional sage-grouse population growth models (Garton et al. 2011; Coates et al. 2015; Garton et al. 2015).

To account for potential confounding effects of anthropogenic disturbance, we obtained well data from the Wyoming Oil and Gas Conservation Commission from 1995 through 2012 and used spud date to determine the year when drilling began (WOGCC 2012). We obtained monthly precipitation data from 1994 through 2012 (4 km resolution; PRISM Climate Group 2016) to account for precipitation on annual population growth. We estimated annual, spring (Mar–May), summer (Jun–Aug), fall (Sep–Nov), and winter (Dec–Feb) precipitation by aggregating monthly precipitation estimates.

Sagebrush treatments and wildfire occurring from 1994 to 2012 in sage-grouse Core Areas were compiled by the WGFD and the Conservation Research Center of Teton Science School (CRCTSS 2012). Treatments were defined as activities that reduced sagebrush canopy cover in sage-grouse habitats of 0.4 ha or larger and included chemical applications (2,4-D and tebuthiuron), mechanical thinning (mowing and mastication), and prescribed burning. Wildfires were defined similarly when their spatial footprints were 0.4 ha or larger. Treatment polygons were originally clipped to state or federally administered lands; we obtained raw treatment data and followed methods of CRCTSS (2012) to include treatments and wildfires that occurred on private lands. We used the Monitoring Trends in Burn Severity database to include any wildfires that were not included in the CRCTSS dataset during the same time period (Eidenshink et al. 2007). We classified treatments into 4 categories: chemical, mechanical, prescribed fire, and cumulative (total) treatments. We calculated the total area of treatments and wildfires within circular analysis regions around each lek (scales described below). In some cases, treatments or wildfire occurred across the same spatial footprint during subsequent years. For example, a theoretical treatment occurred during 1994 and was followed by another treatment that covered a portion of the previous treatment footprint in 1996. In these instances, treatments or wildfire were reclassified to reflect the most recent treatment or wildfire following its implementation. The original treatment or wildfire was maintained, but truncated to reflect the remaining area that was not influenced by the most recent activity.

Data Analysis

We modeled population growth with generalized estimating equations (GEE) using package 'geepack' in R (Yan 2002; Yan & Fine 2004; Hojsgaard et al. 2006; R Development Core Team 2015), where we assigned individual leks to clusters with an autoregressive correlation structure appropriate for longitudinal data (Wang & Carey 2003). Annual rate of change followed a normal distribution. Previous studies have demonstrated that male lek attendance and persistence may be influenced by environmental and anthropogenic activities across a range of scales in proximity to leks and population responses often exhibit lag temporal effects following development (Walker et al. 2007; Harju et al. 2010; Holloran et al. 2010; Gregory & Beck 2014)—we thus reasoned that sage-grouse populations may respond similarly to habitat treatments. To assess scales and lag effects, we evaluated the area of habitat treatments and wildfires within 1.0, 2.5, 5.0, 6.4, 8.4, and 10.0 km radii scales around leks to build three separate models assessing 1, 3, and 5-year time lags. We included well pad density (number of wells/km^2) within the intermediate scale (5.0 km) of each lek for all wells present during year t-1 in all models. The resolution of precipitation data (4 km) did not allow us to precisely match these scales, therefore we evaluated precipitation at the raster cell containing the lek (cell), at approximately 5 km around each lek (5 km scale), and approximately 10 km around each lek (10 km scale), during year t-1 in all models. We estimated time lags in response to vegetation treatments and wildfire by allowing at least one full growing season following implementation of treatments. For example, we evaluated a 1-year time lag for population growth in response to treatments that occurred 2 years prior to Nt. We used a sequential approach with the Quasi-likelihood information criterion (QIC; Pan 2001; Burnham & Anderson 2002) to evaluate predictor variables within variable subsets.

Well density, precipitation, wildfire, and treatment variables were centered and Z-transformed to facilitate direct comparison between variables and ensure model convergence (Becker et al. 1988). For each lag model, we carried forward the Gompertz density dependence (no lag or 1-year lag) with the most model support and well density variable if univariate models had QIC values lower than the null model and 85% confidence intervals of parameter estimates did not overlap zero (Arnold 2010). We performed variable screening for precipitation, wildfire, and treatment models by determining the most predictive of the three analysis scales for precipitation variables and the most predictive of the six analysis scales for wildfire and treatment variables by retaining the scale with the lowest QIC value when 85% confidence intervals did not overlap zero. We assessed both linear and quadratic effects for wildlife and treatment variables. The most supported scale for area of wildfire was brought forward to final modelling. For remaining precipitation and treatment variables, we retained the variable with the lowest QIC value if correlation coefficients $|r| \geq 0.6$. We brought forward remaining variables within each variable subset if model support indicated an improvement over the null model. Remaining variables within each subset were combined to assess model improvement relative to the best Gompertz density dependence only model. Models within 4 QIC of the Gompertz density dependence only model were considered competitive (Arnold 2010). We performed post-hoc evaluation of final lag models to evaluate possible interactions between precipitation and treatment variables.

Results

Approximately 3% (1,511 km^2) of our 50,957 km^2 study area was treated from 1994–2012; 270 km^2 (17.8% of total area treated) were treated with chemical applications, mechanical treatments occurred across 196 km^2 (13.0% of total), and 1045 km^2 (69.2% of total) were treated with prescribed fire. In addition, wildfire occurred across 676 km^2 (30.9% of total) of sagebrush habitats from 1994–2012. Treatments occurred at elevations ranging from 1304 to 2657 m, and average treatment size was 1.3 ± 0.2 km^2 (range: 0.004 to 197 km^2). Our 1-year lag models included 8,293 estimates of population growth from 945 leks from 1996–2012. We modeled population growth with 7,779 estimates from 942 leks from 1998–2012 in 3-year lag models and used 7,180 estimates of population growth from 936 leks during 2000–2012 in 5-year lag models.

In all models, Gompertz with no time lag received the most support describing density dependence and was carried forward (Tables 1–4). For the 1-year time lag model, well pad density, summer precipitation, winter precipitation within 10 km, wildfire within 8.4 km, and chemical and mechanical treatments with 10 km were brought forward to final modelling (Table 1). The final model was 55.53 QIC points lower than the Gompertz only model. Well pad density was negatively associated with population growth ($\hat{\beta}_1$ = -0.043 ± 0.017 SE). Summer ($\hat{\beta}_1$ = -0.015 ± 0.017 SE) and winter precipitation ($\hat{\beta}_1$ = -0.043 ± 0.020 SE) were also negatively associated with population growth; however, 85% confidence intervals around the parameter estimate for summer precipitation included zero. Wildfire within 8.4 km ($\hat{\beta}_1$ = -0.052 ± 0.013 SE) and mechanical treatments within 10 km ($\hat{\beta}_1$ = -0.034 ± 0.016 SE) were negative predictors of population growth, whereas chemical treatments within 10 km were positively associated with population growth ($\hat{\beta}_1$ = 0.009 ± 0.017 SE); however, chemical treatments were considered uninformative variables because 85% confidence intervals around the parameter estimate included zero. We found support for a positive relationship between mechanical treatments with 10 km and winter precipitation ($\hat{\beta}_1$ = 0.074 ± 0.044 SE) indicating that population growth was less sensitive to mechanical treatments occurring 2 years prior to the current years population growth estimate when winter precipitation was greater during the previous winter.

For the final 3-year time lag model, well pad density, fall precipitation, wildfires within 10 km and mechanical treatments (quadratic effect) within 1 km were brought forward to final modeling (Table 2). The final model was 68.32 QIC points lower than the Gompertz only model. Well pad density was negatively associated with population growth ($\hat{\beta}_1$ = -0.049 ± 0.015 SE) and fall precipitation was positively associated with population growth ($\hat{\beta}_1$ = 0.014 ± 0.018 SE); however 85% confidence intervals of the parameter estimate for fall precipitation overlapped zero. Wildfire within 10 km ($\hat{\beta}_1$ = -0.070 ± 0.016 SE) and mechanical treatments within 1 km ($\hat{\beta}_1$ = -0.063 ± 0.059 SE; quadratic term, $\hat{\beta}_1$ = 0.001 ± 0.004 SE) were negatively associated with population growth. Confidence intervals for the parameter estimate of mechanical treatments within 1 km overlapped zero, however. We found no support for interactive effects between mechanical treatments and fall precipitation.

Variables in the final 5-year time lag model included well pad density, fall precipitation within 5 km, spring precipitation, wildfire within 8.4 km, and mechanical treatments within 10 km. The final model was 100.44 QIC points lower than the Gompertz only model (Table 3). Well pad density was negatively associated with population growth ($\hat{\beta}_1$ = -0.052 ± 0.016 SE). Spring precipitation was negatively associated with population growth ($\hat{\beta}_1$ = -0.078 ± 0.017 SE), whereas fall precipitation within 10 km was positively associated with population growth ($\hat{\beta}_1$ = 0.035 ± 0.018 SE). We found negative associations with wildfire within 8.4 km ($\hat{\beta}_1$ = -0.071 ± 0.019 SE) and mechanical treatments ($\hat{\beta}_1$ = -0.034 ± 0.018 SE) in the 5-year time lag model.

We found support for a positive interaction between mechanical treatments within 10 km and spring precipitation ($\hat{\beta}_1 = 0.0424 \pm 0.013$ SE, $P = 0.001$) indicating that population growth was less sensitive to mechanical treatments occurring 6 years prior to the current years population growth estimate when spring precipitation was greater during the previous year.

Discussion

The primary objective of our study was to evaluate how sagebrush treatments influenced annual sage-grouse population growth rates. We found negative association between the amount of mechanically treated sagebrush within 10 km and sage-grouse population growth in our 1 and 5-year lag models. While we lacked fine scale demographic information to identify specific mechanisms to support our findings, annual counts provide suitable estimates to track trends in abundance through time (Connelly et al. 2004; Johnson & Rowland 2007).

Studies that have evaluated sage-grouse response to treatments in Wyoming big sagebrush have reported mixed results (see Beck et al. 2012). For instance, Connelly et al. (2000a) found a reduction in male lek attendance 1-to-5 years after prescribed burning in Wyoming big sagebrush habitats in the Big Desert of southeastern Idaho. Fischer et al. (1996) found similar sage-grouse abundance on burned and unburned areas in Wyoming big sagebrush in the same study area 1-to-3 years after burning. In contrast, sage-grouse pellet densities were higher in tebuthiuron treated sites relative to mechanical treatments or control areas in mountain big sagebrush in south-central Utah (Dahlgren et al. 2006). Dahlgren et al. (2006) attributed increased use of tebuthiuron treated sites by sage-grouse to increased forb production; however, shrub cover was still relatively high in treated sites (~20%). Furthermore, some evidence exists for increased male lek counts associated with small treatments (< 200 ha) in high elevation mountain big sagebrush communities compared to leks in surrounding areas (Dahlgren et al. 2015).

We incorporated demographic factors (density dependence), environmental conditions (precipitation and wildfire), and anthropogenic disturbance (well pad density) to account for factors that have been attributed to sage-grouse population dynamics previously. Density dependence was consistently supported in all models. The influence of density dependence on sage-grouse population growth has been reported by other studies using annual male sage-grouse lek counts (Garton et al. 2011; Coates et al. 2015; Garton et al. 2015). Precipitation was also consistently associated with population growth; however, the main effect of precipitation received little model support with the exception of our 1 and 5-year lag models. Precipitation positively influences population growth and individual vital rates (Blomberg et al. 2012; Blomberg et al. 2013; Guttery et al. 2013; Caudill et al. 2014). Annual climate partially drives herbaceous production in sagebrush communities (Noy-Meir 1973) and insect abundance is positively associated with increased herbaceous production (Wenninger & Inouye 2008), suggesting bottom-up processes likely influence yearly forage availability and security cover that may influence sage-grouse reproductive success (Blomberg et al. 2012; Guttery et al. 2013). We found that winter precipitation was negatively and fall precipitation was positively associated with population growth in our 1-year and 5-year lag models, respectively. We found consistent support that well pad density and wildfire were negatively associated with population growth in all models. These findings corroborate a large body of research reporting negative sage-grouse response to anthropogenic development (Walker et al. 2007; Doherty et al. 2010a; Harju et al.

2010; Holloran et al. 2010; Gregory & Beck 2014), wildfire (Blomberg et al. 2012; Coates et al. 2015), or both (Hess & Beck 2014b).

Myriad studies have demonstrated the importance of structural cover of sagebrush communities used yearlong by sage-grouse to provide concealment cover (Schroeder et al. 1999; Gregg & Crawford 2009; Kirol et al. 2012; Dinkins et al. 2016) as well as meeting the nutritional requirements of adults and chicks (Johnson & Boyce 1990; Barnett & Crawford 1994). Because sagebrush treatments typically reduce sagebrush cover and height to levels lower than sage-grouse use for nesting or roosting sites (Connelly et al. 2000b; Hess & Beck 2012a), treated habitats may only serve to improve foraging opportunities for sage-grouse until treated sagebrush recovers to sufficient levels to provide cover. If herbaceous production is limiting sage-grouse populations, benefits of vegetation treatments may be achieved if treatments provide increased foraging opportunities while concurrently maintaining landscapes of suitable and intact sagebrush structural cover important for sage-grouse seasonal habitats. However, the juxtaposition and variability of unaltered sagebrush habitats often meet guidelines for sage-grouse habitats (i.e., Doherty et al. 2010b). Our results indicated that mechanical treatments negatively influence annual sage-grouse population growth up to 6 years following treatments, but increased winter or fall precipitation may function to offset the negative response to treatments. If vegetation treatments near leks result in functional habitat loss, it is conceivable that both juvenile males and females may be less likely to establish breeding territories near leks with greater amounts of treatments (e.g. Holloran et al. 2010).

Restoration practices must align with localized threats influencing wildlife populations (e.g., Barnas et al. 2015) and determine if practical solutions can be afforded to sage-grouse populations through management actions (Boyd et al. 2014). Some evidence suggests that small scale treatments in mountain big sagebrush communities may benefit breeding habitats for sage-grouse (Dahlgren et al. 2006; Dahlgren et al. 2015), yet little support exists for treatments in Wyoming big sagebrush communities (Beck et al. 2012). Further research is needed to identify the mechanisms associated with habitat use and demographic responses of sage-grouse to these habitat manipulations. Nevertheless, a lack of vegetative response following treatments, particularly Wyoming big sagebrush communities, dictates that sound science and precautionary principles (Myers 1993; Connelly 2013) be applied when determining if treatments are warranted in the future. Loss and fragmentation of sagebrush habitats has been identified as a significant threat for remaining sage-grouse populations (Knick et al. 2003). Because sagebrush habitats recover slowly following disturbance and limited evidence suggests that habitat treatments improve herbaceous understories important for sage-grouse during the breeding season, we recommend that managers take caution when designing studies to alter intact sagebrush habitats, particularly when management is focused on habitat requirements for one life stage (Dahlgren et al. 2006; Doherty et al. 2010b; Taylor et al. 2012).

There is a need to evaluate and assess the single-species management approach that has been applied to sage-grouse conservation. Short term benefits to sage-grouse populations do not necessarily provide long term solutions that could potentially be afforded by more ecosystem focused conservation strategies (e.g., Boyd et al. 2014). In Wyoming, sagebrush rangelands provide habitats to nearly 450 avian, mammalian, herptile, and fish species (WGFD 2010) and many of these species could be influenced by treatments designed for sage-grouse habitat restoration. Sage-grouse may serve as an umbrella species for many sagebrush occurring wildlife species (Rich & Altman 2001; Rowland et al. 2006; Gamo et al. 2013; Copeland et al. 2014); therefore, management practices targeting sage-grouse should not negatively affect other sagebrush occurring species (Rowland et al. 2006). Disturbance is a natural process in sagebrush communities and current fire rotations are shorter than historic levels (Bukowski & Baker 2013), creating mosaics of successional sagebrush. Efforts to maintain large, continuous sagebrush landscapes provides a more ecosystem level approach for maintaining sagebrush habitats and will likely be more beneficial to sage-grouse and other sagebrush occurring wildlife in the future.

Acknowledgments

The authors thank the Wyoming Sage-Grouse Conservation Fund of the Wyoming Game and Fish Department; Bates Hole/Shirley Basin, Big Horn Basin, Southwest, Southcentral, and Wind River/Sweetwater River Local Sage-Grouse Working Groups; the Margaret and Sam Kelly Ornithological Research Fund; and the Wyoming Wildlife and Natural Resource Trust for funding support. We thank WGFD (T. Christiansen), Wyoming Geographic Science Center (N. Graff), and CRCTSS (M. Graham) for providing data. This material is based upon work supported by the University of Wyoming, Wyoming Reclamation and Restoration Center through its Graduate Assistantship program.

LITERATURE CITED

Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178

Baker WL (2011) Pre-Euro-American and recent fire in sagebrush ecosystems. Pages 185-201 In: Knick ST, Connelly JW (eds) Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press Berkeley, California

Barnas KA, Katz SL, Hamm DE, Diaz MC, Jordan CE (2015) Is habitat restoration targeting relevant ecological needs for endangered species? Using Pacific salmon as a case study. Ecosphere 6:Art110

Barnett JK, Crawford JA (1994) Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range management 47:114-118

Beck JL, Connelly JW, Reese KP (2009) Recovery of greater sage-grouse habitat features in Wyoming big sagebrush following prescribed fire. Restoration Ecology 17:392-403

Beck JL, Connelly JW, Wambolt CL (2012) Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management 65:444-455

Becker RA, Chambers JM, Wilks AR (1988) The new S language: A programming environment for data analysis and graphics. Wadsworth and Brooks Cole. Belmont, California

Bergman EJ, Bishop CJ, Freddy DJ, White GC, Doherty PF, Jr. (2014) Habitat management influences overwinter survival of mule deer fawns in Colorado. Journal of Wildlife Management 78:448-455

Bergman EJ, Doherty PF, Jr., White GC, Freddy DJ (2015) Habitat and herbivore density: response of mule deer to habitat management. Journal of Wildlife Management 79:60-68

Block WM, Franklin AB, Ward JP, Ganey JI, White GC (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. Restoration Ecology 9:292-303

Blomberg EJ, Sedinger JS, Atamian MT, Nonne DV (2012) Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3: art55

Blomberg EJ, Sedinger JS, Nonne DV, Atamian MT (2013) Annual male lek attendance influences count-based population indices of greater sage-grouse. Journal of Wildlife Management 77:1583-1592

Boyd CS, Johnson DD, Kerby JD, Svejcar TJ, Davies KW (2014) Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? Rangeland Ecology and Management 67:358-368

Bukowski BE, Baker WL (2013) historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. Ecological Applications 23:546-564

Bunnell KD, Flinders JT, Mitchell DC, Warder JH (2004) Occupied and unoccupied sage grouse habitat in Strawberry Valley, Utah. Journal of Range Management 57:524-531

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York

Caudill D, Guttery MR, Bibles B, Messmer TA, Caudill G, Leone E, Dahlgren DK, Chi R (2014) Effects of climatic variation and reproductive trade-offs vary by measure of reproductive effort in greater sage-grouse. Ecosphere 5:art154

Coates PS, Ricca MA, Prochazka BG, Doherty KE, Brooks ML, Casazza ML (2015) Long-term effects of wildfire on greater sage-grouse-integrating population and ecosystem concepts for management in the Great Basin: U.S. Geological Survey Open File Report 2015-1165

Connelly JW (2013) Federal agency responses to greater sage-grouse and the ESA: getting nowhere fast. Northwest Science 88:61-64

Connelly JW, Knick ST, Schroeder MA, Stiver SJ (2004) Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming

Connelly JW, Reese KP, Fischer RA, Wakkinen WL (2000a) Response of a sage grouse breeding population to fire in southeastern Idaho. Wildlife Society Bulletin 28:90-96

Connelly JW, Schroeder MA, Sands AR, Braun CE (2000b) Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985

[CRCTSS] Conservation Research Center of Teton Science Schools (2012) Wyoming Sagebrush disturbance in greater sage-grouse Core Areas (1994-Present). ESRI ArcGIS Geodatabase Polygon Feature Class. Jackson, Wyoming. Wyoming Game and Fish Department

Copeland HE, Pocewicz A, Naugle DE, Griffiths T, Keinath D, Evans J, Platt J (2013) Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. PLoS One: 8:e67261

Copeland HE, Sawyer H, Monteith KL, Naugle DE, Pocewicz A, Graf N, Kauffman MJ. 2014. Conserving migratory mule deer through the umbrella of sage-grouse. Ecosphere 5:art117

Dahlgren DK, Chi R, Messmer TA (2006) Greater sage-grouse response to sagebrush management in Utah. Wildlife Society Bulletin 34:975-985

Dahlgren DK, Larsen RT, Danvir R, Wilson G, Thacker ET, Black TA, Naugle DE, Connelly JW, Messmer TA (2015) Greater sage-grouse and range management: insights from a 25 year case study in Utah and Wyoming. Rangeland Ecology and Management 68:375-382

Dahlgren DK, Guttery MR, Messmer TA, Caudill D, Elmore RD, Chi R, Koons DN (2016) Evaluating vital rate contributions to greater sage-grouse population dynamics to inform conservation. Ecosphere 7:e01249

Davies KW, Bates JD (2014) Attempting to restore herbaceous understories in Wyoming big sagebrush communities with mowing and seeding. Restoration Ecology 22:608-615

Davies KW, Bates JD (2010) Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the norther Great Basin. Rangeland Ecology and Management 63:461-466

Davies KW, Bates JD, Johnson DD, Nafus AM (2009) Influence of mowing *Artemisia tridentata* ssp. *wyomingensis* on winter habitat for wildlife. Environmental Management 44:84-92

Davies KW, Bates JD, Miller RF (2007) Short-term effects of burning Wyoming big sagebrush steppe in southeast Oregon. Rangeland Ecology and Management 60:515-522

Davies KW, Bates JD, Nafus AM (2012a) Mowing Wyoming big sagebrush communities with degraded herbaceous understories: has a threshold been crossed? Rangeland Ecology and Management 65:498-505

Davies KW, Bates JD, Nafus AM (2012b) Vegetation response to mowing dense mountain big sagebrush stands. Rangeland Ecology and Management. 65:268-276

Davies KW, Boyd CS, Beck JL, Bates JD, Svejcar TJ, Gregg MA (2011) Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573-2584

Dennis B, Ponciano JM, Lele SR, Taper ML, Staples DF (2006) Estimating density dependence, process noise, and observation error. Ecological Monographs. 76:323-341

Dinkins JB, Smith KT, Beck JL, Kirol CP, Pratt AC, Conover MR (2016) Microhabitat conditions in Wyoming's Sage-grouse Core Areas: effects on nest site selection and survival. PLoS ONE 11:e0150798

Doherty KE, Naugle DE, Evans JS (2010a) A currency for offsetting energy development impacts: horse-trading sage-grouse on the open market. PLoS ONE 5:e10339

Doherty KE, Naugle DE, Walker BL (2010b) Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544-1553

Dunbar MR, Gregg MA, Crawford JA, Giordano MR, Tornquist SJ (2005) Normal hematologic and biochemical values for prelaying greater sage-grouse (*Centrocercus urophasianus*) and their influence on chick survival. Journal of Zoo and Wildlife Medicine 36:422-429

Eidenshink J, Schwind B, Brewer K, Zhu Z, Quayle B, Howard S (2007) A project for monitoring trends in burn severity. Fire Ecology 3:3-22

Fedy BC, Aldridge CL (2011) The importance of within-year repeated counts and the influences of scale on long-term monitoring of sage-grouse. Journal of Wildlife Management 75:1022-1033

Fischer RA, Reese KP, Connelly JW (1996) An investigation on fire effects within xeric sage-grouse brood habitat. Journal of Range Management 49:194-198

Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen J (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423

Gamo RS, Beck, JL (2017) Effectiveness of Wyoming's Sage-grouse Core Area policy: Influences on energy development and male lek attendance. Environmental Management 59:DOI 10.1007/s00267-016-0789-9

Hagen CA, Connelly JW, Schroeder MA (2007) A meta-analysis of greater sage-grouse Centrocercus urophasianus nesting and brood-rearing habitats. Wildlife Biology 13:42-50

Hancock MH, Amphlett A, Proctor R, Dugan D, Willi J, Harvey P, Summers RW (2011) Burning and mowing as habitat management for capercaillie *Tetrao urogallus*: an experimental test. Forest Ecology and Management 262:509-521

Harju SM, Dzialak MR, Taylor RC, Hayden-Wing LD, Winstead JB (2010) Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437-448

Hess JE, Beck JL (2012a) Burning and mowing Wyoming big sagebrush: do treated sites meet minimum guidelines for greater sage-grouse breeding habitat? Wildlife Society Bulletin 36:85-93

Hess JE, Beck JL (2012b). Disturbance factors influencing greater sage-grouse lek abandonment in north-central Wyoming. Journal of Wildlife Management 76:1625-1634

Hess JE, Beck JL (2014) Forb, insect, and soil response to burning and mowing Wyoming big sagebrush in greater sage-grouse breeding habitat. Environmental Management 53:813-822

Hobson KA, Schieck J (1999) Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecological Applications 9:849-863

Hojsgaard S, Halekoh U, Yan J (2006) The R package geepack for generalized estimating equations. Journal of Statistical Software 15:2-11

Holloran MJ, Kaiser RC, Hubert WA (2010) Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65-72

Hunter ML, Jr. (1993) Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65:115-120

Gamo RS, Carlisle JD, Beck JL, Bernard JAC, Herget ME (2013) Greater sage-grouse in Wyoming: an umbrella species for sagebrush dependent wildlife. The Wildlife Professional 7:56-59

Garton EO, Connelly JW, Horne JS, Hagen CA, Moser AM, Schroeder MA (2011) Greater sage-grouse population dynamics and probability of persistence. Pages 293-382 In: Knick ST, Connelly LW (eds) Greater sage-grouse Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California

Garton EO, Wells AG, Baumgardt JA, Connelly JW (2015) Greater sage-grouse population dynamics and probability of persistence. Final Report to Pew Charitable Trust

Gregg MA, Crawford JA (2009) Survival of greater sage-grouse chicks and broods in the northern Greater Basin. Journal of Wildlife Management 71:646-651

Gregg MA, Dunbar MR, Crawford JA, Pope MD (2006) Total plasma protein and renesting by greater sage-grouse. Journal of Wildlife Management 70:472-478

Gregory AJ, Beck JL (2014) Spatial heterogeneity in response of male greater sage-grouse lek attendance to energy development. PloS ONE 9:e97132

Guttery MR, Dahlgren DK, Messmer TA, Connelly JW, Reese KP, Terletzky PA, Burkpile N, Koons DN (2013) Effects of landscape-scale environmental variation on greater sage-grouse chick survival. PloS ONE 8:e65582

Johnson DH, Rowland MM (2007) The utility of lek counts for monitoring greater sage-grouse. University of Idaho College of Natural Resources Experiment Station Bulletin 88:43-56

Johnson GD, Boyce MS (1990) Feeding trials with insects in the diet of sage grouse chicks. Journal of Wildlife Management 54:89-91

Johnson KH, Braun CE (1999) Viability and conservation of an exploited sage grouse population. Conservation Biology 13:77-84

Kirol CP, Beck JL, Dinkins JB, Conover MR (2012) Microhabitat selection for nesting and brood-rearing greater sage-grouse in xeric big sagebrush. Condor 114:75-89

Knick ST, Dobkin DS, Rotenberry JT, Schroeder MA, Vander Haegen WM, van Riper III C (2003) Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634

Knight DH, Jones GP, Reiners WA, Romme WH (2014) Mountains and plains: the ecology of Wyoming landscapes. Second edition. Yale University Press, New Haven, Connecticut

Lesica P, Cooper SV, Kudray G (2007) Recover of big sagebrush following fire in southwest Montana. Rangeland Ecology and Management 60:261-269

Lockyer ZB, Coates PS, Casazza ML, Espinosa S, Delehanty DJ 2015. Nest-site selection and reproductive success of greater sage-grouse in a fire-affected habitat in northwestern Nevada. Journal of Wildlife Management 79:785-797

Mills LS, Doak DF, Wisdom MJ (2009) Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13:815-829

Myers N (1993) Biodiversity and the precautionary principle. Ambio 22:74-79

Nelle PJ, Reese KP, Connelly JW (2000) Long-term effects of fire on sage grouse habitat. Journal of Rangeland Management 53:586-591

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25-51

Pan W (2001) Akaike's Information Criterion in generalized estimating equations. Biometrics 57:120-125

Payton AC, Hayes SJ, Borthwick SM, Japuntich RD. 2011. Short-term response of shrubs, graminoids and forbs to mechanical treatment in a sagebrush ecosystem in Colorado. Natural Resources and Environmental Issues 16:art24

Peters DC, Brooke JM, Tanner EP, Unger AM, Keyser PD, Harper CA, Clark JD, Morgan JJ (2015) Impact of experimental habitat manipulation on northern bobwhite survival. Journal of Wildlife Management 79:605-617

Perryman BL, Olson RA, Petersburg S, Naumann T (2002) Vegetation response to prescribed fire in Dinosaur National Monument. Western North American Naturalist 62:414-422

PRISM Climate Group. (2016) Oregon State University, http://prism.oregonstate.edu

Pyke DA (2011) Restoring and Rehabilitation sagebrush habitats. Pages 531-548 In: Knick ST, Connelly JW (eds) Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press Berkeley, California

Pyke DA, Chambers JC, Pellant M, Knick ST, Miller RF, Beck JL, Doescher PS, Schupp EW, Roundy BA, Brunson M, McIver JD (2015) Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat—Part 1. Concepts for understanding and applying restoration: U.S. Geological Survey Circular 1416, 44 p.

Raithel JD, Kauffman MJ, Pletscher DH (2007) Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795-803

Reese KP, Bowyer RT (2007) Monitoring populations of sage-grouse. College of Natural Resources Experiment Station Bulletin 88. University of Idaho, Moscow, Idaho

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/

Rich T, Altman B. 2001. Under the sage-grouse umbrella; will management for sage-grouse protect other birds and animals in the sagebrush steppe? Bird Conservation 14:10

Rhodes EC, Bates JD, Sharp RN, Davies KW (2010) Fire effects on cover and dietary resources of sage-grouse habitat. Journal of Wildlife Management 74:755-764

Rowland MM, Leu M (2011) Study Area Description. Pages 10–45 In: Hanser SE, Leu M, Knick ST, Aldridge CL (eds) Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas

Rowland MM, Wisdom MJ, Suring LH, Meinke CW (2006) Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation 129:323-335

Schroeder MA, Young JR, Braun CE (1999) Sage grouse (*Centrocercus urophasianus*). Pages 1-28 In: Poole A, Gill F (eds) The Birds of North America. The Birds of North America Inc., Philadelphia, Pennsylvania

State of Wyoming (2011) Greater sage-grouse core area protection. Office of the Governor, Executive Order Number 2011-5. http://wgfd.wyo.gov/web2011/Departments/Wildlife/pdfs/SAGEGROUSE_EO_COREROTECTION0000651.pdf

Stiver SJ, Apa AD, Bohne JR, Bunnell SD, Deibert PA, Gardner SC, Hilliard MA, McCarthy CW, Schroeder MA (2006) Greater sage-grouse comprehensive conservation strategy. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming

Sveum CM, Crawford JA, Edge WD (1998) Use and selection of brood-rearing habitat by sage-grouse in south central Washington. Great Basin Naturalist 58:344-351

Taylor RL, Walker BL, Naugle DE, Mills LS (2012) Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336-347

Thompson KM, Holloran MJ, Slater SJ, Kuipers JL, Anderson SH (2006) Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. Western North American Naturalist 66:332-342

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. Federal Register 80:59858-59942

Walker BL, Naugle DE, Doherty KE (2007) Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654

Wang Y, Carey V (2003) Working correlation structure misspecification, estimation, and covariate design: implications for generalised estimating equations performance. Biometrika 90:29-41

Wenninger EJ, Inouye RS (2008) Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. Journal of Arid Environments 72:24-33

Wortley L, Hero JM, Howes M (2013) Evaluating ecological restoration success: a review of the literature. Restoration Ecology 21:537-543

[WGFD] Wyoming Game and Fish Department (2011) Wyoming Game and Fish Department protocols for treating sagebrush to benefit sage-grouse. https://wgfd.wyo.gov/WGFD/media/content/PDF/Habitat/Sage%20Grouse/SG_TREATINGSAGEBRUSHPROTOCOL.pdf

[WGFD] Wyoming Game and Fish Department. (2010) Wyoming state wildlife action plan. Wyoming Game and Fish Department. Cheyenne, WY

[WOGCC] Wyoming Oil and Gas Conservation Commission. 2012. http://www.wogcc.wyo.gov

Yan J (2002) Geepack: yet another package for generalized estimating equations. R-News. 2/3:12-14

Yan J, Fine JP (2004) Estimating equations for association structures. Statistics in Medicine 23:859-880

Table 1. Top and competing models within variable subsets and combined models explaining one-year time lags of sage-grouse annual population growth within Core Areas in Sage-grouse Management Zone II, Wyoming, USA, 1996–2012.

Model	Model fit statistics		
	QIC	ΔQIC	w_i
Density-dependence			
Gompertz$_{\text{(no lag)}}$	20474.93	0.00	1.00
Gompertz$_{\text{(one year lag)}}$	25562.16	5087.23	0.00
Null	25596.20	5121.27	0.00
Well Pad Density			
Well Pad Density	25594.94	0.00	0.65
Null	25596.20	1.26	0.35
Precipitation			
Summer + Winter$_{10\text{km}}$	25587.57	0.00	0.99
Null	25596.20	8.63	0.01
Wildfire			
Wildfire$_{8.4\text{km}}$	25592.79	0.00	0.85
Null	25596.20	3.41	0.15
Vegetation Treatments			
Chemical$_{10\text{km}}$ + Mechanical$_{10\text{km}}$	25588.83	0.00	0.98
Null	25596.20	7.37	0.02
Combined			
Gompertz$_{\text{(no lag)}}$ + Well Density + Summer + Winter$_{10\text{km}}$ + Wildfire$_{8.4\text{km}}$ + Chemical$_{10\text{km}}$ + Mechanical$_{10\text{km}}$	20419.40	0.00	1.00
Gompertz$_{\text{(no lag)}}$	20474.93	55.53	0.00

Table 2. Top and competing models within variable subsets and combined models explaining three-year time lags of sage-grouse annual population growth within Core Areas in Sage-grouse Management Zone II, Wyoming, USA, 1998–2012.

Model	Model fit statistics		
	QIC	ΔQIC	w_i
Density-dependence			
Gompertz$_{\text{(no lag)}}$	18116.30	0.00	1.00
Gompertz$_{\text{(one year lag)}}$	22824.90	4708.60	0.00
Null	22914.59	4798.29	0.00
Well Pad Density			
Well Pad Density	22908.45	0.00	0.96
Null	22914.59	6.14	0.04
Precipitation			
Fall	22900.20	0.00	1.00
Null	22914.59	14.39	0.00
Wildfire			
Wildfire$_{10km}$	22902.51	0.00	1.00
Null	22914.59	12.08	0.00
Vegetation Treatments			
[1]Mechanical$_{1km}$	22904.93	0.00	0.99
Null	22914.59	9.66	0.01
Combined			
Gompertz$_{\text{(no lag)}}$ + Well Density + Fall +Wildfire$_{10km}$+ [1]Mechanical$_{1km}$	18047.98	0.00	1.00
Gompertz$_{\text{(no lag)}}$	18116.30	68.32	0.00

[1] Quadratic term used in model

Table 3. Top and competing models within variable subsets and combined models explaining five-year time lags of sage-grouse annual population growth within Core Areas in Sage-grouse Management Zone II, Wyoming, USA, 2000–2012.

	Model fit statistics		
Model	QIC	ΔQIC	w_i
Density-dependence			
$\text{Gompertz}_{\text{(no lag)}}$	15897.96	0.00	1.00
$\text{Gompertz}_{\text{(one year lag)}}$	19766.50	3868.54	0.00
Null	19844.23	3946.27	0.00
Well Pad Density			
Well Pad Density	19836.60	0.00	0.98
Null	19844.23	7.63	0.02
Precipitation			
$\text{Fall}_{5\text{km}}$ + Spring	19828.24	0.00	1.00
Null	19844.23	15.99	0.00
Wildfire			
$\text{Wildfire}_{8.4\text{km}}$	19834.39	0.00	0.99
Null	19844.23	9.84	0.01
Vegetation Treatments			
$\text{Mechanical}_{10\text{km}}$	19839.97	0.00	0.89
Null	19844.23	4.26	0.11
Combined			
$\text{Gompertz}_{\text{(no lag)}}$ + Well Density + $\text{Fall}_{5\text{km}}$ + Spring + $\text{Wildfire}_{8.4\text{km}}$ + $\text{Mechanical}_{10\text{km}}$	15797.52	0.00	1.00
$\text{Gompertz}_{\text{(no lag)}}$	15897.96	100.44	0.00

Table 4. Variable coefficients, standard errors (SE), and 85% confidence intervals (LCL and UCL) from top Generalized Estimating Equation models comparing one-year, three-year, and five-year lags effects of density dependence, precipitation, and habitat treatments on estimated greater sage-grouse annual population growth (r) in Core Areas of Sage-grouse Management Zone II, Wyoming, USA. Models included main effects only

	One-year lag				**Three-year lag**				**Five-year lag**			
Parameter	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**
Intercept	0.899	0.034	--	--	0.957	0.038	--	--	0.914	0.041	--	--
Density Dependence												
Gompertz$_{(\text{no lag})}$	-0.345	0.011	-0.361	-0.329*	-0.356	0.012	-0.373	-0.338*	-0.344	0.013	-0.362	-0.325*
Well Density												
Well Pad Density	-0.043	0.017	-0.066	-0.019*	-0.049	0.015	-0.070	-0.028*	-0.052	0.016	-0.075	-0.029*
Precipitation												
Spring	--	--	--	--	--	--	--	--	-0.078	0.017	-0.102	-0.053*
Summer	-0.015	0.017	-0.039	0.009	--	--	--	--	--	--	--	--
Fall	--	--	--	--	0.014	0.018	-0.012	0.039	--	--	--	--
Fall$_{5\text{km}}$	--	--	--	--	--	--	--	--	0.035	0.018	0.009	0.061*
Winter$_{10\text{km}}$	-0.042	0.020	-0.071	-0.013*	--	--	--	--	--	--	--	--
Wildfire												
Wildfire$_{8.4\text{km}}$	-0.052	0.013	-0.071	-0.032*	--	--	--	--	-0.071	0.019	-0.098	-0.043*
Wildfire$_{10\text{km}}$	--	--	--	--	-0.070	0.016	-0.094	-0.046*	--	--	--	--
Treatments												
Mechanical$_{1\text{km}}$	--	--	--	--	-0.063	0.059	-0.148	0.022	--	--	--	--
Mechanical$_{10\text{km}}$	-0.034	0.016	-0.057	-0.012*	--	--	--	--	-0.034	0.018	-0.060	-0.007*
Chemical$_{10\text{km}}$	0.009	0.017	-0.015	0.033	--	--	--	--	--	--	--	--

*85% confidence intervals that do not include zero

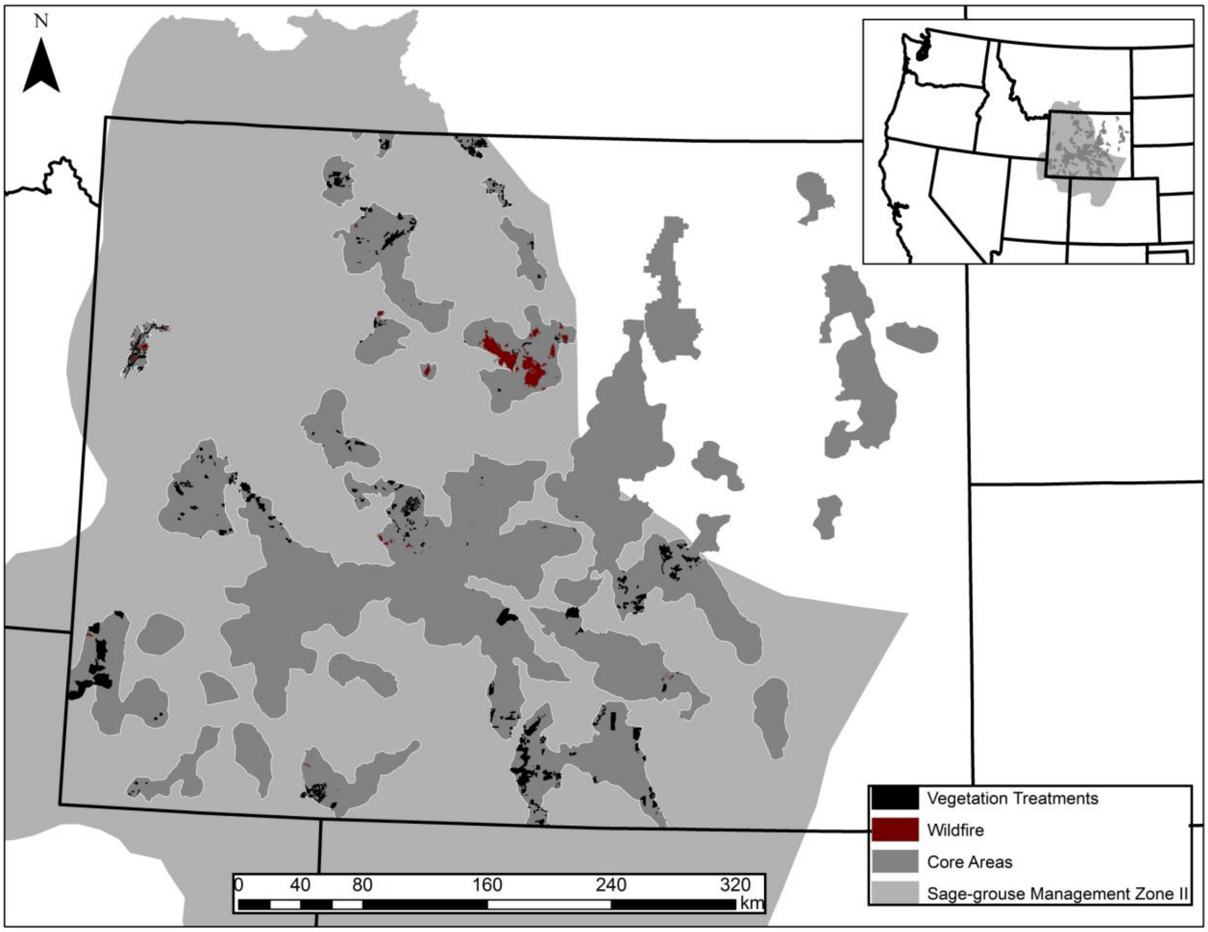


Figure 1. Map of the study area depicting vegetation treatments and wildfires occurring from 1994–2012 in Wyoming's Core Areas within Sage-Grouse Management Zone II, Wyoming, USA.

CHAPTER THREE

Reproductive State leads to Intraspecific Habitat Partitioning and Fitness Tradeoffs in Greater Sage-Grouse

Kurt T. Smith, Jeffrey L. Beck, and Christopher P. Kirol

Department of Ecosystem Science and Management, College of Agriculture and Natural Resources, University of Wyoming, Dept. 3354, 1000 E University Ave, Laramie, Wyoming, 82071, USA.

In the format for manuscripts submitted to *Wildlife Research*

Abstract

Context. Inter- and intraspecific habitat partitioning is widespread across taxa, yet limited information is available on differences in intraspecific habitat selection of same sex individuals among differing reproductive states. Understanding habitat selection by conspecifics of different reproductive states may help optimize conservation efforts, particularly for gallinaceous bird species such as greater sage-grouse (*Centrocercus urophasianus*), which are long-lived, but have only moderate reproductive rates.

Aims. We hypothesized that microhabitat use differed between grouse under different reproductive states and that reproductive effort by brood-rearing female sage-grouse decreased adult summer survival.

Methods. We compared microhabitat characteristics used by brood-rearing and broodless female sage-grouse and evaluated the influence of reproductive investment on adult female survival.

Key results. We found that brood-rearing and broodless female sage-grouse partitioned habitat at the microhabitat scale. Broodless females were more likely to survive the summer suggesting tradeoffs in fitness strategies.

Conclusions. Our findings suggest that broodless females were roosting and foraging in concealed habitats with greater visual obstruction but less food forb availability. In contrast, brood-rearing females likely selected riskier microhabitats with less shrub cover and greater herbaceous understory to predictably maximize foraging opportunities and promote growth of their chicks.

Implications. Adult female survival is critical for population persistence of sage-grouse and other long-lived Galliformes, yet conservation efforts generally focus on habitats used during nesting and brood-rearing. Our results indicate habitat partitioning is a risk-adverse strategy ensuring higher survival for broodless females while optimizing resources for brood-rearing females, suggesting conservation efforts focus on conserving habitats used by brood-rearing and broodless sage-grouse.

Additional keywords: behavior; survival; reproduction

INTRODUCTION

Species that occupy heterogeneous landscapes may utilize a spectrum of habitats throughout their life-cycles, potentially making inference about habitat use and identifying habitats for conservation difficult (Donovan and Thompson 2001). Assessing interspecific habitat use and partitioning between species and intraspecific habitat partitioning among conspecifics clarifies inferences about habitat selection (e.g., Banuelos *et al.* 2008; Alves *et al.* 2013). Interspecific habitat partitioning is common across taxa including fish (Werner *et al.* 1977), birds (Burger *et al.* 1977), and mammals (Cumming *et al.* 1996). Intraspecific habitat partitioning between sexes is also widespread across taxa, and several hypotheses have been proposed to understand sexual habitat segregation (Bowyer 2004; Ruckstuhl 2007). For example, the predation risk hypothesis suggests that males select high quality foraging habitats with higher predation risk, whereas females trade off forage quality to enhance offspring survival (Main and Coblentz 1996; Ruckstuhl 2007; Alves *et al.* 2013). Habitat-based segregation (Main and Coblentz 1996; Conradt 1999) may also apply to individuals of the same sex under different reproductive states, which must be accounted for when assessing individual variability of resource use (Bolnick *et al.* 2003). Because habitat choices often influence survival (Wilson and Nussey 2010), accounting for sex-specific or reproductive state variability is necessary for assessing habitat conservation. Reproductive costs imposed on individuals represent tradeoffs between current reproductive effort and future survival under limited energy constraints (Harshman and Zera 2007). These tradeoffs may occur in relatively long lived species when reproducing individuals balance survival with rearing young to maximize lifetime reproductive success (Erickstad *et al.* 1998). Individuals in different reproductive states may utilize various habitats to mitigate these tradeoffs. For example, red deer (*Cervus elaphus*; Alves *et al.* 2013) and noctule bats (*Nyctalus noctula*; Mackie and Racey 2007) use different habitats under different reproductive states, whereby non-reproductive females select different habitats or foraging resources than reproductive individuals. The success of reproductive females depends on offspring survival, whereas unsuccessful females must survive to reproduce in subsequent breeding periods to maximize lifetime reproductive success. For species with high maternal parental investment, differences in habitat selection may result as differential responses to risk stimuli under distinct reproductive states (Frid and Dill 2002; Laundre *et al.* 2010), where females with young may be faced with balancing predation risk with foraging opportunities for the adult and dependent young (Main and Coblentz 1996; Ruckstuhl 2007); however, limited information on habitat partitioning across reproductive states currently exist.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a species of great conservation concern (U.S. Fish and Wildlife Service 2015), currently occupying approximately 668,000 km^2 of sagebrush (*Artemisia* spp.) across <60% of their historic range (Schroeder *et al.* 2004). Sage-grouse face significant threats from range-wide habitat loss and degradation (Connelly *et al*. 2004). Research has repeatedly demonstrated sexual habitat partitioning in sage-grouse during different times of the year (see Connelly *et al.* 2011a), but habitat partitioning of females under different reproductive states has received little attention. Sage-grouse, unlike most other gallinaceous species, more closely align with a *K*-selection strategy because they are a relatively long lived species with only moderate reproductive rates (Pianka 1970; Connelly *et al.* 2011b). Research has demonstrated that population growth in sage-grouse is particularly sensitive to adult female survival (Johnson and Braun 1999; Schroeder *et al*. 1999; Taylor *et al.* 2012; Dahlgren *et al.* 2016) and range-wide nest success estimates for sage-grouse are generally low, with many females failing to produce a brood during most years (Schroeder *et al.* 1999; Connelly *et al.* 2011b). Because adult female survival is critical to sage-grouse persistence, conservation actions that promote adult female survival across reproductive states may be most beneficial to sage-grouse populations (Taylor *et al.* 2012; Dahlgren *et al.* 2016). Survival of adult female sage-grouse is typically lowest during the breeding season (Moynahan *et al.* 2006; Baxter *et al.* 2013; Blomberg *et al.* 2013) and survival has been shown to be influenced by reproductive effort, where brood-rearing investment is negatively correlated with annual adult survival (Blomberg *et al.* 2013).

Identifying microhabitats used by brood-rearing and non-brood-rearing (hereafter broodless) females is important when prioritizing habitat for sage-grouse; however, most research has focused on nesting or brood-rearing microhabitats (e.g., Hagen *et al.* 2007; Connelly *et al.*

2011a), leaving a knowledge gap regarding habitat selection of broodless females. Some research suggests that broodless females generally move to mesic sagebrush habitats earlier in the summer than females with broods and may be more mobile while roosting in areas that are more distant from foraging locations (Gregg *et al.* 1993). Brood-rearing females are generally more restricted in their movement because chicks are not capable of flight until approximately 2 weeks after hatch (Wallstad 1971). During that time, many factors can lead to reduced survival by sage-grouse chicks, including predation, adverse weather and low nutrient availability (Drut *et al.* 1994; Huwer *et al.* 2008; Gregg and Crawford 2009; Blomberg *et al.* 2012; Guttery *et al.* 2013). Reduced movement by adult females with broods and limited mobility of chicks during early life may indicate that habitat choice is especially critical during this time to maximize chick growth and minimize predation risk. In fact, there may be a significant relationship between brood movement and survival, where more mobile broods may have increased exposure to predators (Drut *et al.* 1994; Gregg 2006). Selection of habitats is likely less important for broodless females as they are more mobile and can select different locations for roosting and diurnal foraging to minimize these risks (Dumroese *et al.* 2015).

Landscape (Shepherd *et al.* 2011; Kirol *et al.* 2015) and microhabitat scale (Gregg *et al.* 1993; Bunnell *et al.* 2004) habitat selection has been assessed for broodless females, but we are unaware of any studies that have evaluated microhabitat selection of brood-rearing and broodless female sage-grouse simultaneously while relating differences in habitat selection to female survival risk. Differences in selection among brood-rearing and broodless females of other grouse species (e.g., Banuelos *et al.* 2008) highlights the importance of understanding habitat partitioning across different reproductive states and how this might relate to adult female survival during the same period. While the predation risk hypothesis was originally proposed to explain habitat partitioning in relation to gender differences in reproductive strategies (Main and Coblentz 1996), it may explain habitat partitioning between female sage-grouse under different reproductive states. We hypothesized that brood-rearing females occupy high quality foraging habitats to meet nutritional needs of chicks with limited mobility at the expense of greater predation risk, whereas broodless females occupy distinct roosting and foraging locations to minimize predation risk. Specifically, we predicted brood-rearing females select habitats with greater foraging resources and have lower summer survival compared to broodless females, which select habitats with lower predation risk. To test our predictions, we compared microhabitat selection and adult female survival of brood-rearing and broodless female sage-grouse during the breeding season.

MATERIALS AND METHODS

Study area

Our study area occurred in portions of Fremont and Natrona counties, in central Wyoming, USA (42.63’N, 107.92’W) and encompassed ~3,098 km^2. Elevation ranged from 1644 to 2439 m and included approximately 81% Federal, 7% State, and 12% privately administered lands. Annual precipitation ranged from approximately 13.3 to 33.7 cm (NOAA 2016). Vegetation communities in the study area were dominated by mountain (*Artemisia tridentata vaseyana*) and Wyoming big sagebrush (*A. t. wyomingesis*), with inclusions of basin big sagebrush (*A. t. tridentanta*), black sagebrush (*A. nova*), greasewood (*Sarcobatus vermiculatus*), and silver sagebrush (*A. cana*). Major land uses include livestock grazing.

Capture and monitoring

We captured and radio-marked female sage-grouse near leks in spring 2011–2013 by spot-lighting and hoop-netting (Giesen *et al.* 1982; Wakkinen *et al.* 1992). We used roosting locations of radio-marked females captured in spring to capture and radio-mark additional females in August each year. We attached radio transmitters (22 g, Model A4060; Advanced Telemetry Systems Incorporated, Isanti, MN, USA) to females with a PVC-covered wire necklace. We began locating female sage-grouse weekly during late April each year with R-1000 hand-held receivers and 3-element antennas (Communication Specialists, Orange, CA, USA). We used fixed-wing aircraft flights to locate individuals not located from ground searches. All sage-grouse were captured, marked, and monitored in accordance with approved protocols (Wyoming Game and Fish Department Chapter 33-801 permit and University of Wyoming Institutional Animal Care and Use Committee protocol 03132011).

We monitored all females weekly irrespective of nesting or brood status through 15-Aug of each year. Consequently, if a female was not documented on a nest or a nesting female was determined to be unsuccessful, we continued to monitor the female and considered that individual to be broodless unless a re-nesting attempt was documented. We located nests of radio-marked females by triangulating the signal until the female was spotted or when the location was isolated to a single nest shrub or shrubs. Once a female was determined to be nesting, we monitored the nest weekly until the female was no longer located in the area to determine nest fate. We monitored nests from a distance of ≥30 m and left the area in an erratic pattern to reduce the potential of the researcher influencing nest predation (i.e., leaving a scent trail to the nest; Kirol *et al*. 2012). For successfully hatched nests (i.e., at least one hatched egg; Rotella *et al.* 2004) we determined if the female was with a brood by visual observations of chicks or brooding behavior by the female (Kirol *et al.* 2012). If no brooding behavior was detected during two successive telemetry visits, we estimated the date of brood loss as the midpoint between the last date when the female was determined to be with a brood and the first visit when a brood was not detected. We further assessed brood fate by night time spotlight counts at approximately 35 days post-hatch and considered broods successful when at least one chick was present with the hen at this time (Walker 2008; Kirol *et al.* 2015).

Microhabitat sampling and analysis

We evaluated vegetative and ground cover microhabitat parameters at brood-rearing locations (early and late brood-rearing periods), summer broodless female locations, and random locations along 2, perpendicular 30-m transects centered at each grouse and random location aligned in cardinal directions. We chose these microhabitat variables because they have been shown to be important for sage-grouse microhabitat selection in other studies (e.g., Hagen *et al.* 2007; Kirol *et al.* 2012; Dinkins *et al.* 2016; Table 1). We defined the early brood-rearing period as the 2-week period following nest hatch (Bergerud and Gratson 1988; Thompson *et al.* 2006), and estimated microhabitat characteristics at 2 locations during 2011 and 1 location during 2012 and 2013 for each brood-rearing female during this time period. For late brood-rearing, we recorded habitat characteristics at 2 locations in 2011 and 1 location in 2012 and 2013 when chicks were estimated to be between 20 and 35 days of age. Broodless female locations were sampled during late June and early July each year. We estimated herbaceous and ground cover attributes using the Daubenmire (1959) technique in 20 x 50 cm quadrats (n = 17 quadrats location^{-1}) placed at pre-determined locations along both 30-m transects. We recorded shrub canopy cover with the line intercept method and computed percentage cover for each shrub species (Canfield 1941; Wambolt *et al.* 2006). We recorded shrub density by counting shrubs rooted within 1-m belt transects positioned along the right side of each 30-m transect and assessed visual obstruction using a Robel pole (dm; Robel *et al.* 1970) placed in the center of each location, and recorded measurements from a distance of 5, 10, and 15 m at 1 m height from each cardinal direction. We measured the droop height of current and residual perennial grasses in each 20 x 50 cm quadrat and height of the tallest leader, excluding inflorescences for each shrub encountered along each 30-m line transect. We examined microhabitat at random locations constrained by a random distance (direction 100–500 m) and direction from each sage-grouse use location (Aldridge and Boyce 2008).

Because we were interested in potential differences in selection by sage-grouse under different reproductive states compared to available habitat, we used multinomial logistic regression models using function multinom in package nnet in R (Venables and Ripley 2002; R Core Team 2015), where resource use was identified as microhabitat sampling locations for radio-marked early brood-rearing, late brood-rearing, or broodless female sage-grouse, and resource availability was defined as random locations. Multinomial logistic regression is useful for modeling habitat selection when there are >2 response categories. This method allowed for simultaneous comparisons of microhabitat selection by early brood-rearing, late brood-rearing and broodless females in a single model and allowed comparisons of each response group relative to the same predictor variables in the same model. Similar approaches have been used to assess the influence of predictor variables on nesting and brood-rearing sage-grouse (Dinkins *et al*. 2014) and brood-rearing and broodless capercaillie (*Tetrao urogallus cantabricus*; Banuelos *et al.* 2008).

We categorized predictor variables into four subsets; shrub canopy cover, horizontal visual obstruction, herbaceous cover, and ground cover characteristics. We used a sequential modeling approach (Arnold 2010) by initially evaluating predictor variables within each subset. Prior to model selection, non-informative variables with 85% confidence intervals of parameter estimates overlapping 0 were removed from each subset. In addition, we computed Pearson's correlation matrix to test for collinearity among predictors in each subset and did not allow variables to compete in the same model when correlation coefficients (r) were ≥ |0.6|. We explored all combinations of variables that were brought forward following initial variable screening procedures within each subset (Burnham and Anderson 2002). We identified the best model subset using Akaike's information criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2004). The model with the lowest AIC score was identified as being the best fit model; however, models with Akaike weights within 90% of the top model were considered competitive (Arnold 2010). Competitive models within variable subsets were brought forward to the final level of model selection and allowed to compete across subsets to assess model improvement. Once a final model was developed, we assessed the influence of individual covariates within that model by assessing 90% confidence intervals of parameter estimates. If confidence intervals overlapped 0, we considered covariates to be marginal predictors of selection for individual sage-grouse microhabitat use across reproductive states.

Adult female survival

We evaluated adult female survival relative to total reproductive effort, brooding effort, and distance moved between subsequent relocations. Total reproductive effort was defined as the estimated number of weeks spent incubating and brood-rearing, whereas brooding effort was the number of weeks spent brood-rearing following a successful nesting attempt. We truncated total reproductive effort and brooding effort to reflect uncertainty in brood retention following night time spotlight counts at 35 days (5 weeks) post-hatch. Chicks often become more visible as they grow; however, brood flocking behavior makes parental assessment difficult after approximately 5 weeks (Dalke *et al*. 1963; Dahlgren *et al*. 2010). Therefore, the maximum value of total reproductive effort of ~ 9 weeks was reflective of the incubation period for successful nests (27 days; 25-29 day incubation period [Schroeder, Young, and Braun 1999]) plus the estimated age when nighttime spotlight counts were conducted (35 ± 0.3 [SE] days post-hatch). Average distance moved was estimated as the linear distance between consecutive relocations divided by the number of days between relocation events.

We calculated Kaplan-Meier product-limit survival estimates (Kaplan and Meier 1958) modified for staggered entry (Pollock *et al.* 1989) to estimate survival rates for marked females from approximately 1-May to 15-Aug each year. We used Cox's proportional hazards regression (Cox PH; Cox 1972) to identify relationships between predictor variables and sage-grouse reproductive seasonal survival with the counting process (Anderson and Gill 1982; Therneau and Grambsch 2000). Cox PH assisted in assessing variables that had the greatest influence on adult survival (Hosmer and Lemeshow 1999). Because our observation intervals were approximately 7 days, we modeled weekly female survival from nesting (1 May) through 15 Aug during each year for all females (13.5 week survival period; Winterstein *et al.* 2001). We used left and right censoring to properly incorporate individuals entering and leaving the study at different times (Winterstein *et al.* 2001). If a female was never located on a nest, we used the average day of nest initiation for each year as the day that individual entered the sample. We estimated mortality dates from the last known telemetry monitoring interval, and used the mid-point between the last 2 locations (most recent location determined alive and date when located dead) as the estimated mortality date. Individuals that did not die during the study were right censored.

We used AICc (Burnham and Anderson 2002) to evaluate model support for Cox PH models. We assessed correlation between variables and did not allow variables to compete in the sample model when r ≥ |0.6|. Remaining variables were brought forward, where we explored all possible variable combinations for model assessment. We tested proportional hazards assumptions with Schoenfeld residuals for each covariate in the top model (Schoenfeld 1982).

RESULTS

We sampled 233 female sage-grouse (68 early brood-rearing, 49 late brood-rearing, 116 broodless female), and 233 random microhabitat plots from 133 radio-marked female sage-grouse from 1 May–15 Aug 2011–2013. Adult female survival from 1-May to 15-Aug was 78 ± 8% (SE) in 2011, 83 ± 4% in 2012, and 79 ± 4% in 2013. Apparent nest success was 26.1%, 44.8%, and 55.3% during 2011, 2012, and 2013, respectively. Brood success was 66.6% in 2011, 68.0% in 2012, and 53.3% in 2013. The percentage of broodless females during 2011, 2012, and 2013 breeding seasons ranged from 69.5–82.6%. Average daily movement distance between estimated relocations was 216.9 ± 16.5 m (SE) for brood-rearing females and 219.8 ± 11.1 m (SE) for broodless females.

Microhabitat Selection

Our final level of model selection indicated that two models were competitive explaining microhabitat selection across all sage-grouse locations and included all variable subsets that we assessed (Table 2). The top model included all variable subsets, but was competitive with the model containing shrub canopy cover, horizontal visual obstruction, and herbaceous ground cover variables (ΔAIC = 1.06, w_i = 0.58). Because model fit was only slightly improved with the inclusion of the ground cover variable subset, which included 3 additional variables, we considered the second model to be the most parsimonious model within the two competitive models and considered it further.

Variables from the shrub canopy cover subset included big sagebrush cover, shrub cover variability, and shrub cover (quadratic form). Big sagebrush density (individual plants m^{-2}) was positively associated with early brood-rearing selection, and a marginal predictor of late brood-rearing and broodless female microhabitat selection (Tables 3 and 4; Fig. 1A). Shrub cover variability (%) was positively associated with late brood-rearing, but uninformative for early brood-rearing or broodless female microhabitat selection (Tables 3 and 4, Fig. 1B). Canopy cover of all shrub species (Shrub Cover) received minimal support across all sage-grouse reproductive states and was not considered further. Visual obstruction (quadratic term for dm) was positively correlated with all reproductive states, but was only a marginal predictor for late brood-rearing (Tables 3 and 4, Fig. 1C). Herbaceous ground cover variables included in final models were species richness and non-food forb cover. Species richness was positively correlated with early brood and late brood, and was marginally correlated with broodless female microhabitat selection (Tables 3 and 4, Fig. 1D). Early and late brood habitat selection were negatively correlated with non-food forb cover, and was a marginal predictor of broodless female microhabitat selection (Tables 3 and 4, Fig. 1E).

Survival

Initial variable screening indicated that 85% confidence intervals for hazard ratios of brood-rearing effort and distance moved between relocations overlapped 1. Therefore, the most predictive model of adult female survival to 13.5 weeks included the single variable that estimated total reproductive effort (Table 5). For every 10% increase in reproductive effort (1 week), the adult female hazard rate increased by approximately 11.7 % (Fig. 2).

DISCUSSION

Our study focused on evaluating whether reproductive state influenced partitioning of habitat and if this was related to female survival. Our results provide evidence for habitat partitioning by female sage-grouse across reproductive states at the microhabitat scale. During the same period, adult female survival was negatively related to reproductive effort—females that were not rearing chicks were more likely to survive the summer. Differences in habitat use among individuals in other Tetraonid species have been documented (Banuelos *et al.* 2008; Blanco-Fontao *et al.* 2013) and some macrohabitat-scale research suggests that habitats used by reproductive female sage-grouse differ from non-breeding individuals (Shepherd *et al.* 2011; Kirol *et al.* 2015). To our knowledge, ours is the first study to simultaneously identify differences in microhabitat selection between brood-rearing and broodless female sage-grouse. Bunnell *et al.* (2004) examined microhabitat differences between brood-rearing and adult sage-grouse, but did not differentiate between males and broodless females, thus contrasting findings to our study are incomparable. Further, survival consequences of microhabitat partitioning by reproductive and broodless female sage-grouse has not been assessed in the context of different habitat use. We found that adult female survival was influenced by total reproductive effort, where individuals that spent more time nesting and brood rearing had higher risk of mortality. Reduction in adult female survival relative to reproductive investment has been documented in other sage-grouse populations (Moynahan *et al.* 2006; Sika 2006; Blomberg *et al.* 2013). Here we suggest that differences in adult survival under different reproductive states can, in part, be explained by differences in habitat use by brood-rearing and broodless females.

Early brood-rearing females generally selected microhabitats with greater big sagebrush density, intermediate visual obstruction, greater food forb species richness, and less non-food forb herbaceous cover. The importance of structure, cover, and food for early brood-rearing sage-grouse has been well documented and are consistent with our findings that early brood-rearing females selected areas of intermediate sagebrush cover with greater herbaceous understories during nesting and brood rearing (Sveum *et al.* 1998; Connelly *et al.* 2000; Bunnell *et al.* 2004; Hagen *et al.* 2007; Doherty *et al.* 2010; Kirol *et al.* 2012) to meet the nutritional requirements of chicks (Johnson 1987; Johnson and Boyce 1990; Barnett and Crawford 1994; Dumroese *et al.* 2015), while providing structural cover for concealment from predators and thermal protection (Schroeder *et al*. 1999; Gregg and Crawford 2009; Kirol *et al.* 2012). As chicks grow, females with chicks generally move to more mesic late brood-rearing sites with resource rich forbs (Wallestad 1971; Atamian *et al.* 2010). In our study, late brood-rearing females selected sagebrush habitats with lower sagebrush densities, greater variability in shrub cover, greater food forb species richness, and less non-food forb herbaceous cover when compared to available habitat. Hagen *et al.* (2007) reported late brood-rearing females select for greater forb and grass cover, and use of shrub cover in proportion to its availability, which is generally corroborated by our findings.

Habitat partitioning was evident between broodless and brood-rearing females. Broodless females only selected for greater horizontal visual obstruction, whereas all other microhabitat features showed only moderate support in our models. Broodless females showed contrasting selection patterns for big sagebrush density, food forb species richness, and non-food forb cover compared to early brood-rearing females. Habitat selection trends were more similar between broodless and late brood-rearing females; perhaps the most distinct differences in microhabitat between individuals in these reproductive states was selection for visual obstruction. Visual obstruction estimates total horizontal obstruction and includes all micro-topographic and vegetation (e.g., shrub, grass, herbaceous) attributes that provide concealment cover for individuals. The importance of visual obstruction for nesting sage-grouse has been documented in other studies (Kirol *et al.* 2012; Dinkins *et al.* 2016). Shrub cover and herbaceous understory within sagebrush communities are often inversely related (Olson and Whitson 2002), and early brood-rearing females were likely selecting areas with sufficient nutritional resources in a way that maximizes structural concealment cover (i.e., intermediate herbaceous understory and shrub overstory cover).

Sage-grouse chicks almost exclusively consume insects and associated forbs during early brood-rearing when nutritional requirements are high for growth and survival (Johnson 1987; Johnson and Boyce 1990; Gregg and Crawford 2009). Gallinaceous chicks likely feed throughout the day to meet their nutritional requirements (Maxson 1977), perhaps at a cost of increased predation risk to both adults and chicks. Similar to our study, Sika (2006) found that days spent brood-rearing were negatively associated with adult survival. Because exogenous resources are the dominant nutritional resources associated with sage-grouse reproductive effort and nesting success (Gregg 2006), reproductive costs likely do not influence survival outside of the reproductive season; rather, nutritional quality during the pre-incubation period is most predictive of productivity (Barnett and Crawford 1994; Gregg 2006). Our findings support our hypothesis that adult survival was influenced by brooding behaviors leading to intraspecific habitat partitioning, rather than nutritional deficits associated with other reproductive activities such as nesting or egg production (*sensu* Blomberg *et al*. 2013). While we do not have data on predator communities in our study area, sage-grouse research has repeatedly demonstrated that habitat selection is a balance between meeting biological or reproductive demands and avoiding predation through concealment or avoidance of riskier habitats (Hagen 2011; Dinkins *et al.* 2012). It reasons that increased conspicuousness during the brood-rearing reproductive state may be at the expense of increased predation risk in selected habitats. Our results suggest that females may be more vulnerable to predation as a function of brood protection, decreased vigilance during foraging, and selection of habitats that provide chick foraging opportunities at the expense of reduced sagebrush concealment cover. Blanco-Fontao *et al.* (2013) suggested that habitat partitioning in greater prairie chickens (*Tympanuchus cupido*) resulted in females selecting more protein rich diets in autumn compared to males who likely selected habitats to reduce predation risk. Similarly, we found that broodless females roosted in areas with denser sagebrush cover that provided greater concealment from predators, but lacked diverse herbaceous understory associated with higher forage quality and greater forb species richness. Because broodless females were not rearing broods, they were likely roosting and foraging in habitats that maximized concealment from predators (Lima 1985) while meeting their more basic nutritional needs. The same parent-offspring conflict (Trivers 1974) has been demonstrated in other Tetraonids, with higher summer mortality of brood-rearing females and habitat partitioning by broodless females that exploit denser cover (Maxon 1978).

Ungulates provide a well-documented case of habitat partitioning and suggest that in some populations, males and females should be effectively managed as separate species (Conradt 1999; Bowyer 2004; Ruckstuhl 2007). Similarly, sufficient differences in habitat selection among individual Tetraonids (Banuelos *et al.* 2008; Blanco-Fontao *et al.* 2013), including sage-grouse under different reproductive states (this study), suggests that this principle should be applied when identifying the array of habitats used by both brood-rearing and broodless female sage-grouse. Sage-grouse habitat management generally focuses on nesting and brood-rearing habitats, however habitat partitioning between brood-rearing and broodless females demonstrated here suggests the need to re-evaluate strategies for sage-grouse habitat conservation. Because adult survival is a critical component of sage-grouse population persistence, particularly in years of poor population productivity when adult female survival may have the greatest influence on population demography (Taylor *et al.* 2012; Dahlgren *et al.* 2016), conserving habitats used by broodless females should also be a top priority of conservation efforts. Maintaining heterogeneous sagebrush landscapes that provide dense overstory cover for broodless females interspersed with more open sagebrush habitats with concomitant herbaceous understories for foraging and brood-rearing is necessary to maintain the variability and juxtaposition of sage-grouse habitats necessary for all individuals within a population.

ACKNOWLEDGMENTS

We received logistical support from T. Christiansen and S. Harter from the Wyoming Game and Fish Department, and S. Oberlie and T. Vosburgh from the Bureau of Land Management-Lander Field Office. This work would not have been possible without the cooperation and help of several landowners and research technicians. This work was supported by the Wyoming Game and Fish Department (grant number WYGF40415); Wyoming Sage-grouse Conservation Fund of the Wyoming Game and Fish Department from Bates Hole, Big Horn Basin, Southwest, South-Central and Wind River/Sweetwater River Local Sage-grouse Working Groups [grant numbers 1001401, 1001970, and 1002656]; the Margaret and Sam Kelly Ornithological Research Fund [grant number170016758]; and Wyoming Wildlife and Natural Resource Trust [grant number 1002157].

LITERATURE CITED

Aldridge, C.L., and Boyce, M.S. (2008). Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. *Israel Journal of Ecology & Evolution* **54**, 389-419.

Alves, J.A., Alves da Silva, A., Soares, A.M.V.M., and Fonseca, C. (2013). Sexual segregation in red deer: is social behaviour more important that habitat preferences? *Animal Behaviour* **85**, 501-509.

Anderson, P.K., and Gill, R.D. (1982). Cox's regression model for counting processes: a large sample study. *Annals of Statistics* **10**, 1100-1120.

Arnold, T.W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* **76**, 391-406.

Atamian, M.T., Sedinger, J.S., Heaton, J.S., and Blomberg, E.J. (2010). Landscape-level assessment of brood rearing habitat for greater sage-grouse in Nevada. *Journal of Wildlife Management* **74**, 1533-1543.

Banuelos, M.J., Quevedo, M., and Obeso, J.R. (2008). Habitat partitioning in endangered Cantabrian capercaille *Tetrao urogallus cantabricus*. *Journal of Ornithology* **149**, 245- 252.

Barnett, J.K., and Crawford, J.A. (1994). Pre-laying nutrition of sage grouse hens in Oregon. *Journal of Range Management* **47**, 114-118.

Baxter, R.J., Larsen, R.T., and Flinders, J.T. (2013). Survival of resident and translocated greater sage-grouse in Strawberry Valley, Utah: a 13-year study. *Journal of Wildlife Management* **77**, 802-811.

Bergerud, A.T., and M.W. Gratson (1988). Survival and breeding strategies of grouse. In ‘Adaptive Strategies and Population Ecology of Northern Grouse’. (Eds. A.T. Bergerud, and M.W. Gratson.) pp. 473-577. (University of Minnesota Press: Minnesota, USA).

Blanco-Fontao, B., Sandercock, B.K., Obeso, J.R., McNew, L.B., and Quevedo, M. (2013). Effects of sexual dimorphism and landscape composition on the trophic behavior of greater prairie chicken. *PLoS ONE* **8**, e79986.

Blomberg, E.J., Sedinger, J.S., Atamian, M.T., and Nonne, D.V. (2012). Characteristics of climate and landscape disturbance influence the dynamic of greater sage-grouse populations. *Ecosphere* **3**, 55.

Blomberg, E.J., Sedinger, J.S., Nonne, D.V., and Atamian, M.T. (2013). Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. *Journal of Avian Biology* **44**, 149-158.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., and Forister, M.L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1-28.

Bowyer, R.T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *Journal of Mammalogy* **85**, 1039-1052.

Bunnell, K.D., Flinders, J.T., Mitchell, D.C., and Warder, J.H. (2004). Occupied and unoccupied sage grouse habitat in Strawberry Valley, Utah. *Journal of Range Management* **57**, 524- 531.

Burger, J., Howe, M.A., Hahn, C., and Chase, J. (1977). Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. *Auk* **94**, 743-758.

Burnham, K.P., and Anderson, D.R. (2004). Multimodal inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* **33**, 261-304.

Burnham, K.P., and Anderson, D.R. (Eds.) (2002). 'Model Selection and Multimodal Inference: a Practical Information-Theoretic Approach, 2nd edition.' (Springer Science + Business Media: New York, USA.)

Canfield, R.H. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry* **39**, 388-394.

Connelly, J.W., Knick, S.T., Schroeder, M.A., and Slater, S.J. (2004). Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming, USA.

Connelly, J.W., Rinkes, E.T., and Braun, C.E. (2011a). Characteristics of greater sage-grouse habitats: a landscape species at the micro and macro scales. In 'Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats' (Eds. S.T. Knick, and J.W. Connelly.) pp. 69-83. (Studies in Avian Biology, Volume 38. University of California Press: California, USA.)

Connelly, J.W., Rinkes, E.T., and Braun, C.E. (2011b). Characteristics and dynamics of greater sage-grouse populations. In ‘Greater Sage-Grouse Ecology and Conservation of a Landscape Species and its Habitats.’ (Eds. S.T. Knick, and J.W. Connelly.) pp. 53-68. (Studies in Avian Biology, Volume 38. University of California Press: California, USA.)

Connelly, J.W., Schroeder, M.A., Sands, A.R., and Braun, C.E. (2000). Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* **28**, 967-985.

Conradt, L. (1999). Social segregation is not a consequence of habitat segregation in red deer and feral Soay sheep. *Animal Behavior* **57**, 1151-1157.

Cox, D.R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society Series B* **34**, 187-220.

Cumming, H.G., Beange, D.B., and Lavoie, G. (1996). Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. *Rangifer* **9**, 81-94.

Dalke, P.D., Pyrah, D.B., Stanton, D.C., Crawford, J.E., and Schlatterer, E.F. (1963). Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* **27**, 810-841.

Dahlgren, D.K., Guttery, M.R., Messmer, T.A., Caudill, D., Elmore, R.D., Chi, R., and Koons, D.N. (2016). Evaluating vital rate contributions to greater sage-grouse population dynamics to inform conservation. *Ecosphere* **7**, e01249.

Dahlgren, D.K., Messmer, T.A., Thacker, E.T., and Guttery, M.R. (2010). Evaluation of brood detection techniques: recommendations for estimating greater sage-grouse productivity. *Western North American Naturalist*, **70**, 233-237.

Daubenmire, R. (1959). A canopy-coverage method of vegetational analysis. *Northwest Science* **33**, 43-61.

Dinkins, J.B., Smith, K.T., Beck, J.L., Kirol, C.P., Pratt, A.C., and Conover, M.R. (2016). Microhabitat conditions in Wyoming's sage-grouse core areas: effects on nest site selection and survival. *PLoS ONE* **11**, e0150798.

Dinkins, J.B., Conover, M.R., Kirol, C.P., Beck, J.L., and Frey, S.N. (2014). Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. *Condor* **116**, 629-642.

Dinkins, J.B., Conover, M.R., Kirol, C.P., and Beck, J.L. (2012). Greater sage-grouse (Centrocercus urophasianus) select nest sites and brood sites away from avian predators. *Auk* **129**, 600-610.

Doherty, K.E., Naugle, D.E., and Walker, B.L. (2010). Greater sage-grouse nesting habitat: the importance of managing at multiple scales. *Journal of Wildlife Management* **74**, 1544-1553.

Donovan, T.M., and Thompson, F.R., III. (2001). Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* **11**, 871-882.

Drut, M.S., Crawford, J.A., and Gregg, M.A. (1994). Brood habitat use by sage grouse in Oregon. *Great Basin Naturalist* **54**, 170-176.

Dumroese, R.K., Luna, T., Richardson, B.A., Kilkenny, F.F., and Runyon, J.B. (2015).

Conserving and restoring habitat for greater sage-grouse and other sagebrush-obligate wildlife:

the crucial link of forbs and sagebrush diversity. *Native Plants Journal* **16**, 276-299.

Erikstad, K.E., Fauchald, P., Tveraa, T., and Steen, H. (1998). On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* **79**, 1781-1788.

Frid, A., and Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**, 11.

Giesen, K.M., Schoenberg, T.L., and Braun, C.E. (1982). Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* **10**, 224-231.

Gregg, M.A. (2006). Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival (Doctoral dissertation). Available from ProQuest database (3219759).

Gregg, M.A., and Crawford, J.A. (2009). Survival of greater sage-grouse chicks and broods in the northern Great Basin. *Journal of Wildlife Management* **71**, 646-651.

Gregg, M.A., Crawford, J.A., and Drut, M.S. (1993). Summer habitat use and selection by female sage grouse (*Centrocercus urophasianus*) in Oregon. *Great Basin Naturalist* **53**, 293-298.

Guttery, M.R., Dahlgren, D.K., Messmer, T.A., Connelly, J.W., Reese, K.P., Terletzky, P.A., Burkepile, N., and Koons, D.N. (2013). Effects of landscape-scale environmental variation on greater sage-grouse chick survival. *Plos ONE* **8**, e65582.

Hagen, C.A., Connelly, J.W., and Schroeder, M.A. (2007). A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. *Wildlife Biology* **13**, 42-50.

Hagen, C.A. (2011). Predation on greater sage-grouse: facts, process and effects. In ‘Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats’. (Eds. S.T. Knick, and J.W. Connelly.) pp. 95-100. (Studies in Avian Biology, Volume 38. University of California Press: California, USA.)

Harshman, L.G., and Zera, A.J. (2007). The cost of reproduction: the devil in the details. *Trends in Ecology and Evolution* **22**, 80-86.

Hosmer, D.W., and Lemeshow, S. (1999). ‘Applied Survival Analysis: Regression Modeling of Time to Event Data.’ (John Wiley: New Jersey, USA.)

Huwer, S.L., Anderson, D.R., Remington, T.E., and White, G.C. (2008). Using human-imprinted chicks to evaluate the importance of forbs to sage-grouse. *Journal of Wildlife Management* **72**, 1622-1627.

Johnson, G.D. (1987). Effects of rangeland grasshopper control on sage grouse in Wyoming. (Master Thesis). Available from ProQuest database (EP22602).

Johnson, K.H., and Braun, C.E. (1999). Viability and conservation of an exploited sage-grouse population. *Conservation Biology* **13**, 77-83.

Johnson, G.D., and Boyce, M.S. (1990). Feeding trials with insects in the diet of sage grouse chicks. *Journal of Wildlife Management* **54**, 89-91.

Kaplan, E.L., and Meier, P. (1958). Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* **53**, 457-481.

Kirol, C.P., Beck, J.L., Huzurbazar, S.V., Holloran, M.J., and Miller, S.N. (2015). Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. *Ecological Applications* **25**, 968-990.

Kirol, C.P., Beck, J.L., Dinkins, J.B., and Conover, M.R. (2012). Microhabitat selection for nesting and brood-rearing greater sage-grouse in xeric big sagebrush. *Condor* **114**, 75-89.

Laundre, J.W., Hernandez, L., and Ripple, W.J. (2010). The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* **3**, 1-7.

Lima, S.L. (1985). Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* **66**, 60-67.

Mackie, I.J., and Racey, P.A. (2007). Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): implications for conservation. *Biological Conservation* **140**, 70-77.

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology and Evolution* **6**, 183-186.

Main, M.B., and Coblentz, B.E. (1996). Sexual segregation in Rocky Mountain mule deer. *Journal of Wildlife Management* **60**, 497-507.

Maxon, S.J. (1978). Spring home range and habitat use by female ruffed grouse. *Journal of Wildlife Management* **42**, 61-71.

Maxon, S.J. (1977). Activity patterns of female ruffed grouse during the breeding season. *Wilson Bulletin* **89**, 439-455.

Moynahan, B.J., Lindberg, M.S., and Thomas, J.W. (2006). Factors contributing to process variance in annual survival of female sage-grouse in Montana. *Ecological Applications* **16**, 1529-1538.

NOAA National Centers for Environmental Information. (2016). Annual Climatological Summary for station Lander 1 N, WY US COOP:485392, for 2011 and 2012, Asheville, NC, USA. http://www1.ncdc.noaa.gov/pub/orders/cdo/672061.pdf.

Olson, R.A., and Whitson, T.D. (2002). Restoring structure in late successional sagebrush communities by thinning with tebuthiuron. *Restoration Ecology* **10**, 146-155.

Pollock, K.H., Winterstein, S.R., Bunch, C.M., and Curtis, P.D. (1989). Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* **53**, 7-15.

Pianka, E.R. (1970). On R and K selection. *American Naturalist* **104**, 592-597.

R Core Team. (2015). R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Robel, R.J., Briggs, J.N., Dayton, A.D., and Hulbert, L.D. (1970). Relationship between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* **23**, 295-297.

Rotella, J.J., Dinsmore, S.J., and Shaffer, T.L. (2004). Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* **27**, 187-205.

Ruckstuhl, K.E. (2007). Sexual segregation in vertebrates: proximate and ultimate causes. *Integrative and Comparative Biology* **47**, 245-257.

Schoenfeld, D. (1982). Residuals for the proportional hazards regression model. *Biometrika* **69**, 239-241.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Deibert, P.A., Gardner, S.C., Hilliard, M.A., Kobriger, G.D., McAdam, S.M., McCarthy, C.W., McCarthy, J.J., Mitchell, D.L., Rickerson, E.V., and Stiver, S.J. (2004). Distribution of sage-grouse in North America. *Condor* **106**, 363-376.

Schroeder, M.A., Young, J.R., and Braun, C.E. (1999). Sage grouse (*Centrocercus urophasianus*). In 'The Birds of North America.' (Eds. A. Poole, and F. Gill.) pp. 1-28. (The Birds of North America Inc: New York, USA.)

Shepherd, J.F., Reese, K.P., and Connelly, J.W. (2011). Landscape fragmentation and nonbreeding greater sage-grouse. In 'Ecology, Conservation, and Management of Grouse' (Eds. B.K. Sandercock, K. Martin, and G. Segelbacher.) pp. 77-88. (Studies in Avian Biology Volume 39. University of California Press: California, USA.)

Sika, J.L. (2006). Breeding ecology, survival rates, and causes of mortality of hunted and nonhunted greater sage-grouse in central Montana (Master thesis).

Sveum, C.M., Crawford, J.A., and Edge, W.D. (1998). Use and selection of brood-rearing habitat by sage grouse in south central Washington. *Great Basin Naturalist* **58**, 344-351.

Taylor, R.L., Walker, B.L., Naugle, D.E., and Mills, L.S. (2012). Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* **76**, 336-347.

Therneau, T.M., and Grambsch, P.M. (2000). ‘Modeling Survival Data: Extending the Cox Model.’ (Springer: New York, USA.)

Thompson, K.M., Holloran, M.J., Slater, S.J., Kuipers, J.L., and Anderson, S.H. (2006). Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. *Western North American Naturalist* **66**, 332-342.

Trivers, R.L. (1974). Parent-offspring conflict. *American Zoologist* **14**, 249-264.

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. Federal Register **80**, 59858-59942.

Venables, W.N., and Ripley, B.D. (2002). ‘Modern applied statistics with S. 4th edition.’ (Springer: New York, USA.)

Wakkinen, W.L., Reese, K.P., Connelly, J.W., and Fischer, R.A. (1992). An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* **20**, 425-426.

Walker, B.L. (2008). Greater sage-grouse response to coal-bed natural gas development and west Nile virus in the Powder River Basin, Montana and Wyoming (Doctoral dissertation). Available from ProQuest database.

Wallstad, R.O. (1971). Summer movements and habitat use by sage grouse broods in central Montana. *Journal of Wildlife Management* **35**, 129-136.

Wambolt, C.L., Frisina, M.R., Knapp, S.J., and Frisina, R.M. (2006). Effect of method, site, and taxon on line-intercept estimates of sagebrush cover. *Wildlife Society Bulletin* **34**, 440-445.

Werner, E.E., Hall, D.J., Laughlin, D.R., Wagner, D.J., Wilsmann, L.A., and Funk, F.C. (1977). Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada* **34**, 360-370.

Winterstein, S.R., Pollock, K.H., & Bunck, C.M. (2001). Analysis of survival data from radiotelemetry studies. In 'Radio Tracking and Animal Populations.' (Eds. J.J. Millspaugh, and J.M. Marzluff.) pp. 352-380. (Academic Press: Massachusetts, USA.)

Table 1. Variables used in model selection evaluating greater sage-grouse microhabitat selection in central Wyoming, USA, 2011–2013. Ground cover and herbaceous canopy cover were estimated from 17 Daubenmire ($0.1 m^2$) quadrats at each location.

Variable names	Description
Ground Cover (%)	
Bground	Mean bare ground from Daubenmire quadrats
Cactus	Mean cactus cover from Daubenmire quadrats
Crypto	Mean biological soil crust cover from Daubenmire quadrats
Gravel	Mean gravel cover from Daubenmire quadrats
Litter	Mean litter cover from Daubenmire quadrats
Height and Visual Obstruction	
BsageH[1,2]	Mean big sagebrush height (cm) for each plant along 2, perpendicular 30 m transects
ShrubH[1,2]	Mean total shrub height (cm) from each plant along 2, perpendicular 30 m transects
PerGrassH	Averaged maximum perennial grass droop height from Daubenmire quadrats
ResGrassH	Averaged maximum residual grass droop height from Daubenmire quadrats
VO[1]	Visual obstruction estimated from Robel pole (dm)
Herbaceous Canopy Cover (%)	
AnGrass	Mean annual grass cover from Daubenmire quadrats
PerGrass	Mean perennial grass cover from Daubenmire quadrats
ResGrass	Mean residual grass cover from Daubenmire quadrats
FoodF[3]	Mean food forb cover from Daubenmire quadrats
NFoodF	Mean non-food forb cover from Daubenmire quadrats
SpeciesR	Mean food forb species richness from Daubenmire quadrats
Shrub Characteristics	
Bsage[1,2]	Mean big sagebrush cover (%) measured from 2, perpendicular 30 m transects
BsageD	Big sagebrush density (plants m^{-2}) measured along 2, perpendicular 30 m transects
Shrub[1,2]	Mean total shrub cover (%) estimated from 2, perpendicular 30 m transects
ShrubD	Total shrub density (plants m^{-2}) measured along 2, perpendicular 30 m transects

[1] Quadratic transformations assessed

[2] Standard deviation with 2, perpendicular 30 meter transects for cover and height

Table 2. Top and competing ($w_i \geq 10\%$ of top model w_i) multinomial logistic regression models best explaining sage-grouse selection for early-brood, late-brood, and broodless female microhabitat in central Wyoming, USA, 2011–2013.

Model	K	ΔAICc	w_i	Deviance
[BsageD, ShrubSD, Shrub, Shrub^2], [VO, VO^2], [NFoodF, SpeciesR], [Bground, Crypto, Litter]	36	0.00	0.58	894.96
[BsageD, ShrubSD, Shrub, Shrub^2], [VO, VO^2], [NFoodF, SpeciesR]	27	1.10	0.33	916.82
Null	3	161.00	0.00	1128.12

Table 3. Parameter estimates with 90% confidence intervals (LCL and UCL) from top multinomial logistic regression model comparing sage-grouse early brood, late brood, and broodless hen microhabitat selection relative to random habitats in central Wyoming, USA, 2011–2013.

	Early Brood vs. Random				**Late Brood vs. Random**				**Broodless vs. Random**			
Parameter	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**
Intercept	-5.734	0.355	-6.318	-5.150	-4.707	0.746	-5.934	-3.479	-3.862	0.679	-4.980	-2.744
Shrub cover variables												
BsageD	0.435	0.241	0.039	0.832*	-0.541	0.336	-1.093	0.011	-0.139	0.229	-0.516	0.238
ShrubSD	0.026	0.019	-0.005	0.057	0.054	0.016	0.028	0.081*	0.005	0.017	-0.022	0.032
Shrub	0.046	0.066	-0.063	0.154	0.036	0.062	-0.066	0.138	-0.026	0.052	-0.112	0.059
Shrub^2	-0.001	0.001	-0.003	0.001	0.000	0.001	-0.002	0.001	0.001	0.001	-0.001	0.002
Horizontal visual obstruction variables												
VO	1.881	0.425	1.181	2.581*	0.362	0.427	-0.340	1.065	1.648	0.357	1.061	2.235*
VO^2	-0.230	0.066	-0.340	-0.121*	-0.014	0.050	-0.097	0.069	-0.132	0.043	-0.202	-0.061*
Herbaceous canopy cover variables												
SpeciesR	0.828	0.241	0.431	1.225*	1.516	0.262	1.085	1.948*	-0.202	0.250	-0.611	0.208
NFoodF	-0.224	0.064	-0.329	-0.118*	-0.103	0.055	-0.194	-0.011*	0.038	0.031	-0.014	0.090

*90% confidence intervals that do not include zero

Table 4. Mean microhabitat characteristics and standard errors (in parentheses) of sage-grouse early brood, late brood, broodless and random locations in central Wyoming, USA, 2011–2013.

Characteristic	**Early Brood**	**Late Brood**	**Broodless**	**Random**
BsageD	1.5 (0.1)	1.1 (0.1)	1.3 (0.1)	1.3 (0.1)
ShrubSD	22.1 (1.4)	30.4 (2.8)	24.8 (0.9)	19.8 (0.5)
VO	2.7 (0.1)	3.6 (0.3)	3.7 (0.2)	2.2 (0.1)
SpeciesR	0.8 (0.1)	1.1 (0.1)	0.5 (0.1)	0.5 (0.0)
NFoodF	1.3 (0.3)	1.8 (0.4)	3.6 (0.4)	2.8 (0.3)

Table 5. Parameter estimates, risk ratios, and 90% confidence intervals (LCL and UCL) for variables that were used to assess adult female survival to 13.5 weeks in central Wyoming, 2011–2013.

Parameter	**Estimate**	**SE**	**Risk ratio**	**LCL**	**UCL**
Total reproductive effort	0.019	0.010	1.019	1.001	1.036
Brood-rearing effort	0.027	0.018	1.027	0.996	1.059
Distance moved	0.000	0.000	1.000	0.999	1.001

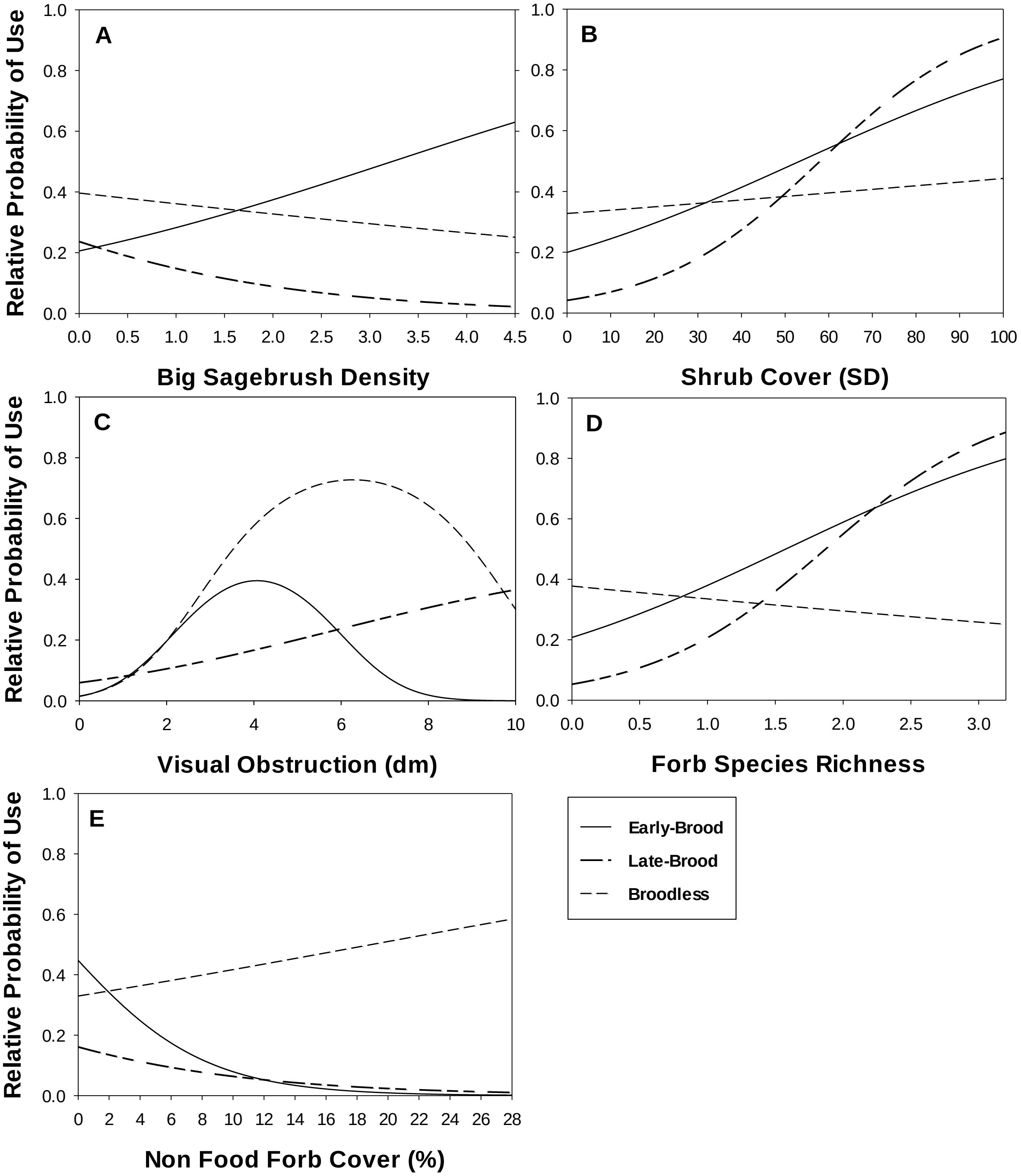


Figure 1. Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of big sagebrush density (A), variability in shrub cover (B), visual obstruction (C), forb species richness (D), and non-food forb cover (E) in central Wyoming, USA, 2011–2013.

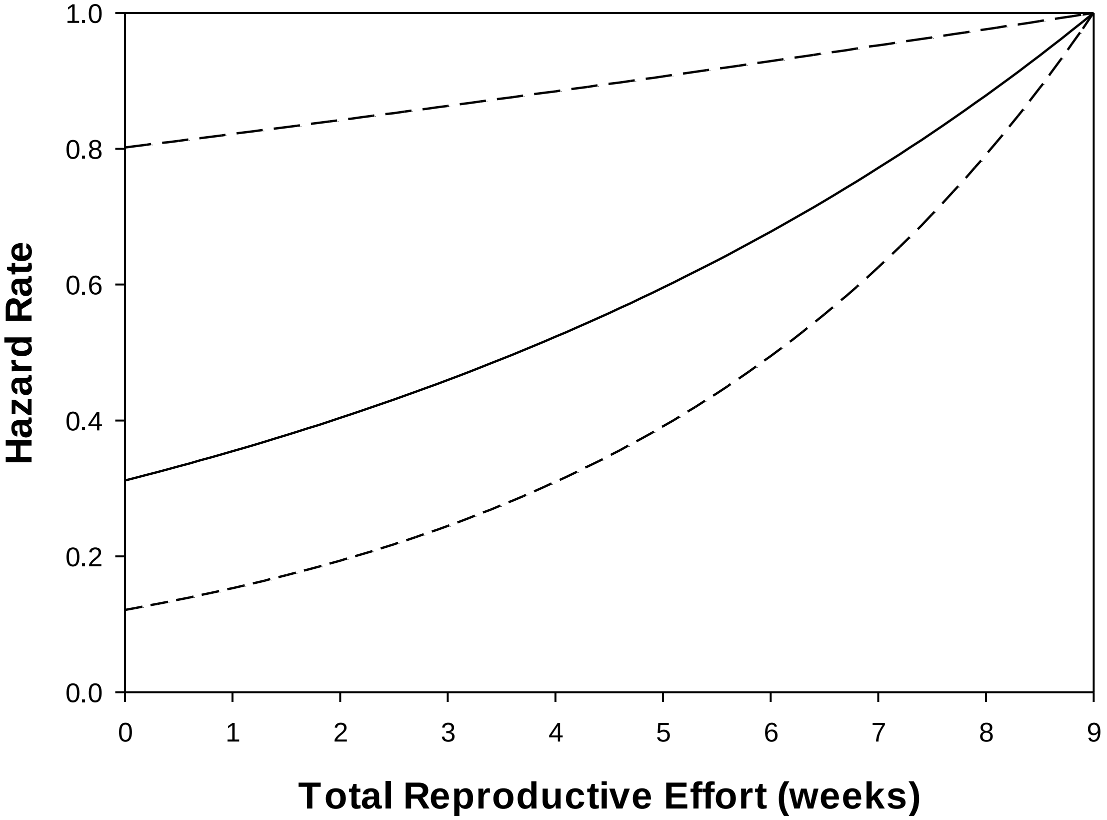


Figure 2. Hazard rates for the most supported model that included total reproductive effort (weeks) predicting adult female sage-grouse survival in central Wyoming, USA, 2011–2013. Hazard rates were plotted with 90% confidence intervals (hashed lines).

CHAPTER FOUR

Effects of Mowing and Tebuthiuron Treatments on the Nutritional Quality of Sagebrush in Central Wyoming

In the format for manuscripts submitted to *Rangeland Ecology and Management*

Abstract.

Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) is the most abundant and well distributed subspecies of big sagebrush and has been treated through chemical application, mechanical treatments, and prescribed burning to improve habitat conditions for species such as greater sage-grouse (*Centrocercus urophasianus*) and mule deer (*Odocoileus hemionus*). Although the response of structural attributes of sagebrush communities to treatments is well understood, there is a need to identify how sagebrush treatments influence the quality of winter food available for wildlife. The purpose of our research was to identify how mowing and tebuthiuron (Spike® 20P Dow AgroSciences, Indianapolis, IN) treatments intended to reduce sagebrush canopy cover influenced dietary quality of Wyoming big sagebrush in central Wyoming. Two study areas were mowed in January and February 2014 and tebuthiuron was applied in two study areas in May 2014. We constructed 6 exclosures in each of 4 study areas (24 total), which encompassed 30 m x 30 m areas of treated and untreated sagebrush within each exclosure. Samples of current annual growth were collected from 18 sagebrush plants from treatment sites and 12 plants from control sites within each exclosure during November 2013–2015. Samples were analyzed for crude protein and plant secondary metabolites known to influence dietary selection of sagebrush by sage-grouse and other sagebrush occurring species.

Our results suggest that mowing and tebuthiuron treatments may slightly increase crude protein concentrations directly after treatments without immediate changes in plant secondary metabolites. Slight increases in dietary quality of sagebrush following treatments coupled with potential trade-offs with loss of biomass associated with treatments corroborates previous research that treating Wyoming big sagebrush habitats may have little benefit for sage-grouse and other sagebrush occurring wildlife. Future work should evaluate not only how treatments influence sage-grouse habitat use and reproductive success, but how treatments influence other wildlife species in fragile sagebrush ecosystems.

INTRODUCTION

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) is the most widely distributed subspecies of big sagebrush and provides important habitat and foraging resources for many wildlife species (Beck et al. 2012). Sagebrush is the primary food source for greater sage-grouse (*Centrocercus urophasianus*; hereafter, 'sage-grouse') during late fall, winter, and spring (Wallestad et al. 1975; Connelly et al. 2000) and may comprise greater than 50% of the winter diets of pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*; Mason 1952; Austin and Urness 1983).

Sage-grouse have experienced long-term range-wide declines (Connelly and Braun 1997) and occur in approximately 56% of their pre-settlement habitats (Schroeder et al. 2004). Declining sage-grouse populations are largely attributed to human mediated loss and fragmentation of sagebrush habitats (Connelly et al. 2004). Sage-grouse are a sagebrush obligate species that rely on a variety of sagebrush-dominated habitats for food and cover throughout the year (Connelly et al. 2004, Crawford et al. 2004). A developing body of research has coupled habitat selection and demographic rates to measure habitat quality and population level consequences for sage-grouse (Aldridge and Boyce 2007; Smith et al. 2014; Kirol et al. 2015). Unfortunately, these studies are not often conducive to long-term monitoring of wildlife following natural or management-directed changes in habitat quality across landscapes. In addition, the majority of research has focused on defining sagebrush habitat quality for sage-grouse in terms of height and structural cover, with myriad studies demonstrating the importance of structure and cover for sage-grouse during different life stages (e.g. Hagen et al. 2007). However, because sagebrush comprises a substantial portion of sage-grouse diets, quality of sagebrush habitats should not be defined solely in terms of structural characteristics.

Habitat treatments in big sagebrush communities have been implemented with the intent of improving sage-grouse habitats by reducing competition between sagebrush overstory and herbaceous understory to improve important foraging resources for sage-grouse during the reproductive period (Beck et al. 2012). Treatments often reduce the age structure and density of sagebrush communities and younger age classes of Wyoming big sagebrush plants contain slightly higher levels of crude protein (Wambolt 2004). In addition, reduction in sagebrush density likely alleviates competitive effects between individual plants, allowing greater resource acquisition of remaining unaltered plants (Casper and Jackson 1997) and possibly greater nutritional quality. Plant secondary metabolites (PSMs) occur in high concentrations in sagebrush (Kelsey et al. 1982) and may have negative metabolic consequences for herbivores consuming sagebrush (Forbey et al. 2013). Dietary consumption of high concentrations of PSMs is common in specialist herbivores such as sage-grouse, which reduce absorption of monoterpenes, and excrete large amounts in their feces (Thacker et al. 2012; Kohl et al. 2015). While digestive enzyme activity is less influenced by monoterpenes in sage-grouse compared to species that have not evolved with a sagebrush diet, enzyme inhibition at high levels of dietary monoterpenes could limit sufficient nitrogen acquisition and result in nutritional deficits (Kohl et al. 2015).

There is considerable evidence that nutritional and chemical quality of the diet is important to herbivores (Beckerton and Middleton 1982, Beckerton and Middleton 1983, Jakubas et al. 1993a,b), including sage-grouse (Remington and Braun 1985, Welch et al. 1988, Frye et al. 2013). Frye et al. (2013) determined that sage-grouse selected black sagebrush (*A. nova*) with lower PSM concentrations over Wyoming big sagebrush in winter in southern Idaho. In addition, sage-grouse also selected individual plants within black sagebrush patches that were higher in nutrient concentrations and lower PSM concentrations than available plants (Frye et al. 2013). Dietary quality of sagebrush may have a significant impact on body condition as grouse enter the reproductive period. For example, ruffed grouse (*Bonasa umbellus*) consuming diets with higher crude protein had higher reproductive success (Beckerton and Middleton 1982). In addition, ruffed grouse consuming winter diets higher in crude protein and lower chemical defenses had higher population densities (Beckerton and Middleton 1982, Beckerton and Middleton 1983, Jakubas et al. 1993b).

Our specific objective was to determine how tebuthiuron application and mechanical removal of sagebrush influenced the dietary quality of Wyoming big sagebrush. Herbicide applications, mechanical treatments, and prescribed burning form the major types of treatments that have been applied in efforts to enhance wildlife habitats in Wyoming big sagebrush (Beck et al. 2009, 2012; Hess and Beck 2012; Davies et al. 2009). Prescribed burning Wyoming big sagebrush to enhance habitat for sage-grouse is problematic in most instances because the shrub structure needed by sage-grouse for nesting, brood-rearing and winter habitat is lost for decades (Beck

1977, Beck et al. 2009, Hess and Beck 2012). Consequently, mechanical treatments may be more suitable to treat sage-grouse habitat because residual sagebrush remains on treated sites and herbicide such as tebuthiuron do not kill all sagebrush plants (Olson and Whitson 2002) and leave behind shrub skeletons that sage-grouse may use for cover (Dahlgren et al. 2006). Only Davies et al. (2009) has investigated the influence of mowing on crude protein of sagebrush leaves and no studies to our knowledge have evaluated the influence of herbicide treatment on dietary quality of sagebrush. Further, increase in crude protein alone does not necessarily indicate an increase in nutritional quality as PSMs strongly influence selection by sage-grouse (Forbey et al. 2013). We thus evaluated how mowing and tebuthiuron applications influenced crude protein and PSMs in leaves of treated and untreated Wyoming big sagebrush plants. We used crude protein as a nutrient variable because it can affect herbivore foraging behavior and reproductive success (Mattson 1980). We chose monoterpenes and polyphenolics (coumarins and total phenolics) because these classes of compounds exert deleterious effects (e.g., toxicity, increased energy expenditure, nutrient binding) on herbivores (Dearing et al. 2005) and occur in relatively high concentrations in sagebrush (Kelsey et al. 1982).

MATERIALS AND METHODS

Study area

Our study area included portions of Fremont and Natrona counties, Wyoming and encompassed ~3,098 km2 (735,879 ac; Figure 1), and was composed of approximately 81% Federal, 6.9% State, and 12.1% privately administered lands. Average annual 30-year normal precipitation and temperature were 26 cm and 6.1 °C, respectively (Prism Climate Group 2016). Elevation ranged from 1642 to 2499 m. Notable vegetation communities in the study area included Wyoming big sagebrush, mountain big sagebrush (*A. t. vaseyana*), basin big sagebrush (*A. t. tridentata*), silver sagebrush (*A. cana*), black sagebrush, and greasewood (*Sarcobatus vermiculatus*). Major land uses during the study included livestock grazing.

Treatments consisted of mechanical mowing and aerially broadcasted tebuthiuron (Spike® 20P, Dow AgroSciences, Indianapolis, IN) to sagebrush in early brood-rearing habitats during winter and spring 2014. Treatments followed guidelines of the Wyoming Game and Fish Department (WGFD) Protocols for Treating Sagebrush to be Consistent with Wyoming Executive Order 2011-5; Greater Sage-Grouse Core Area Protection (WGFD 2011). The only exception to the WGFD protocols was that instead of grazing rest for 2 growing seasons following treatments, we installed exclosures to measure post-treatment vegetative response in the absence of grazing. This was necessitated by the fact that only 1 allotment in the 4 treatment study areas had cross fencing and a rotational grazing system. The remaining treatment study areas occurred in areas with season-long continuous grazing, making evaluations of un-grazed post treatment vegetation responses impossible without exclosures. Therefore, we installed 12, 30 x 60 m exclosures in mowed sites and 12, 30 x 80 m exclosures in tebuthiuron treated sites—exclosures constructed in tebuthiuron-treated areas were larger to account for potential herbicide leaching into the untreated side—during May 2014 to serve as controls for livestock grazing. The general design of these exclosures was to exclude a 30 x 30 m (0.09 ha) area of untreated sagebrush with an adjoining 30 x 30 m area excluding livestock grazing in treated sagebrush (Figure 2). Treatments occurred in a mosaic pattern across 4 general locations (2 tebuthiuron and 2 mowing treatments; Appendix A). During January and February 2014, 489 ha of sagebrush habitats were mowed to a height of 25.4 cm across 2 mowing treatment areas. Mowing treatment study areas were 50.0 km^2 and 33.8 km^2, respectively. Tebuthiuron application occurred in early

May 2014. Contractors applied 0.22 kg/ha active ingredient to 607 ha across 2 study areas, anticipating a 50% kill rate of sagebrush. Tebuthiuron study areas were 24.9 km^2 and 44.8 km^2, respectively. Treatments occurred across less than 5% of each study to be consistent with WGFD guidelines (WGFD 2011).

Field methods

Prior to treatments, we randomly selected 18 plants (with at least 6 plants less than 25.4 cm) within the treated portion of each mowing exclosure to maximize the likelihood of at least 6 plants surviving (assuming less than a 50% kill outcome in treatments) and 12 plants (with at least 6 plants less than 25.4 cm) within the untreated portions of each of the 12 exclosures. We collected 5–8 sprigs from each selected sagebrush plant within each collection site by clipping the stems with pruning shears and minimizing damage to remaining leaves and stems. Each plant was marked with a metal plant tag to allow for long term monitoring of treatment effects on dietary quality of plants. Sagebrush samples were stored in a –20 °C freezer. We were unable to sample at tebuthiuron exclosure locations prior to treatment because these locations were not yet delineated during the pre-treatment sampling period.

During sampling following treatments (November 2014 and 2015), we collected vegetation from 6 previously sampled plants that survived treatment, plus an additional 6 plants in each treatment that were not sampled during the previous sampling period. Collection and analysis of new plants allowed us to account for effects of clipping on diet quality. Post-treatment sampling focused on collecting stems from plants containing new growth during the second winter season. Because we were unable to sample at tebuthiuron exclosure locations prior to treatment, 2014 sampling at tebuthiuron exclosures was consistent with pre-treatment sampling at mowing exclosure locations.

Laboratory methods

Of the original 18 plants sampled within the treated portions of exclosures, we only analyzed those plants that survived through the post-treatment sampling periods. In addition, we ensured that the sizes of plants sampled were similar between treatment and control plots. We found no differences between new or repeatedly sampled shrubs collected during 2014 in the mowing exclosures (control and mow) for any of the plant secondary chemicals analyzed (ANOVA, $P > 0.05$); therefore, new plants were selected for all analyses for 2015 mowing and tebuthiuron treatments. Samples were submerged in liquid nitrogen and sagebrush leaves were removed from woody stems. Samples were compiled and homogenized according to site, treatment and exclosure. Six samples from each exclosure were selected for the composite samples. We ground samples into a coarse powder using a mortar, pestle and liquid nitrogen until particles were ≤ 2 mm. Samples were then allocated into headspace vials for gas chromatography and micro-centrifuge tubes for chemical analysis of coumarins and total phenolics. For crude protein (% dry matter), a minimum of 1.7 g of coarsely ground sagebrush composites were dried for 48 hours and assessed using combustion method elemental analysis of nitrogen (Dairy One Forage Laboratories, Ithaca, New York). Sagebrush composites (0.1 g) were analyzed for monoterpenes (AUC/mg) with headspace gas chromatography (GC) using an Agilent 7694 Headspace Autosampler coupled with an Agilent 6890N gas chromatograph. One ml of headspace gas was injected into J and W DB-5 capillary columns (30m x 250μm x 0.25μm; Operating conditions:

oven temperature at 100°C, loop temperature at 110°C, transfer line temperature at 120°C, vial equilibrium time of 20 min, a pressurization time of 0.20 min, a loop fill time of 0.50 min, a loop equilibrium time of 0.20 min, and an injection time of 0.50 min; Operating conditions for GC: splitless injector at 250°C, flame ionization detector at 300°C, oven temperature at 40°C for 2 min, then increasing 3°C/min to 60°C, then increasing 5°C/min to 120°C, then increasing 20°C/min to 300°C, and held at 300°C for 7 min; J.S. Forbey, personal communication, 2016). The make-up gas was nitrogen and the carrier gas was helium. The inlet pressure was 80 KPa with a flow rate of 1.0 mL/min. Volatile monoterpenes were identified by matching retention times to cocktails of known monoterpene composition and concentration. Retention times and peak areas were calculated using HP ChemStation version B.01.00 (Santa Clara, California, USA). Peak areas were calculated by integrating chromatogram curves; compounds with peak areas greater than 1% of the total area were used in the analysis.

Coumarins (umol/g) and total phenolics (umol/g) were assessed using colorimetric assays. Samples (50 mg) were extracted for two 3-minute periods in 1.0 ml GC-grade methanol in a sonicating water bath and filtered through glass wool. For the coumarin assay, 50 μl subsamples were pipetted into a 96-well plate in triplicate. Color intensity was measured using a BioTek Synergy MX multi-mode plate reader (BioTek, Winooski, Vermont, USA) at an absorbance of 350 nm excitation and 460 nm emission at room temperature. Scopoletin (number 5995-86-8, Acros Organics) diluted in methanol was used as a standard (0 to 80 μM). We used an adapted Folin-Ciocalteau assay to measure total phenolics (Ainsworth and Gillespie 2007). Samples were diluted with methanol to fit within the standard curve. Gallic acid (number 92-6-15, Acros Organics) diluted in methanol was used as a standard (0 to 580 μM). For each sample and standard, 20 μl of the dilution was pipetted in triplicate into 96 well plates. Next, 100 μl of 10%

Folin-Ciocalteau reagent was added to each well, mixed and 80 μl of 700 mM (7.5%) sodium carbonate was added and mixed. Plates were allowed to incubate for 2 hours, and were then shaken on the plate reader for 60 seconds before reading. Color intensity was measured using a BioTek Synergy MX multi-mode plate reader at an absorbance of 765 nm at room temperature.

Statistical analysis

We used linear mixed models (package nlme; Pinheiro et al. 2016) to test the response of sagebrush dietary quality (crude protein, monoterpenes, coumarins, and total phenolics) to mowing and tebuthiuron treatments. Fixed factors included treatment type and year, with exclosures (with year and type nested within exclosure) treated as a random effect. We performed separate models for each treatment type (mowing or tebuthiuron) and dietary response to compare differences between treatments and controls within exclosures. In addition, we assessed differences between mowing and tebuthiuron treatments during 2014 and 2015, where the response of paired control plots was subtracted from treatments. We used least square means with Tukey adjustments to assess *post hoc* differences between treatment and controls or mowing and herbicide treatments across sampling years (package lsmeans; Length 2016). We removed any outliers from analysis and assessed normality of model residuals. We performed all statistical analyses in R statistical software (R version 3.2.4, R Core Team 2016) and set statistical significance at $\alpha = 0.05$.

RESULTS

Mowing treatments

Comparison of mowing exclosures revealed no differences in crude protein between treatment and control ($F_{1, 22} = 1.76$, $P = 0.198$), year ($F_{2, 44} = 1.65$, $P = 0.205$), or treatment by year interaction ($F_{2, 44}$ =2.31, P = 0.111). However, *post hoc* analysis indicated that mowing treatments had higher crude protein compared to controls during 2015 (*post hoc*, P = 0.027; Figure 3). For monoterpenes, we found no difference between treatment and controls at mowing exclosures (Treatment: $F_{1,22}$ = 0.040, P = 0.843; Treatment x Year: $F_{2,44}$ = 1.60, P = 0.214). We detected a difference across years ($F_{2, 44}$= 7.32, P = 0.002), with lower monoterpene concentrations in 2013 compared to 2014 (*post hoc*, P = 0.023) and 2015 (*post hoc*, P = 0.002). Similarly, we found no differences in coumarin concentrations between treatment and controls at mowing exclosures (Treatment: $F_{1,22}$ = 0.049, P = 0.837; Treatment x Year: $F_{2,44}$ = 0.21, P = 0.813); however, coumarin concentrations differed across years ($F_{2,44}$ = 16.47, P < 0.001), with coumarins lower in 2015 compared to 2013 and 2014 (*post hoc*, P < 0.001). For total phenolics, we did not detect differences between treatment and controls (Treatment: $F_{1,22}$ = 0.55, P = 0.465; Treatment x Year: $F_{2,44}$ = 0.49, P = 0.617), but found differences across years ($F_{2,44}$ = 22.97, P < 0.001), with 2015 samples having lower total phenolic concentrations compared to 2013 and 2014 (*post hoc*, P < 0.001).

Tebuthiuron treatments

We found differences between herbicide and control treatments ($F_{1,22}$ = 9.78, P = 0.005) and year ($F_{1,22}$ = 21.90, P < 0.001), but did not detect a significant treatment by year interaction ($F_{1,22}$ = 0.18, P = 0.677; Figure 3). We found higher crude protein in tebuthiuron treatments compared to paired controls during 2014 (*post hoc*, P = 0.006) and 2015 (*post hoc*, P = 0.014), and overall crude protein levels were greater in 2014 compared to 2015 (*post hoc*, P < 0.001). For monoterpenes, we did not detect differences between treatment and controls ($F_{1,22}$ = 0.12, P = 0.735) across years ($F_{1,22}$ = 3.11, P = 0.092) or for the treatment x year interaction ($F_{1,22}$ = 0.032, P = 0.859). We found no differences in coumarin concentrations between treatment and control in tebuthiuron in exclosures (Treatment: $F_{1,22} = 0.49$, $P = 0.490$; Treatment x Year: $F_{1,22} = 0.12$, $P = 0.734$); however, we did detect differences across years ($F_{1,22} = 7.35$, $P = 0.013$), with greater coumarin concentrations in 2014 compared to 2015. Similarly, we did not detect differences in concentrations of total phenolics between tebuthiuron and control treatments ($F_{1,22} = 0.79$, $P = 0.384$) or the treatment x year interaction ($F_{1,22} = 2.67$, $P = 0.116$), but total phenolics were greater in 2015 ($F_{1,22} = 11.22$, $P = 0.003$).

Comparison of mowing and tebuthiuron treatments

Comparison between paired differences of treatment and controls indicated a difference in crude protein between tebuthiuron and mowing treatments ($F_{1,22} = 11.58$, $P = 0.003$; Figure 4). There were no differences between year ($F_{1,22} = 0.19$, $P = 0.663$) and the treatment by year interaction was not significant ($F_{1,22} = 1.20$, $P = 0.28$). Crude protein was greater at tebuthiuron treated exclosures compared to mowing exclosures during 2014 (*post hoc*, $P = 0.003$), but no differences were detected during 2015 (*post hoc*, 0.073; Figure 2). We found no differences between treatments, years, or treatment x year interactions for monoterpenes, coumarins, or total phenolics.

DISCUSSION

Relatively little information exists about the effects of management practices on the dietary quality of shrubs. Although several studies have investigated how management practices influence diversity and composition of sagebrush communities (Davies et al. 2011a; Davies et al. 2012), only Davies et al. (2009) have investigated the influence of mowing on dietary quality of sagebrush and our study is the first to evaluate the influence of herbicide treatments on sagebrush dietary quality. We found that mowing and herbicide treatments resulted in sagebrush plants with greater leaf crude protein content compared to untreated controls. We did not collect pre-treatment information on herbicide treatments; nonetheless our results suggest that sagebrush plants treated with herbicide had greater leaf crude protein content compared to mowing treatments at least during the first year following treatments. However, we did not detect differences in PSMs between treated and untreated plants, or between treatment types, but our results corroborate others that found annual variation in PSMs (Cedarleaf et al. 1983; Wilt and Miller 1992).

Changes in the availability of quality food pose a threat to a variety of terrestrial species. Recent work from Idaho revealed strong evidence that the nutritional and chemical quality of sagebrush, not structural cover, explained habitat selection by sage-grouse (Frye et al. 2013) and pygmy rabbits (*Brachylagus idahoensis*; Ulappa et al. 2014). This research suggested that wildlife managers should be concerned with preserving the dietary quality of sagebrush and should identify how management-driven changes to habitats influence the dietary quality of sagebrush specifically in areas dominated by Wyoming big sagebrush. Wyoming big sagebrush communities have undergone significant changes due to invasion of non-native grass species, wildlife, and management practices that reduce sagebrush (Davies et al. 2011b; Beck et al. 2012). Increases in CO_2, drought, and temperatures associated with climate change are likely to reduce the dietary quality of remaining sagebrush (Bidart-Bouzat and Imeh-Nathaniel 2008, Karban 2011, Robinson et al. 2012). Future sage-grouse populations may experience both the loss of biomass and reduction in the dietary quality of existing sagebrush, which could be mitigated or exacerbated by management practices (Forbey et al. 2013).

Sage-grouse are reliant on sagebrush for food during winter (Wallestad et al. 1975) and treatments may be utilized by sage-grouse during this time, provided snow cover does not preclude access to remaining sagebrush canopy. Further, sagebrush is an important dietary component of female sage-grouse during the pre-laying period prior to new forb growth (Connelly et al. 2000; Gregg et al. 2006). It is often argued that sagebrush plant age is related to plant nutritional quality; however, Kelsey et al. (1982) and Wambolt (2004) report negligible differences in crude protein levels with plant age class. Davies et al. (2009) found slight increases in crude protein level in treated Wyoming big sagebrush habitats up to 6 years following mechanical treatments, but cautioned that minor increases in nutritional quality of treated sagebrush is unlikely to offset the negative impacts of long term reduction in cover and density for sage-grouse and other wildlife. We detected slight increases in crude protein in mowing and tebuthiuron-treated sagebrush, corroborating findings of Davies et al. (2009). However, we agree with Davies et al. (2009) that slight increases in crude protein in mowed sagebrush unlikely offset the reduction in cover, density, and biomass of sagebrush habitats for wildlife. In contrast, tebuthiuron treatments leave behind shrub skeletons that sage-grouse may use for cover (Dahlgren et al. 2006). If sufficient cover remains within herbicide treatments, increased palatability of sagebrush may improve habitat quality as a result of herbicide treatments. Beckerton and Middleton (1982) found that captive female ruffed grouse fed diets with approximately 2% greater crude protein on a per percentage dry matter basis, had greater clutch sizes and mean egg weights, but did not exhibit increased hatching success. An approximate 10% increase in crude protein in the diet of captive female ruffed grouse did increase hatching success, but clutch sized, mean egg weight, and hatching success were similar to wild females (Beckerton and Middleton 1982). In addition, we did not detect differences in PSM concentrations relative to mowing or herbicide treatments, which may better predict dietary selection by sage-grouse compared to crude protein levels alone (Frye et al. 2013). Based on these findings, it is unlikely that marginal increases in crude protein as a result of mowing and herbicide treatments would improve reproductive success for sage-grouse.

The sagebrush ecosystem is among the most imperiled ecosystems in the United States (Davies et al. 2011b) and loss and fragmentation of sagebrush habitats has been identified as a significant threat for remaining sage-grouse populations (Knick et al. 2003); managers should take great caution when altering remaining sagebrush habitats. While some evidence suggests that treatments may improve breeding habitats for sage-grouse in mountain big sagebrush communities (Dahlgren et al. 2006; Dahlgren et al. 2015), our results provide additional evidence that treating Wyoming big sagebrush communities to benefit sage-grouse may not result in a desirable outcome. Specifically, sagebrush communities recovery slowly following disturbances (Baker 2011), often do not increase important forb and insect abundance for sage-grouse diets during the breeding season (Fischer et al. 1996; Nelle et al. 2000; Davies et al. 2007; Rhodes et al. 2010; Davies et al. 2012; Hess and Beck 2014), result in reduction of sagebrush cover important for nesting and brood-rearing habitats (Hagen et al. 2007), and provide only a slight increase in nutritional quality for winter diets (Davies et al. 2009; this study). In addition, emphasis on improving habitats for sage-grouse does not reflect the numerous wildlife species that rely on sagebrush communities yearlong. For example, identifying how to maximize the availability of palatable sagebrush will benefit other herbivores such as pronghorn and pygmy rabbits, which specialize on sagebrush for food and mule deer and elk (*Cervus elaphus*) that would benefit from higher quality food during winter. Further work is needed to understand the relationship between diet and reproductive success of sage-grouse as well as how habitat management targeted at sage-grouse influences habitat quality for other sagebrush occurring wildlife.

LITERATURE CITED

Aldridge, C.L, Boyce, M.S. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Ainsworth, E.A., Gillespie, K.M. 2007. Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin-Ciocalteu reagent. Nature Protocols 2:875–877.

Austin, D.D., Urness, P.J. 1983. Overwinter forage selection by mule deer on a seeded big sagebrush-grass range. Journal of Wildlife Management 47:1203–1207.

Baker, W.L. 2011. Pre-Euro-American and recent fire in sagebrush ecosystems. Pages 185–201 In: Knick, S.T., Connelly, J.W. (eds) Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California.

Beck, T.D.I., 1977. Sage grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18–26.

Beck, J.L., Connelly, J.W., Reese, K.P., 2009. Recovery of greater sage-grouse habitat features in Wyoming big sagebrush following prescribed fire. Restoration Ecology 17:393–403.

Beck, J.L, Connelly, J.W., Wambolt, C.L., 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management 65:444–455.

Beckerton, P.R., Middleton, A.L.A., 1982. Effects of dietary-protein levels on ruffed grouse reproduction. Journal of Wildlife Management 46:569–579.

Beckerton, P.R., and Middleton, A.L.A., 1983. Effects of dietary-protein levels on body-weight, food-consumption, and nitrogen-balance in ruffed grouse. Condor 85:53–60.

Bidart-Bouzat, M.G., Imeh-Nathaniel, A., 2008. Global change effects on plant chemical defenses against insect herbivores. Journal of Integrative Plant Biology 50:1339–1354.

Casper, B.B., Jackson, R.B. 1997. Plant competition underground. Annual Review of Ecology and Systematics 28:545–570.

Cedarleaf, J.D., Welch, B.L., Brotherson, J.D. 1983. Seasonal variation of monoterpenoids in big sagebrush [*Artemisia tridentata*]. Journal of Range Management 36:492–494.

Connelly, J.W., Braun, C.E. 1997. Long-term changes in sage-grouse Centrocercus urophasianus populations in western North America. Wildlife Biology 3:229–234.

Connelly, J.W., Knick, S.T., Schroeder, M.A., Stiver, S.J., 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. In: WAOFAW. Agencies, editor. Cheyenne, Wyoming.

Connelly, J.W., Schroeder, M.A., Sands, A.R., Braun, C.E., 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Crawford, J.A., Olson, R.A., West, N.E., Mosley, J.C., Schroeder, M.A., Whitson, T.D. Miller, R.F, Gregg, M.A., Boyd, C.S., 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.

Dahlgren, D.K, Chi, R., Messmer, T., 2006. Greater sage-grouse response to sagebrush management in Utah. Wildlife Society Bulletin 34:975–985.

Dahlgren, D.K., Larsen, R.T., Danvir, R., Wilson, G., Thacker, E.T., Black, T.A., Naugle, D.E., Connelly, J.W., Messmer, T.A. 2015. Greater sage-grouse and range management: insights from a 25 year case study in Utah and Wyoming. Rangeland Ecology and Management 68:375–382.

Davies, K.W., Bates, J.D., Johnson, D.D., Nafus, A.M., 2009. Influence of mowing *Artemisia tridentata* ssp. *wyomingensis* on winter habitat for wildlife. Environmental Management 44:84–92.

Davies, K.W., Bates, J.D., Miller, R.F. 2007. Short-term effects of burning Wyoming big sagebrush steppe in southeast Oregon. Rangeland Ecology and Management 60:515–522.

Davies, K.W., Bates, J.D., Nafus, A.M. 2011a. Are there benefits to mowing Wyoming big sagebrush plant communities? An evaluation in southeastern Oregon. Environmental Management 48:539–546.

Davies, K.W., Bates, J.D., Nafus, A.M. 2012. Mowing Wyoming big sagebrush communities with degraded herbaceous understories: has a threshold been crossed? Rangeland Ecology and Management 65:498–505.

Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, T.J., Gregg, M.A., 2011b. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573–2584.

Dearing, M.D., Foley, W.J., McLean, S. 2005. The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. Annual Review of Ecology, Evolution, and Systematics 36:169–189.

Fischer, R.A., Reese, K.P., Connelly, J.W. 1996. An investigation on fire effects within xeric sage-grouse brood habitat. Journal of Range Management 49:194–198.

Forbey, J.S., Wiggins, N.L., Frye, G.G., Connelly, J.W. 2013. Hungry grouse in a warming world: emerging risks from plant chemical defenses and climate change. Wildlife Biology 19:374–381.

Frye, G.G., Connelly, J.W., Musil, D.D., Forbey, J.F., 2013. Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology 94:308–314.

Gregg, M.A., Dunbar, M.R., Crawford, J.A., Pope, M.D. 2006. Total plasma protein and renesting by greater sage-grouse. Journal of Wildlife Management 70:472–478.

Hagen, C.A., Connelly, J.W., Schroeder, M.A. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13:42–50.

Hess, J.E., Beck, J.L. 2014. Forb, insect, and soil response to burning and mowing Wyoming big sagebrush in greater sage-grouse breeding habitat. Environmental Management 53:813–822.

Hess, J.E., Beck, J.L, 2012. Burning and mowing Wyoming big sagebrush: do treated sites meet minimum guidelines for greater sage-grouse breeding habitats? Wildlife Society Bulletin 36:85–93.

Jakubas, W.J., Karasov, W.H., Guglielmo, C.G., 1993a. Coniferyl benzoate in quaking aspen (*Populus tremuloides*)- its effect on energy and nitrogen digestion and retention in ruffed grouse (*Bonasa-umbellus*). Physiological Zoology 66:580–601.

Jakubas, W.J., Wentworth, B.C., Karasov, W.H., 1993b. Physiological behavioral-effects of coniferyl benzoate on avian reproduction. Journal of Chemical Ecology 19:2353–2377.

Karban, R., 2011. The ecology and evolution of induced resistance against herbivores. Functional Ecology 25:339–347.

Kelsey, R.G., Stephens, J.R., Shafizadeh. 1982. The chemical-constituents of sagebrush foliage and their isolation. Journal of Range Management 35:617–622.

Kirol, C.P., Beck, J.L, Huzurbazar, S.V., Holloran, M.J., Miller, S.N. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:968–990.

Knick, S.T., Dobkin, D.S., Rotenberry, J.T., Schroeder, M.A., Vander Haegen, W.M., van Riper C. III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Kohl, K.D., Pitman, E., Robb, B.C., Connelly, J.W., Dearing, M.D., Forbey, J.S. 2015. Monoterpenes as inhibitors of digestive enzymes and counter-adaptations in a specialist avian herbivore. Journal of Comparative Physiology B. 185:425–435.

Lenth, R.V. 2016. Least-Squares Means: The R package lsmeans. Journal of Statistical Software 69:1–33.

Mason, E. 1952. Food habitats and measurements of Hart Mountain antelope. Journal of Wildlife Management 16:387–389.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

Nelle, P.J., Reese, K.P., Connelly, J.W. 2000. Long-term effects of fire on sage grouse habitat. Journal of Range Management 53:586–591.

Olson, R.A., Whitson, T.D., 2002. Restoring structure in late successional sagebrush communities by thinning with tebuthiuron. Restoration Ecology 10:146–155.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D, R Core Team. 2016. _nlme: Linear and nonlinear mixed effects models_. R package version 3.1-127. http://CRAN.R-project.org/package=nlme.

PRISM Climate Group. 2016. PRISM Climate DATA. http://www.prism.oregonstate.edu

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org.

Remington, T.E., Braun, C.E., 1985. Sage grouse food selection in winter, North Park, Colorado. Journal of Wildlife Management 49:1055–1061.

Rhodes, E.C., Bates, J.D., Sharp, R.N., Davies, K.W. 2010. Fire effects on cover and dietary resources of sage-grouse habitat. Journal of Wildlife Management 74:755–764.

Robinson, E.A., Ryan, G.D., Newman, J.A., 2012. A meta-analytical review of the effects of elevated CO2 on plant arthropod interactions highlights the importance of interacting environmental and biological variables. New Phytologist 194:321–336.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Deibert, P.A., Gardner, S.C., Hiliard, M.A., Kobriger, G.D., McAdam, S.M., McCarthy, C.W., McCarthy, J.J., Mitchell, D.L., Rickerson, E.V., Stiver, S.J. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Smith, K.T., Kirol, C.P., Beck, J.L., Blomquist, F.C. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:article15.

Thacker, E.T., Gardner, D.R., Messmer, T.A., Guttery, M.R., Dahlgren, D.K. 2012. Using gas chromatography to determine winter diets of greater sage-grouse in Utah. Journal of Wildlife Management 76:588–592.

Ulappa, A.C., Kelsey, R.G., Frye, G.G., Rachlow, J.L., Shipley L.A., Bond, L., Pu, X., Forbey, J.S. 2014. Plant protein and secondary metabolites influence diet selection in a mammalian specialist herbivore. Journal of Mammalogy 95:834–842.

Wallestead, R.O. Peterson, J.G., Eng, R.L. 1975. Foods of adult sage grouse in central Montana. Journal of Wildlife Management 39:628–630.

Wambolt, C.L. 2004. Browsing and plant age relationships to winter protein and fiber of big sagebrush subspecies. Journal of Range Management 57:620-623.

Welch, B.L, Pederson, J.C., Rodgriguez, R.L., 1988. Selection of big sagebrush by sage grouse. Great Basin Naturalist 48:274–279.

Wilt, F.M, Miller, G.C. 1992. Seasonal variation of coumarin and flavonoid concentrations in persistent leaves of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*). Biochemical Systematics and Ecology 20:53–67.

Wyoming Game and Fish Department [WGFD]. 2011. Wyoming Game and Fish Department protocols for treating sagebrush to benefit sage-grouse. http://gf.state.wy.us/wildlife_management/sagegrouse/index.asp

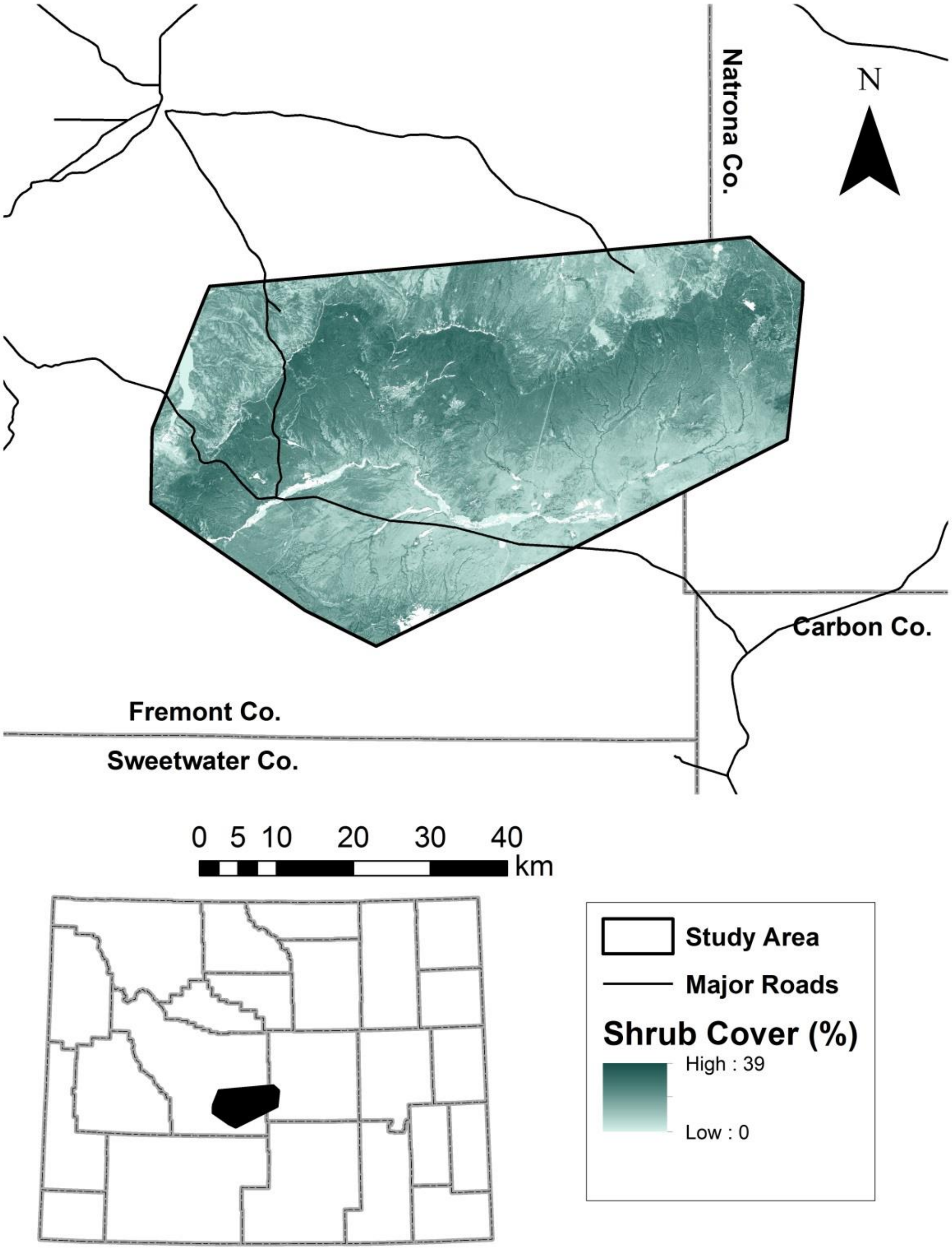


Figure 1. Study area location map, Fremont and Natrona counties, Wyoming, USA.

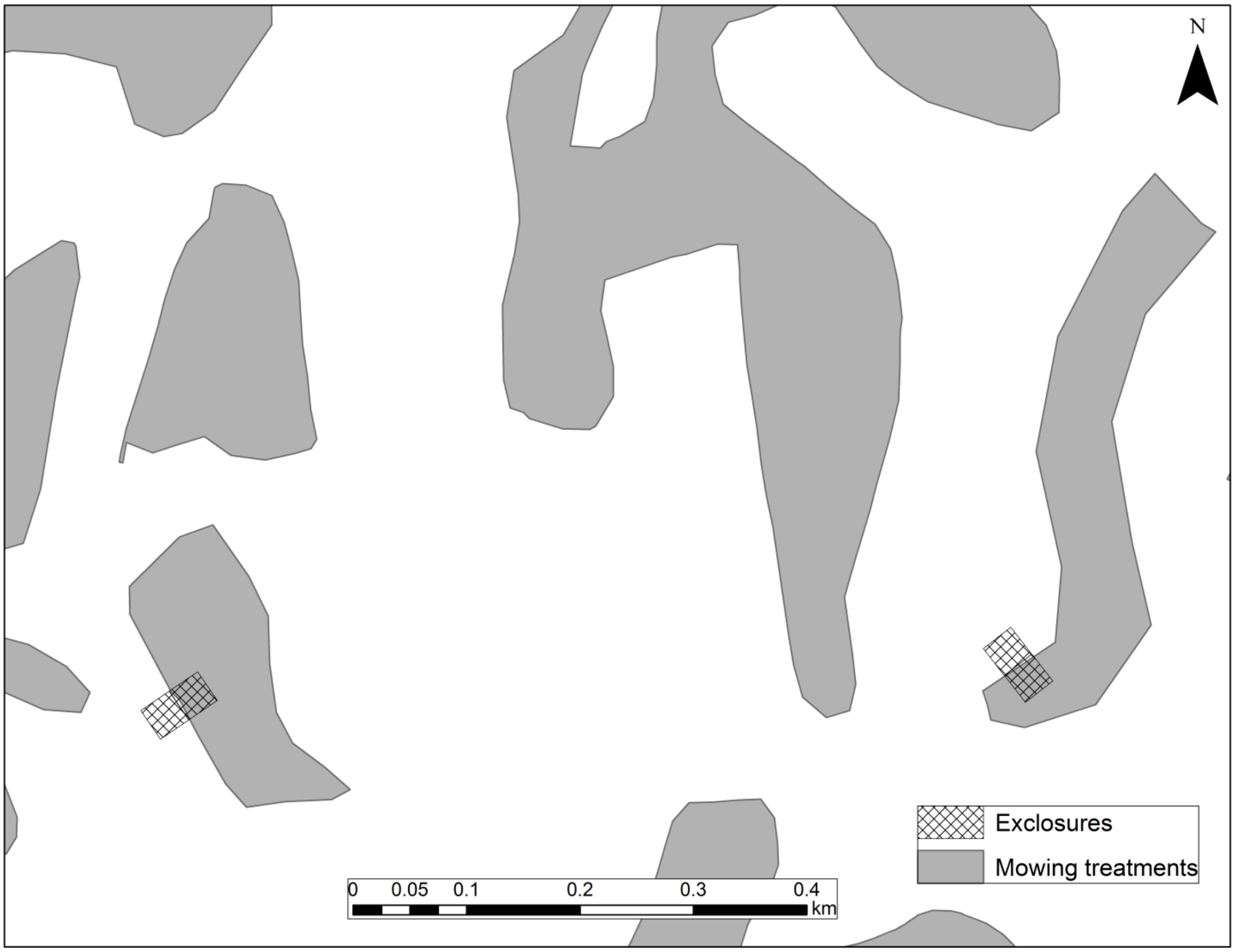


Figure 2. Example of a subset of mowing treatments (grey) and two exclosures (hatched) where sagebrush leaves were sampled, Fremont County, Wyoming, USA, 2013–2015.

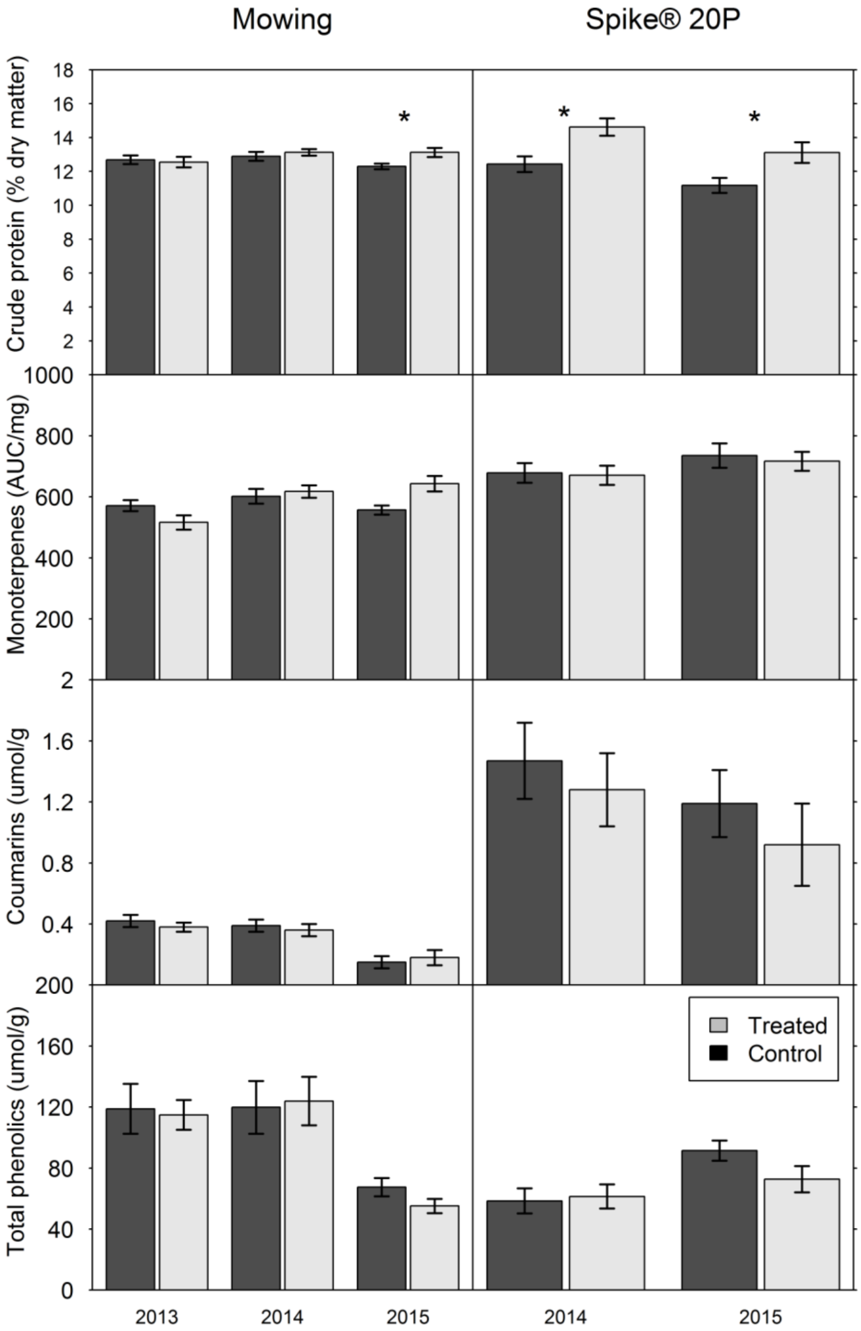


Figure 3. Mean (± SE) crude protein (% dry matter), monoterpenes (AUC/mg), coumarins (umol/g), and total phenolics (umol/g) of sagebrush leaves in mowing (2013–2015) and control (left column), and herbicide (2014–2015) and control exclosures. Asterisks indicate yearly differences between treatment and control plots (P < 0.05).

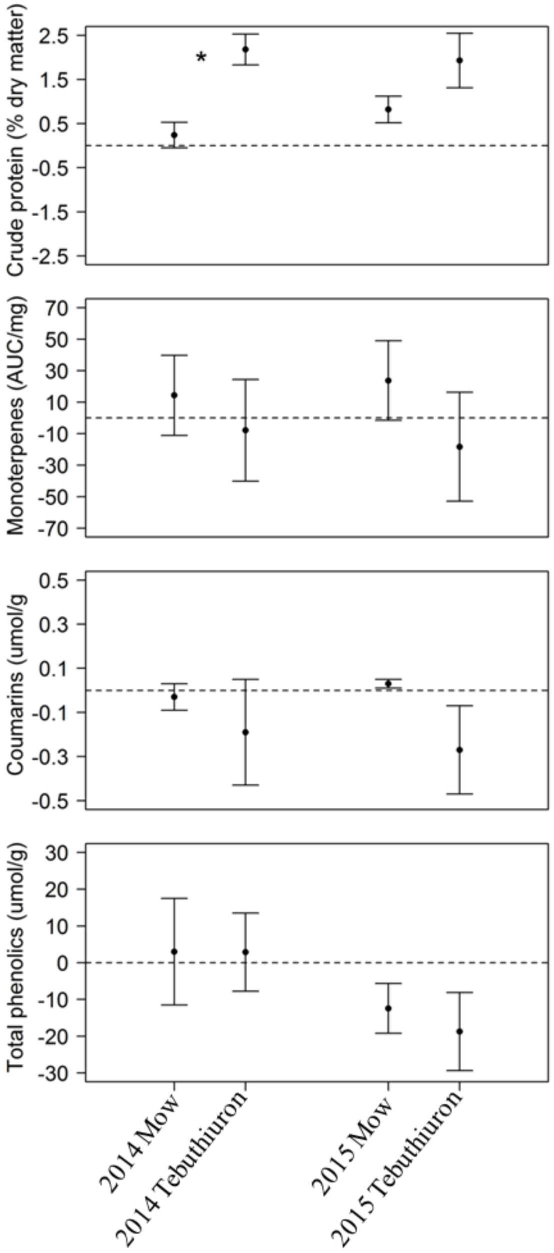


Figure 4. Mean paired differences (± SE) in crude protein (% dry matter), monoterpenes (AUC/mg), coumarins (umol/g), and total phenolics (umol/g) in sagebrush leaves collected at mowing and herbicide treatment exclosures, 2014–2015. Asterisks indicate yearly differences between treatment types ($P < 0.05$).

CHAPTER FIVE

Reconstructing Greater Sage-Grouse Chick Diets: Selection, Body Condition, and Diet Availability at Brood-Rearing and Altered Habitats

RH: Chick Sage-grouse Diet Selection in Response to Treatment

KURT T. SMITH[1], Department of Ecosystem Science and Management
University of Wyoming
Laramie, WY 82071
Email: ksmith94@uwyo.edu; Phone: 570-337-5321

JEFFREY L. BECK, Department of Ecosystem Science and Management
University of Wyoming
Laramie, WY 82071

AARON C. PRATT, Department of Ecosystem Science and Management
University of Wyoming
Laramie, WY 82071

JASON R. LEVAN, Department of Ecosystem Science and Management
University of Wyoming
Laramie, WY 82071

[1] *Email*: ksmith94@uwyo.edu

In the format for manuscripts submitted to *Journal of Wildlife Management*

KEYWORDS: body condition, *Centrocercus urophasianus*, chick diets, dietary selection, forbs, greater sage-grouse, insects

ABSTRACT

Availability of nutritious foods for juvenile grouse (*Tetraonidae*) has important implications as poor foraging conditions during development may lead to reduced fitness in adulthood. Growth and survival by juvenile grouse is nutritionally demanding, making the availability of major foods critical to population productivity. Selection of brood-rearing habitats by female greater sage-grouse (*Centrocercus urophasianus*) with chicks thus has broad implications to survival of

juveniles and persistence of populations. Previous research using crop contents documented insects and forbs compose the diet of chick sage-grouse for the first few months post hatch. We coupled stable isotopes analysis of feathers and field measurements to quantify diet selection and then correlated that with measures of chick body condition. To better understand dietary relationships of chick sage-grouse we sought to reconstruct sage-grouse chick dietary history using stable isotopes to: 1) evaluate whether selection by female grouse for brood-rearing habitats was related to chick dietary consumption, and 2) assess the relationship between dietary consumption and body condition. As a third objective, we evaluated whether the abundance of forbs and insects at treated big sagebrush habitats that were intended to improve forage quality and availability for sage-grouse were similar to habitats selected by brood-rearing females. Females with broods selected habitats in areas where diet resources occurred in proportion to their availability, with the exception that brooding females selected areas with greater forb abundance 4 weeks after hatch. Diet consumption of chicks at brood-rearing locations was unrelated to the availability of forbs and insects, but consumption of plant diets increased with chick age. Chicks that consumed proportionally greater amounts of plants during their first week of life tended to weigh more and have longer wing chords. Forb and insect abundance in mowed and tebuthiuron-thinned Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) did not differ from untreated habitats and were equal to or less than habitats used by brood-rearing grouse up to two years after treatment. The importance of quality foods for sage-grouse is well recognized and habitat management aimed at improving habitats for juvenile sage-grouse should focus on increasing the abundance and availability of dietary forbs; however, there is a need to identify whether desirable effects are achievable in big sagebrush habitats to benefit sage-grouse populations.

INTRODUCTION

Habitat loss and degradation are primary threats to the quality of habitats used by avian species (Johnson 2007). Thus, maintaining or improving habitat quality in heterogeneous landscapes has important implications to survival, reproduction, and population productivity. Food quality and availability are substantial components of habitat quality for birds and forage quality may be directly linked to habitat preference, potentially influencing offspring development and fitness during adulthood. North American prairie grouse (*Tetraonidae*) have experienced declines associated with habitat loss, degradation, and fragmentation (Storch 2007), necessitating a need to understand and conserve the quality of habitats for remaining populations. Reproductive success, particularly nest and brood survival, are major contributors to population growth in grouse (Bergerud 1988). Juvenile mortality is notable, primarily occurring during the first two weeks of life (Hannon and Martin 2006). As such, habitat management has focused on improving nest success and brood survival in efforts to maintain or increase grouse populations (e.g., Dahlgren et al. 2006). Gallinaceous birds are primarily herbivorous, however, invertebrate diets are important for proper growth and survival of dependent young during early life (Savory 1989); low food availability is a contributing factor influencing early life mortality (Hannon and Martin 2006). Poor food resources may directly influence survival, but may also influence development during ontogeny; however, consequences of poor forage conditions during early development are less well understood (Lindstrom 1999). Nonetheless, poor early nutrition may have profound effects on juvenile development that may be expressed in later life stages, which could result in reduced body size, survival, and fecundity (Schluter and Gustafsson 1993, Verhulst et al. 1997, Rose et al. 1998), and negatively influence individual reproductive success (Metcalfe and Monaghan 2001) and potentially lead to delayed density dependent effects at the population level (Beckerman et al. 2002). Therefore, understanding diets that produce larger juveniles in better body condition may provide important insights into the effect of diet on juvenile survival during the critical period between fledging and adulthood (e.g., Owen and Black 1989, Maness and Anderson 2013, Blomberg et al. 2014).

Most studies that have evaluated diet associated with greater sage-grouse (*Centrocercus urophasianus*) brood-rearing habitat have assessed the relationship between areas selected by females with broods compared to availability of diet items at randomly sampled locations. Female greater sage-grouse (hereafter 'sage-grouse') with broods select areas with greater arthropod abundance (Harju et al. 2013, Schreiber et al. 2015) and greater abundance and cover of herbaceous plants (Drut et al. 1994a, Sveum et al. 1988, Casazza et al. 2011, Kirol et al. 2012). Greater availability of insects and forbs has been attributed to increased chick survival during this period (Gregg and Crawford 2009, Dahlgren et al. 2010, Casazza et al. 2011).

Nutritional demand is high for juvenile sage-grouse, and consumption of insects and forbs is related to individual growth and body condition (Johnson and Boyce 1990, Huwer et al. 2008, Blomberg et al. 2013). Many studies have demonstrated the relationship between gallinaceous chick survival and the contribution of different dietary items they consume (e.g., Johnson and Boyce 1993, Moss et al. 1993, Picozzi et al. 1999). Johnson and Boyce (1990) demonstrated that captive-reared sage-grouse chicks required invertebrates in their diets for survival up to 10 days after hatch. In addition, chick body growth has been positively associated with the proportion of insects consumed (Johnson and Boyce 1990) and the amount of forb cover available to chicks during foraging bouts (Huwer et al. 2008). Chick growth rates have also been positively associated with quick transitions to primarily herbivorous diets during early life (Blomberg et al. 2013).

Reduced annual recruitment due to poor brood-rearing habitats has been considered a major factor contributing to sage-grouse population declines (Connelly and Braun 1997). Chick survival, therefore, has compelling implications for persistence of sage-grouse populations. Sage-grouse are relatively long lived with moderate reproductive rates compared to other gallinaceous birds and population growth is more sensitive to survival of adults and chicks, rather than productivity (Taylor et al. 2012). However, adult survival is generally higher and less variable than chick survival (Taylor et al. 2012), suggesting that management directed actions to improve habitat quality may have greater potential to influence chick survival (Mills et al. 1999).

Treatments to improve big sagebrush (*Artemisia* spp.) habitats for sage-grouse are often intended to increase herbaceous production to provide additional food sources for both adult and juvenile sage-grouse. If herbaceous production is limiting sage-grouse populations, big sagebrush treatments may be most beneficial to grouse when they increase the availability of forbs and concomitant insects necessary for juvenile growth. Yet, the relative use of treatments by sage-grouse and their effectiveness in providing habitats associated with positive population level effects remain poorly understood (Beck et al. 2012). An understanding of the ability of treated sagebrush habitats to provide dietary resources important for sage-grouse chicks will provide important information to explain how sagebrush treatments influence the availability of important for juvenile diets. If treated habitats contain greater availability of forbs and insects compared to areas selected by brood-rearing females or other untreated habitats, treatments may provide important foraging opportunities for sage-grouse chicks that could potentially lead to greater chick survivability.

Analysis of diets using stable isotopes has emerged as a powerful technique to reconstruct diets of avian taxa, provided that consumer material used to estimate diet can be related to a relevant time period of interest (Hobson and Clark 1992). Stable isotopes in feather tissue reflects diets during periods of feather growth; following growth, feather material becomes metabolically inert (Hobson and Clark 1992, Hobson and Wassenaar 1997, Martinez del Rio et al. 2009), providing a framework to determine potential changes in diets along a time series corresponding to feather synthesis (e.g., Blomberg et al. 2013). Sage-grouse chick secondary feathers offer a means to assess dietary consumption during early life. Secondary feathers emerge shortly after hatch (Johnsgard 1983) and grow continuously until approximately four weeks after hatch (Blomberg et al. 2013, K. Smith and A. Pratt unpublished data) until they are replaced during the post juvenile molt (Johnsgard 1983). To better understand dietary relationships of chick sage-grouse we sought to reconstruct sage-grouse chick dietary history using stable isotopes to: 1) evaluate whether selection by female grouse for brood-rearing habitats was related to chick dietary consumption, and 2) assess the relationship between dietary consumption and body condition. As a third objective, we evaluated whether the abundance of forbs and insects at treated big sagebrush habitats that were intended to improve forage quality and availability for sage-grouse were similar to habitats selected by brood-rearing females.

STUDY AREA

The Bighorn Basin study area occurred in Big Horn, Washakie, and northeastern Hot Springs County, in northcentral Wyoming (elevation range: 1157–2976 m). Major land uses in the area included bentonite mining, livestock grazing, and a variety of recreational activities. The Jeffrey City study area occurred in portions of Fremont and Natrona counties in central Wyoming (elevation range: 1529–2524 m). Livestock grazing was the major land use in this study area. Important vegetation communities in both study areas included big sagebrush (*Artemisia tridentata* spp.), black sagebrush (*A. nova*), rabbittbrush (*Ericameria nauseosa* and

Chrysothamnus viscidiflorus), and greasewood (*Sarcobatus vermiculatus*). Gardners's saltbush (*Atriplex gardneri*), and shadscale saltbush (*A. confertifolia*) were common in the Bighorn Basin study area. Detailed study area descriptions are found in Smith et al. (2016). During winter and spring 2014, early brood-rearing habitats in Wyoming big sagebrush (*A.t. wyomingensis*) in the Jeffrey City study area were treated with mechanical mowing (to a height of 25.4 cm) to 489 ha across 2 independent 50.0 km^2 and 33.8 km^2 study areas and tebuthiuron (Spike® 20P, Dow AgroSciences, applied at 0.22 kg/ha active ingredient by Ag Flyers, Inc., Torrington, WY) across 607 ha in 2 independent 24.9 km^2 and 44.8km^2 study areas. We used female brood-rearing locations and areas that were predicted to be highly selected brood-rearing habitats to identify each of the 4 randomly selected treatment study areas (2 tebuthiuron and 2 mowing treatments; Appendix A).

METHODS

Capture and Monitoring

We captured and marked female sage-grouse near leks in spring and at summer roosting locations during July and August by nighttime spot-lighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). We attached either radio transmitters (22 g, Model A4060; Advanced Telemetry Systems Incorporated, Isanti, MN, USA) to females with a PVC-covered wire necklace or Global Positioning System (GPS) transmitters (22-g PTT-100 Solar Argos/GPS PTT [Microwave Telemetry, Columbia, MD, USA] or Model 22 GPS PTT [North Star Science and Technology, King George, VA, USA]) via rump mount. GPS transmitters were solar-powered and uploaded locations (± ~ 20-m error) to satellites (CLS America, Largo, MD, USA) every 3 days. GPS Transmitters were programmed to acquire 3 locations per day (local time ignoring Daylight Savings Time) from 1 November to 14 March (at 0900, 1200, and 1500), 4 locations per day from 15 March to 30 April and 25 August to 30 October (at 0700, 1000, 1300, 1600), 5 locations per day from 1 May to 24 August (at 0600, 0900, 1200, 1500, 1800), and an additional location every night at midnight (2400). Sage-grouse were captured, marked, processed, and monitored in adherence with approved protocols (Bighorn Basin study [Wyoming Game and Fish Department Chapter 33-800 permit and University of Wyoming Institutional Animal Care and Use Committee protocols 03142011 and 20140228JB00065]; Jeffrey City study [Wyoming Game and Fish Department Chapter 33-801 and University of Wyoming Institutional Animal Care and Use Committee protocols 03132011 and 20140128JB0059]).

We monitored females weekly through approximately 15 August each year. Nests were located by circling each VHF-marked female's signal until surveyors visually observed the female on a nest or isolated the nest location on the ground. We subsequently monitored nests with triangulation from a distance of at least 30 m to minimize potential nest disturbance. We visually inspected nest locations of GPS-equipped females after the female left a location of clustered GPS points which indicated a nest (Dinkins et al. 2016). We determined nest success (at least one hatched egg; Rotella et al. 2004) by examining eggshell and eggshell membranes after the female left the nest location. Brood productivity and survival were estimated from females with successfully hatched nests by visually observing chicks or by identifying brooding behavior of the female during weekly telemetry visits. We determined brood loss following two telemetry visits with no brooding behavior displayed by the female or lack of chick observations. We further assessed brood fate by night time spotlight counts at approximately 35-d post-hatch. During night-time counts, we captured 2–3 chicks (if present) per brood and plucked the fifth secondary feather from each chick. We selected the fifth secondary wing feather because its growth begins slightly later than more distal secondary feathers and minimizes the influence of egg yolk nutrients on nutritional analysis (Romanoff 1944, Johnsgard 1983, Blomberg et al. 2013). At the time of capture, we weighed each chick to the nearest 1 g and measured its wing chord length to the nearest 1 mm prior to release. Feathers were stored individually in freezers prior to processing for isotopic analysis.

Diet Sampling

For successful broods, we sampled forbs and insects at 1 location and 1 dependent-random location per week during the first 4 weeks post-hatch for each female to identify potential brood foraging locations (2013–2015 in Jeffrey City and 2013 in Bighorn Basin). Random locations were constrained to a random direction and distance (0.1–0.5 km) from each paired location (Aldridge and Boyce 2008). We collected forb and insect samples within and adjacent to treated areas in the Jeffrey City study area (2014 and 2015). In each of the 4 treatment areas, each year we sampled 10 randomly selected treated locations and 10 un-treated locations in intact sagebrush habitats that were directly adjacent to treated sites (within 0.5 km of a treated area). Sampling dates of treated and un-treated areas corresponded to the brood-rearing period during each year; we began sampling locations within one week after the first successfully hatched nest was documented. At each location, we established a sampling plot demarcated by 2, 30-m transects, intersecting the center of the sampling location and extending in each cardinal direction. We clipped perennial food forbs (see Kirol et al. 2012 for list of perennial food forbs) within 4, 1-m^2 quadrats placed along each transect at a randomly selected distance of 3, 6, 9, and 12-m without replacement from the center of the plot. Directly adjacent to each perennial food-forb quadrat, we placed an additional 1 m^2 quadrat for insect sampling. We fitted quadrats used to sample insects with mesh window screening to prevent insect escapement. We used an insect vacuum (duration, 2 minutes per quadrat; Model 1612, The John W. Hock Company, Gainesville, FL, USA; Schreiber et al. 2015) to sample relative insect abundance in each quadrat. Forb and insect samples were combined from each quadrat to estimate mass per 4 m^2 at each sampling plot and stored in a freezer prior to processing. By compiling insect data in mass per 4 m^2 we were able to avoid reporting dry insect mass less than the error of our electronic scale. We dried forb and insect samples in a forced-air drying oven at 60° C for 48 hours to obtain dry mass (Beck and Peek 2005). We estimated the dry mass (g DM/ 4 m^2) of forbs and insects at each location to determine the proportional availability of each diet item by site. We randomly selected a subset of forb and insect samples to identify potential food items for our dietary mixing model (*n* = 25 samples per study area and year; described below). Samples were selected to represent dietary availability during the brood-rearing period in each study area and year, to reflect potential yearly and seasonal changes in stable isotope composition of diet items.

Stable Isotope Sample Preparation and Analysis

Feathers were cleaned in 2:1 chloroform:methanol solutions (Hopkins and Ferguson 2012) and allowed to air dry for 48 h in a fume hood. We used model predictions derived from Blomberg et al. (2013) to determine the age of each sample beginning at the distal tip of each feather. Blomberg et al. (2013) used feather growth bars positioned along the rachis to determine the age of feather samples using total feather length and known-age individuals. We used estimated ages of each brood at the time each brood-rearing female was located during weekly telemetry visits to compare dietary composition estimated with feathers with timing of dietary sampling at brood locations. We removed feather vane material along one side of the rachis to correspond to approximate one week of feather growth for each weekly sample (feather sample location at estimated age ± ~ 3 days of feather growth). Feathers, insect, and forb samples were analyzed for

$\delta^{15}N$ at the University of Wyoming Stable Isotope Facility with a continuous flow Finnigan Delta + XP isotope ratio mass spectrometer. Results are reported in units of ‰ relative to atmospheric N_2. Measured uncertainty was less than ± 0.2‰.

Statistical Analysis

Brood feeding site selection–All statistical analyses were performed in Program R (R Core Team 2015). We used conditional logistic regression to compare diet availability at brood-rearing location and dependent random locations with 'clogit' in the survival package (Therneau and Grambsch 2000, Therneau 2015). We used broods as a strata term and evaluated forb mass, insect mass, and the ratio of forb mass to insect mass (hereafter; proportion of available plant diet) collected during each week as predictor variables. Because brood-rearing is often defined as early (2-week period following nest hatch; Thompson et al. 2006) and late periods (post 2-week period; Connelly et al. 2011), we considered predictors which averaged forbs, insects, and proportion of available plant diet during the first two weeks and the last two weeks at used and dependent random locations, respectively. In addition, we evaluated the mean and range of forbs, insects, and the proportion of available plant diet across all weeks. We removed unsupported variables in single variable models based on whether 85% confidence intervals around odds ratios included 1 (Hosmer and Lemeshow 2000). We computed Pearson's correlations for remaining predictor variables to assess collinearity among predictors and evaluated all combinations of uncorrelated variables ($|r| < 0.6$) to develop candidate models. We considered the model that only included the strata term (i.e., brood) as the null model and identified the most supported model relative to the null model using Akaike's information criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2004). We considered models within 4 AICc of the best fit model competitive (Arnold 2010).

Dietary consumption at selected brood-rearing locations–We used a single element, two-source mixing model to evaluate the contribution of plants and invertebrates in the weekly diet of each chick estimated from $\delta^{15}N$ in feathers (consumer) relative to potential food items (source) with package ‘simmr’ (Parnell 2016). The model output provided estimates of the relative proportion of plant diet during each week for each individual. We used discrimination factors between diet source and consumer of avian feather tissue ($\Delta^{15}N = 3.84 \pm 0.26‰$ [SE]) derived from Caut et al. (2009). Prior to running the mixture models, we used analysis of variance and linear regression models to determine if $\delta^{15}N$ of source material differed between study area, year, and sampling date within each year. We detected differences between study area and year ($P < 0.05$), but did not detect differences across sampling date. We performed separate mixing models for each study area and year to account for differences in $\delta^{15}N$ of source materials.

To evaluate dietary selection (estimated from feather $\delta^{15}N$) relative to dietary mass at brood use locations, we used generalized linear mixed models with package ‘lme4’ (Bates et al. 2015). We used δ15N from feather samples as a proxy for the proportion of plant diet during each week compared to the mass of dietary items at brood-rearing locations instead of estimated proportion of plant diet generated from mixing models to limit potential bias from using isotope discrimination factors that were not derived from our study system (Martinez del Rio et al. 2009, Phillips et al. 2014). Moreover, estimates of feather $\delta^{15}N$ and proportion of plant diet from mixing models were highly correlated ($r = 0.94$). We averaged $\delta^{15}N$ across chicks in each brood and included brood in all models, which were uniquely defined for each year and study area, as random intercept terms to account for yearly differences in diet availability and a lack of independence among individuals in the same brood during the 4-week sampling period. We considered both linear and quadratic effects of forb, insect, proportion of available plant diet, and week as predictor variables. We used AICc to determine the most plausible linear or quadratic model for each variable, and explored all combinations of remaining uncorrelated variables ($|r| < 0.6$; Burnham and Anderson 2004), when single variable models had greater support than the random intercept model only. Predictors were centered and Z-transformed prior to analysis (Becker et al. 1988) to ensure model convergence.

Relative body condition–We used body mass and wing chord length separately as relative metrics of chick body condition. We used the residuals from generalized linear models with chick age and year to develop age-corrected mass and wing chord length estimates to account for individuals that were captured at different ages (Blomberg et al. 2013). We used generalized linear mixed models with package ‘lme4’ (Bates et al. 2015) to evaluate age-corrected relative body condition indices relative to individual ∂^{15}N feather samples. We considered models with predictor variables including feather ∂^{15}N during each week, mean feather ∂^{15}N during weeks 1 and 2 (early brood-rearing) and weeks 3 and 4 (late brood-rearing), the mean ∂^{15}N across all weeks, and the range of feather ∂^{15}N across weeks. We considered variables as linear and quadratic effects. We used AICc to determine the most plausible linear or quadratic model for each variable, and explored all combinations of remaining uncorrelated variables ($|r| < 0.6$; Burnham and Anderson 2004). All models included brood as random intercept terms to account for potential differences in diet availability by year and lack of independence among individuals among the same brood. Model support was assessed relative to the random intercepts only model with AICc.

Availability of dietary resources at brood use compared to treated sites–We used analysis of variance (ANOVA) with treatment type (mow, tebuthiuron, control mow, and control tebuthiuron) as between-subject effects to compare potential differences in forb and insect mass in treated and un-treated areas during each year. We used additional ANOVAs to compare forb and insect mass at brood use locations and mowing and tebuthiuron treatments separately by year. We assessed differences between groups with Tukey's honest significant difference tests (Yandell 1997).

RESULTS

To identify brood diet selection in 2013–2015, we sampled forb and insect abundance at 232 brood-rearing locations and 232 paired random locations from 58 females (Bighorn Basin [*n* = 16]; Jeffrey City [*n* = 42]) that successfully raised a brood to at least 35-d post-hatch. To evaluate dietary consumption at selected brood-rearing locations we used information from 76 broods (Bighorn Basin [*n* = 16]; Jeffrey City [*n* = 60]), and evaluated dietary influences on relative body condition from 153 individuals (Bighorn Basin [*n* = 45]; Jeffrey City [*n* =108]) from those broods. To evaluate availability of chick foods at treated and un-treated sites, we sampled forb and insect abundance at 20 mowed and 20 tebuthiuron locations and 40 un-treated locations during 2014 and 2015 in the Jeffrey City study area for a total of 160 samples.

Brood Feeding Site Selection

Plausible models explaining brood-rearing site selection for dietary items included variables with forb mass during week 4, forb mass during the early brood-rearing period (weeks 1 and 2), insect mass during the late brood-rearing period (weeks 3 and 4), and the average proportion of plant diet across all weeks (Table 1). All variables in each competitive model, with the exception of forb mass during week 4, had odds ratios with 85% confidence intervals that included 1. Moreover, the model including the single variable, forb mass during week 4 had the lowest AICc value and was the most parsimonious model; therefore, we considered this the most supported model. Forb mass during week 4 was positively correlated with brood-rearing habitat selection; model predictions suggest that for every 5 g/4 m^2 increase in food forb abundance, relative probability of selection increased by approximately 2%.

Dietary Consumption at selected brood-rearing locations

Mixing models indicated that plant food items were approximately 50% of the diet of sage-grouse chicks through 4 weeks post-hatch, but displayed a general increase through time. However, this relationship varied slightly between study areas and across years (Figure 1). Competitive models explaining dietary consumption at brood-rearing locations included all variables that were assessed (Table 2). However, we considered the top model which only included week as the most supported model because 85% confidence intervals for parameter estimates of forbs, insects, and proportion of plant diet included zero in all competitive models. Week ($\hat{\beta} = -0.095 \pm 0.024$ SE) was negatively related to feather $\partial^{15}N$, suggesting that broods were consuming more forbs as they aged, which corroborates results from the mixing model.

Relative Body Condition

The mixed effect model that contained a quadratic effect of feather $\partial^{15}N$ during week 1 was the most supported model relating age-corrected body mass (Table 3). Similarly, the quadratic effect of feather $\partial^{15}N$ during week 1 was the most supported model relating age-corrected wing chord length (Table 4). Competitive models for both age-corrected body mass and wing chord length included the range of feather $\partial^{15}N$, feather $\partial^{15}N$ during the late brood-rearing period, feather $\partial^{15}N$ during week 3, and feather $\partial^{15}N$ during week 4. However, these variables had parameter estimates with 85% confidence intervals that overlapped zero in all models describing both dependent variables. Feather $\partial^{15}N$ during week 1 was negatively correlated with age-corrected mass ($\hat{\beta}$ = -318.63 ± 107.40 SE), indicating that chicks consuming a relatively higher proportion of plant diet during their first week of life tended to be larger (Figure 2A). Similarly, age-corrected wing chord length was negatively correlated with feather $\partial^{15}N$ during week 1 ($\hat{\beta}$ = -53.24 ± 17.91 SE), suggesting that individuals with larger wing chords tended to consume a relatively greater proportion of plant diet during their first week (Figure 2B).

Availability of Dietary Resources at Brood Use Compared to Treated Sites

We found no differences in forb mass across treatment type or between treatment and un-treated locations during 2014 and 2015 ($P > 0.05$; Table 5, Figure 3). Insect mass differed between 2014 and 2015, with greater mass in 2014 compared to 2015 ($P < 0.05$; Figure 3); however insect mass did not differ between treatments and un-treated locations or between treatment types within years ($P > 0.05$; Figure 3). We found differences in both forb and insect mass between brood-rearing, and mowing and tebuthiuron treated locations (Figure 4). Brood-rearing locations generally had greater forb mass than mowing and tebuthiuron treatments (Figure 4). Mowing treatments contained the lowest forb mass during 2014 and 2015 compared to brood-rearing or tebuthiuron treatments ($P < 0.05$), whereas forb mass between brood-rearing locations and tebuthiuron treatments did not differ ($P > 0.05$). Forb mass at brood-rearing locations was 2.7-times higher and 3.7-times higher than at mowed locations in 2014 and 2015, respectively (Table 5). Forb mass at tebuthiuron treatment locations was 1.5- and 1.9-times higher than at mowed locations in 2014 and 2015, respectively. Insect mass differed across years, but did not differ between brood-rearing locations or treatments ($P > 0.05$).

DISCUSSION

Our study sought to evaluate dietary resource availability at brood-rearing locations, understand dietary consumption by chicks estimated from feather ∂^{15}N at selected habitats, and determine how diets influenced the relative body condition of sage-grouse chicks. Our findings generally suggested that females with broods were selecting habitats with diets in proportion to their availability, with the exception that brooding females selected areas with greater forb abundance 4 weeks after hatch. In contrast, several studies have found positive associations with brood-rearing habitats and forb (Drut et al. 1994a, Sveum et al. 1988, Casazza et al. 2011) and insect abundance (Harju et al. 2013, Schreiber et al. 2015). However, brood-rearing habitat selection is not always related to forb abundance, particularly during early brood rearing (Thompson et al. 2006, Kirol et al. 2012). We did find a positive association with selection for forb abundance during week 4 post hatch, which is corroborated by studies that suggest females with broods move to more forb rich mesic habitats during late brood-rearing (e.g., Connelly et al. 2000). Our study used a dependent random design that constrained the sample of available habitat to within 0.1 and 0.5 km of brood-rearing locations (third-order selection; Johnson 1980). This contrasts with many studies that have evaluated brood habitat selection within the lens of a study area (second-order selection; Drut et al. 1994a, Casazza et al. 2011, Kirol et al. 2012). Spatial and temporal differences in forb and insect abundance may explain the lack of selection we found for forb and insect abundance during the first 3 weeks after hatch. Female sage-grouse may select nesting areas that enhance chick survival by placing nests in suitable brood-rearing habitats (Gibson et al. 2016a). We speculate that females may have been selecting relatively homogeneous brood-rearing areas that may explain the minimal differences we found in forb and insect abundance between used and paired random locations; however, we do not have data to support this presumption. Our analysis only included females with broods that survived to ~35-d post hatch and did not compare selection of brood-rearing habitats by females who lost broods prior to 35-d, which may further explain our finding that successful females were generally selecting habitats with diet resources in proportion to their availability.

Chick dietary consumption at brood-rearing locations was generally unrelated to dietary availability of forbs and insects, but consumption of plant diets increased with chick age. Adaptive habitat selection theory suggests that females should select areas to maximize foraging opportunities while minimizing predation risk. Consumption of dietary items by juvenile grouse may be directly related to their availability (Savory 1989). For example, red grouse chicks (*Lagopus lagopus scoticus*) ate insect food in relation to their availability (Savory 1977) and forbs and insects were consumed by sage-grouse chicks in greater mass when availability was greater (Drut et al. 1994b). Presumably, dietary consumption by chicks occurs opportunistically within the habitat patch that was chosen by the female. Alternatively, it is possible that our sampling methodology did not accurately reflect foraging locations of broods as we only sampled 1 location per week and estimated dietary consumption from an entire week of feather synthesis.

Moss et al. (1993) determined that red grouse chick condition was correlated with green heather (*Calluna vulgaris*) biomass. Capercaillie (*Tetrao urogallus*) chick survival was positively associated with invertebrate consumption (Picozzi et al. 1999) and the importance of insects and forbs for brood survival has been well established for juvenile sage-grouse (Johnson and Boyce 1990, Drut et al. 1994b, Huwer et al. 2008, Gregg and Crawford 2009, Dahlgren et al. 2010, Casazza et al. 2011, Blomberg et al. 2013). Drut et al. (1994b) found that chicks from 2 different study areas exhibited similar dietary selection, but differences in productivity were related to the relative dry mass of forbs and invertebrates, not the proportion of diet items consumed. Our methods to determine dietary consumption did not allow us to assess relative mass of consumed foods. We found that on average, individuals consumed a lower proportion of plant diet than previously published studies, particularly by individuals that were more than 1 week old (Klebenow and Gray 1968, Peterson 1970, Blomberg et al. 2013). For example, Klebenow and Gray (1968) found that insects consisted of approximately 50% of the diet of 1-week-old chicks, whereas insects composed less than 25% of the diet for older individuals. Similarly, Peterson (1970) found that juvenile diets during the first 4 weeks consisted of approximately 70% plants. These estimates were derived from crop content and methodological differences between studies may explain the differences we found. Nonetheless, using similar methods to infer diet as our study, Blomberg et al. (2013) found that chicks consumed consistently higher proportions of plant diet during the first 4 weeks compared to our results. We found that age-adjusted mass and wing chord length of chicks captured at approximately 35-d were positively related to the proportion of plant diet during their first week of life. Our results indicate that the proportion of plant diet was ~50% across all weeks for the average individual, but this trend was variable between study areas and across years. Proportionally, insects were the primary food source during an individual’s first week of life, but individuals that had a greater proportion of plant diet during their first week weighed more and had longer wing chords.

Our findings that increased consumption of plant material during the first week was related to individual growth may be explained in several ways. First, we assumed that feather synthesis, and therefore, dietary consumption estimates from feather $\partial^{15}N$ come entirely from dietary intake and not endogenous sources. Egg yolk nutrients are thought to be absorbed at approximately 3-4 days after hatch (Romanoff 1944); therefore, egg yolk nutrition could have substantially contributed to dietary estimates during this time if there was variability in absorption rates. Pre-laying female diets largely consist of plant materials prior to insect emergence in spring (Gregg et al. 2006) and the dietary signature from the female could be reflected in juvenile diet estimates if egg yolk nutrition contributes to early secondary feather growth. Larger eggs produced by females in better condition likely have egg yolk content with greater energy reserves (Martin 1987). It reasons that larger individuals could actually be a result of maternal effects contributing to greater resources for juvenile growth. Further research is needed to assess the influence of egg yolk nutrients on dietary contributions and how this could influence the utility of stable isotope methods to infer juvenile diets.

A second possible explanation for the importance of forbs during week 1 on chick body condition is the specific micronutrients and vitamins that forbs contain. Insects provide more protein than plant materials (Sugimura et al. 1984), but forbs contain higher levels of calcium, and Ascorbic acid (Savory 1989). Calcium is necessary for skeletal growth of juvenile birds (e.g., Tilgar et al. 2004). Ascorbic acid is synthesized by grouse; however, endogenous sources of Ascorbic acid may be important for survival (Hanssen et al. 1979), and supplemental diets containing Ascorbic acid have been associated with increased growth rates in juvenile poultry (Kutlu and Forbs 1993, Sahin et al. 2003). High protein based insect diets are crucial for early sage-grouse development (Johnson and Boyce 1990), however, consumption of forbs during this time may also provide important resources necessary for growth. The general shift towards proportionally greater plant diet may be related to gut morphology and development (*sensu* Blomberg et al. 2013), however this relationship has not been explored in sage-grouse.

Regardless of mechanisms that explain juvenile growth, the importance of quality foods for sage-grouse is well recognized and habitat management has aimed to increase forb and concomitant insect abundance in sagebrush habitats. Management actions are unlikely to directly increase insect abundance (Harju et al. 2013), suggesting that increasing the abundance and availability of forbs would improve dietary habitats for sage-grouse. Results from our secondary objective indicate that both forb and insect abundance in treated sagebrush habitats did not differ from untreated habitats. Both mowing and tebuthiuron treated habitats contained forb and insect abundance that were equal to or less than habitats used by brood-rearing females. Improving foraging resources in degraded sagebrush habitats could potentially improve availability and abundance of critical insect and forb foods, however, managers need to identify whether desirable effects can actually be achieved (Davies et al. 2012). Abundance of critical insect and forb foods do not often exhibit positive response following treatments in Wyoming big sagebrush (Fischer et al. 1996, Nelle et al. 2000, Davies et al. 2007, Rhodes et al. 2010, Davies et al. 2012, Hess and Beck 2012, Hess and Beck 2014). Our results corroborate findings of others, however, accurately assessing the ability of treatments to produce important diet items for sage-grouse will require multiple years of data collection.

Environmental variation may function to mitigate or exacerbate the influence of habitat treatments on availability of diet items for sage-grouse. Annual climate drives herbaceous production in sagebrush communities (Noy-Meir 1973) and insect abundance is positively associated with herbaceous production (Wenninger and Inouye 2008). Precipitation positively influences population growth and individual vital rates (Blomberg et al. 2012, Guttery et al. 2013, Caudill et al. 2014) suggesting that forage availability influences sage-grouse reproduction. Females may modify their behavior and habitat use to maintain reproductive success in drought conditions, but reproduction may still be suppressed at the population level

(Gibson et al. 2016b). Management and conservation practices that improve habitat quality for sage-grouse are needed to ensure sage-grouse viability in the future.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. Israel Journal of Ecology and Evolution 54:389–419.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike’s information criterion. Journal of Wildlife Management 74:1175–1178.

Bates, D, M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 678:1–48.

Beck, J. L, and J. M. Peek. 2005. Great Basin summer range forage quality: Do plant nutrients meet elk requirements? Western North American Naturalist 65:516–527.

Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitat. Rangeland Ecology and Management 65:444-455.

Becker, R. A., J. M. Chambers, and A. R. Wilks. 1988. The new S language: A programming environment for data analysis and graphics. Wadsworth and Brooks Cole, Belmont, California, USA.

Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology and Evolution. 17:263–269.

Bergerud, A. T. 1988. Population ecology of North American grouse. Pages 578-685 *in* A. T. Bergerud, and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, USA.

Blomberg, E. J., S. R. Poulson, J. S. Sedinger, and D. Gibson. 2013. Prefledging diet is correlated with individual growth in greater sage-grouse (Centrocercus urophasianus). Auk 130:715–724.

Blomberg, E. J., J. S. Sedinger, D. Gibson, P. S. Coates, and M. L. Casazza. 2014. Carryover effects and climate conditions influence the postfledging survival of greater sage-grouse. Ecology and Evolution 4:4488–4499.

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3:art55.

Burnham, K. P., and D. R. Anderson. 2004. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, USA.

Casazza, M. L., P. S. Coates, and C. T. Overton. 2011. Linking habitat selection and brood success in greater sage-grouse. Pages 151–167 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, Conservation, and Management of Grouse. Studies in Avian Biology 39. University of California Press, Berkeley, USA.

Caudill, D., M. R. Guttery, B. Bibles, T. A. Messmer, G. Caudill, E. Leone, D. K. Dahlgren, and R. Chi. 2014. Effects of climatic variation and reproductive trade-offs vary by measure of reproductive effort in greater sage-grouse. Ecosphere 5:art154.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (Δ^{15}N and Δ^{13}C): The effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

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., E. T. Rinkes, and C. E. Braun. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 3–68 *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 38. University of California press, Berkeley, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

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.

Dahlgren, D. K., T. A. Messmer, and D. N. Koons. 2010. Achieving better estimates of greater sage-grouse chick survival in Utah. Journal of Wildlife Management 74:1286–1294.

Davies, K. W., J. D. Bates, and R. F. Miller. 2007. Short-term effects of burning Wyoming big sagebrush steppe in southeast Oregon. Rangeland Ecology and Management 60:515–522.

Davies, K. W., J. D. Bates, A. M. Nafus. 2012. Mowing Wyoming big sagebrush communities with degraded herbaceous understories: has a threshold been crossed? Rangeland Ecology and Management 65:498–505.

Dinkins, J. B., K. T. Smith, J. L. Beck, C. P. Kirol, A. C. Pratt, and M. R. Conover. 2016. Microhabitat conditions in Wyoming's sage-grouse core areas: Effects on nest site selection and success. PLoS ONE 11:e0150798

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994a. Brood habitat use by sage-grouse in Oregon. Great Basin Naturalist 54:170–176.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994b. Diets and food selection of sage grouse chicks in Oregon. Journal of Range Management 47:90–93.

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.

Gibson, D., E. J. Blomberg, M. T. Atamian, and J. S. Sedinger. 2016a. Nesting habitat selection influences nest and early offspring survival in greater sage-grouse. Condor 118:689–702.

Gibson, D. E., E. J. Blomberg, M. T. Atamian, and J. S. Sedinger. 2016b. Weather, habitat composition, and female behavior interact to modify offspring survival in greater sage-grouse. Ecological Applications DOI:10.1002/eap.1427.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A., and J. A. Crawford. 2009. Survival of greater sage-grouse chicks and broods in the northern Great Basin. Journal of Wildlife Management 73:904–913.

Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and renesting by greater sage-grouse. Journal of Wildlife Management 70:472–478.

Guttery, M. R., D. K. Dahlgren, T. A. Messmer, J. W. Connelly, K. P. Reese, P. A. Terletzky, N. Burkepile, and D. N. Coons. Effects of landscape-scale environmental variation on greater sage-grouse chick survival. PLoS ONE 8:e65582.

Hannon, S. J., and K. Martin. 2006. Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology 269:422–433.

Hanssen, I., H. J. Grav, J. B. Steen, and H. Lysnes. 1979. Vitamin C deficiency in growing willow ptarmigan (*Lagopus lagopus lagopus*). Journal of Nutrition 109:2260–2276.

Harju, S. M, C. V. Olson, L. Foy-Martin, S. L. Webb, M. R. Dzialak, J. B. Winstead, and L. D. Hayden-Wing. 2013. Occurrence and success of greater sage-grouse broods in relation to insect-vegetation community gradients. Human Wildlife Interactions 7:214–229.

Hess, J. E., and J. L. Beck. 2012. Burning and mowing Wyoming big sagebrush: Do treated sites meet minimum guidelines for greater sage-grouse breeding habitats? Wildlife Society Bulletin 36:85–93.

Hess, J. E., and J. L. Beck. 2014. Forb, insect, and soil response to burning and mowing big sagebrush in greater sage-grouse breeding habitat. Environmental Management 53:813–822.

Hobson, K. A., and R. G. Clark. 1992. Assessing avian diet using stable isotopes I: Turnover of ^{13}C in tissues. Condor 94:181–188.

Hobson, K. A., and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. Oecologia 109:142–148.

Hopkins, J. B. III, and J. M. Ferguson. 2012. Estimating the diets of animals using stable isotopes and a comprehensive Bayesian mixing model. PLoS ONE 7:e28478.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, USA.

Huwer, S. L., D. R. Anderson, T. E. Remington, and G. C. White. 2008. Using human-imprinted chicks to evaluate the importance of forbs to sage-grouse. Journal of Wildlife Management 72:1622–1627.

Johnsgard, P. A. 1983. The grouse of the World. University of Nebraska Press, Lincoln, Nebraska, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, G. D. and M. S. Boyce. 1990. Feeding trials with insects in the diet of sage grouse chicks. Journal of Wildlife Management 54:89–91.

Johnson, M. D. 2007. Measuring habitat quality: A review. Condor 109:489–504.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M.R. Conover. 2012. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. Condor 114:75–89.

Klebenow, D. A., and G. M. Gray. 1968. Food habitats of juvenile sage grouse. Journal of Range Management 21:80–83.

Kutlu, H. R., J. M. Forbes. 1993. Changes in growth and blood parameters in heat-stressed broiler chicks in response to dietary ascorbic acid. Livestock Production Science 36:335–350.

Lindstrom, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology and Evolution 14:342–348.

Maness, T. J., and D. J. Anderson. 2013. Predictors of juvenile survival in birds. Ornithological Monographs 78:1–55.

Martin, T. E. 1987. Food as a limit on breeding birds: A life history perspective. Annual Reviews of Ecology and Systematics 18:453–487.

Martinez del Rio, C., N. Wolf, S. A. Carleton, and L. Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews 84:91–111.

Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: Grow now, pay later? Trends in Ecology and Evolution 16:254–260.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13:815–829.

Moss, R., A. Watson, R. A. Parr, I. B. Trenholm, and M. Marquiss. 1993. Growth rate, condition and survival of Red Grouse *Lapopus lagopus scoticus* chicks. Scandinavian Journal of Ornithology 24:303–310.

Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effects of fire on sage grouse habitat. Journal of Rangeland Management 53:586–591.

Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Owen, M., and J. M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58:603–617.

Parnell, A. C. 2016. Simmr: A stable isotope mixing model. R package version 0.3. http://CRAN.R-project.org/package=simmr.

Peterson, J. G. 1970. The food habitats and summer distribution of juvenile sage grouse in central Montana. Journal of Wildlife Management 34:147–155.

Picozzi, N. R. Moss, and K. Kortland. 1999. Diet and survival of Capercaillie *Tetrao urogallus* chicks in Scotland. Wildlife Biology 5:11–23.

Phillips, D. L., R. Inger, S. Bearhop, A. L. Jackson, J. W. Moore, A. C. Parnell, B. X. Semmens, and E. J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92:823–835.

R Core Team. 2015. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL http://www.R-project.org/.

Rhodes, E. C., J. D. Bates, R. N. Sharp, and K. W. Davies. 2010. Fire effects on cover and dietary resources of sage-grouse habitat. Journal of Wildlife Management 74:755–764.

Romanoff, A. L. 1944. Avian spare yolk and its assimilation. Auk 61:235–241.

Rose, K. E., T. H. Clutton-Brock, F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. Journal of Animal Ecology 67:979–986.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Sahin, K., N. Sahin, and O. Kucuk. 2003. Effects of chromium, and ascorbic acid supplementation on growth, carcass traits, serum metabolites, and antioxidant status of broiler chickens reared at high ambient temperatures (32°C). Nutrition Research 23:225–238.

Savory, C. J. 1977. The foods of red grouse chicks *Lagopus lagopus scoticus*. Ibis 119:1–9.

Savory, C. J. 1989. The importance of invertebrate food to chicks of gallinaceous species. Proceedings of the Nutrition Society 48:113–133.

Schluter, D., and L. Gustafsson. 1993. Maternal inheritance of condition and clutch size in the collared flycatcher. Evolution 47:658–667.

Schreiber, L. A., C. P. Hansen, M. A. Rumble, J. J. Millspaugh, R. S. Gamo, J. W. Kehmeier, and N. Wojcik. 2015. Microhabitat selection of brood-rearing sites by greater sage-grouse in Carbon County, Wyoming. Western North American Naturalist 75:348–363.

Smith, K. T., A. C. Pratt, and J. L. Beck. 2016. Does Wyoming's Core Area policy protect winter habitats for greater sage-grouse? Environmental Management 58:585–595.

Storch, I. 2007. Conservation status of grouse worldwide: An update. Wildlife Biology 13:5–12.

Sugimura, K., E. Hori, Y. Kurihara, and S. Itoh. 1984. Nutritional value of earthworms and grasshoppers as poultry feed. Japanese Poultry Science 21:1–7.

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.

Tilgar, V., R. Mand, I. Ots, M. Magi, P. Kilgas, and S. J. Reynolds. 2004. Calcium availability affects bone growth in nestlings of free-living great tits (*Parus major*), as determined by plasma alkaline phosphatase. Journal of Zoology 263:269–274.

Taylor, R. L., B. L. Walker, D. E. Naugle, L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Therneau, T. 2015. A package for survival analysis in S. version 2.38. URL http:/CRAN.R-project.org/package=survival

Therneau, T. M, and P. M. Grambsch. 2000. Modeling survival data: Extending the Cox model. Springer, New York, USA.

Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. Western North American Naturalist 66:332–342.

Verhulst, S., C. M. Perrins, and R. Riddington. 1997. Natal dispersal of great tits in a patchy environment. Ecology 78:864–872.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Wenninger, E. J., R. S. Inouye. 2008. Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. Journal of Arid Environments 72:24–33.

Yandell, B. S. 1997. Practical data analysis for designed experiments. Chapman and Hall, New York, USA.

Table 1. Top and competing models best explaining dietary resources at brood-rearing female sage-grouse locations in the Bighorn Basin and Jeffrey City study areas, Wyoming 2013–2015.

Model	Model fit statistics		
	K	ΔAICc	w_i
Forbs$_{\text{(week 4)}}$	1	0.00	0.27
Forbs$_{\text{(week 4)}}$ + Insects$_{\text{(late)}}$	2	0.60	0.20
Forbs$_{\text{(week 4)}}$ + Forbs$_{\text{(early)}}$	2	1.73	0.12
Forbs$_{\text{(week 4)}}$ + Proportion Forbs$_{\text{(mean)}}$	2	2.02	0.10
Forbs$_{\text{(week 4)}}$ + Forbs$_{\text{(early)}}$ + Insects$_{\text{(late)}}$	3	2.34	0.08
Forbs$_{\text{(week 4)}}$ + Insects$_{\text{(late)}}$ + Proportion Plants$_{\text{(mean)}}$	3	2.70	0.07
Forbs$_{\text{(week 4)}}$ + Forbs$_{\text{(early)}}$ + Proportion Plants$_{\text{(mean)}}$	3	3.75	0.04
NULL	0	8.94	0.00

Table 2. Top and competing mixed-effects models evaluating the relationship between dietary consumption, estimated from feather $\partial^{15}N$, and dietary abundance at selected brood-rearing locations in the Bighorn Basin and Jeffrey City study areas, Wyoming 2013–2015.

Model	Model fit statistics		
	K	ΔAICc	w_i
Week	4	0.00	0.34
Week + Forbs	5	1.43	0.17
Week + Insects	5	1.61	0.15
Week + Proportion Plants	5	1.98	0.13
Week + Forbs + Insects	6	3.21	0.07
Week + Insects + Proportion Plants	6	3.49	0.06
Week + Forbs + Proportion Plants	6	3.51	0.06
NULL	3	13.59	0.00

Table 3. Top and competing mixed-effects models evaluating the relationship between diet and age-corrected mass of greater sage-grouse chicks captured in Bighorn Basin and Jeffrey City study areas during 2013–2015, Wyoming.

Model	Model fit statistics		
	K	ΔAICc	w_i
$^{1}\partial^{15}\text{N}_{(\text{week 1})}$	5	0.00	0.33
$^{1}\partial^{15}\text{N}_{(\text{week 1})} + \partial^{15}\text{N}_{(\text{range})}$	6	1.56	0.15
$^{1}\partial^{15}\text{N}_{(\text{week 1})} + {}^{1}\partial^{15}\text{N}_{(\text{week 3})}$	6	2.04	0.12
$^{1}\partial^{15}\text{N}_{(\text{week 1})} + {}^{1}\partial^{15}\text{N}_{(\text{late})}$	6	2.13	0.11
$^{1}\partial^{15}\text{N}_{(\text{week 1})} + {}^{1}\partial^{15}\text{N}_{(\text{week 4})}$	6	2.17	0.11
$^{1}\partial^{15}\text{N}_{(\text{week 1})} + {}^{1}\partial^{15}\text{N}_{(\text{week 4})} + \partial^{15}\text{N}_{(\text{range})}$	7	3.74	0.05
$^{1}\partial^{15}\text{N}_{(\text{week 1})} + {}^{1}\partial^{15}\text{N}_{(\text{week 3})} + \partial^{15}\text{N}_{(\text{range})}$	7	3.75	0.05
$^{1}\partial^{15}\text{N}_{(\text{week 1})} + {}^{1}\partial^{15}\text{N}_{(\text{range})} + \partial^{15}\text{N}_{(\text{late})}$	7	3.75	0.05
NULL	3	22.84	0.00

[1] Quadratic form

Table 4. Top and competing mixed-effects models evaluating the relationship between diet and age-corrected wing chord length of greater sage-grouse chicks captured in Bighorn Basin and Jeffrey City study areas during 2013–2015, Wyoming.

	Model fit statistics		
Model	K	ΔAICc	w_i
$^{1}\partial^{15}N_{(\text{week 1})}$	5	0.00	0.33
$^{1}\partial^{15}N_{(\text{week 1})} + {}^{1}\partial^{15}N_{(\text{week 3})}$	6	1.73	0.46
$^{1}\partial^{15}N_{(\text{week 1})} + \partial^{15}N_{(\text{range})}$	6	1.85	0.59
$^{1}\partial^{15}N_{(\text{week 1})} + {}^{1}\partial^{15}N_{(\text{late})}$	6	1.86	0.72
$^{1}\partial^{15}N_{(\text{week 1})} + {}^{1}\partial^{15}N_{(\text{week 4})}$	6	2.00	0.84
$^{1}\partial^{15}N_{(\text{week 1})} + {}^{1}\partial^{15}N_{(\text{week 3})} + \partial^{15}N_{(\text{range})}$	7	3.81	0.89
$^{1}\partial^{15}N_{(\text{week 1})} + {}^{1}\partial^{15}N_{(\text{range})} + \partial^{15}N_{(\text{late})}$	7	3.87	0.93
$^{1}\partial^{15}N_{(\text{week 1})} + {}^{1}\partial^{15}N_{(\text{week 3})} + \partial^{15}N_{(\text{range})}$	7	3.95	0.98
NULL	3	19.26	0.00

[1] Quadratic form

Table 5. Mean (SE) forb and insect abundance (g DM/4 m^2) at treated (mowed and tebuthiuron) and un-treated locations collected during 2014 and 2015 (Jeffrey City), and brood-rearing locations during 2013–2015 (Jeffrey City and Bighorn Basin), Wyoming, USA.

	Forbs			Insects		
Sample	2013	2014	2015	2013	2014	2015
Mow	--	13.5 (2.0)	10.4 (2.8)	--	0.5 (0.1)	0.1 (0.0)
$\text{Mow}_{\text{(control)}}$	--	18.4 (4.0)	21.1 (5.0)	--	0.5 (0.1)	0.1 (0.0)
Tebuthiuron	--	28.0 (5.9)	20.3 (2.9)	--	0.5 (0.1)	0.2 (0.0)
$\text{Tebuthiuron}_{\text{(control)}}$	--	20.9 (4.7)	19.9 (3.8)	--	0.4 (0.1)	0.2 (0.0)
Brood-rearing	26.3 (4.6)	36.4 (6.3)	38.3 (4.5)	0.1 (0.0)	0.6 (0.0)	0.2 (0.0)

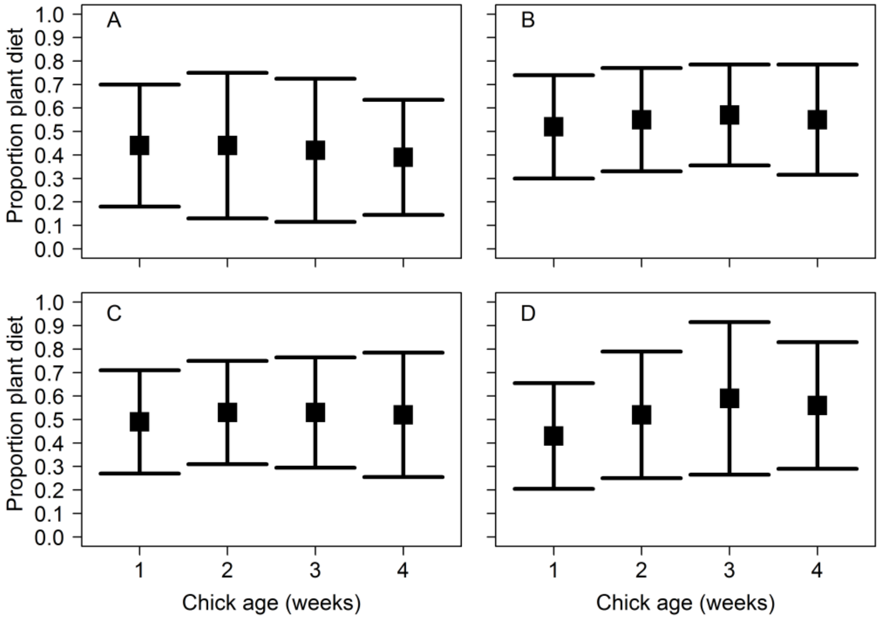


Figure 1. Estimated proportion of plant diet with chick age (weeks 1–4 post hatch) from individual greater sage-grouse chicks captured in A) Bighorn Basin during 2013, and Jeffrey City study areas during B) 2013, C) 2014, and D) 2015. Squares indicate the mean and outer lines the range of values estimated from mixing models.

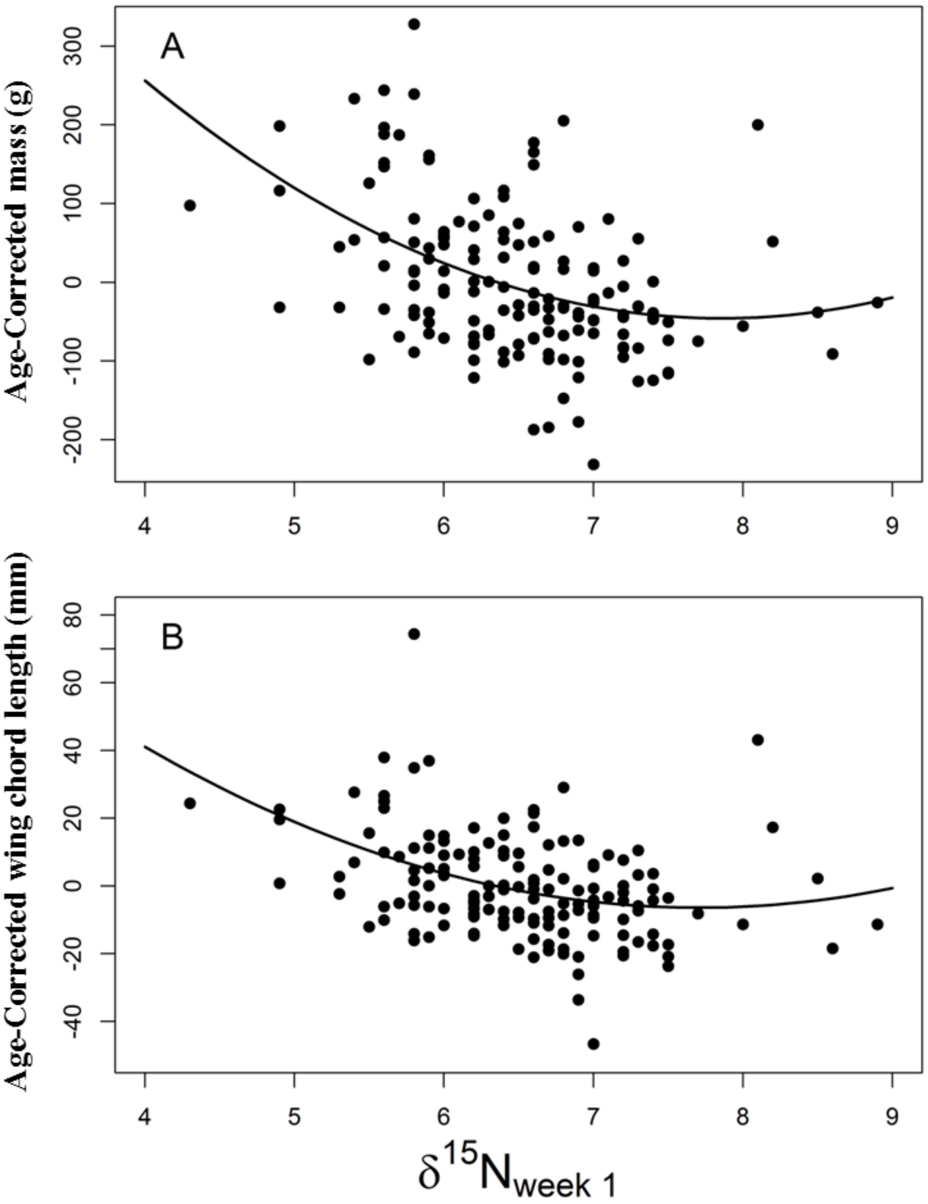


Figure 2. Relationship between feather ∂^{15}N during week 1 and A) age-corrected mass (g) and B) age-corrected wing chord length (mm) for individual chicks from Bighorn Basin (*n* = 45) and Jeffrey City (*n* = 108) study areas, Wyoming USA, 2013–2015.

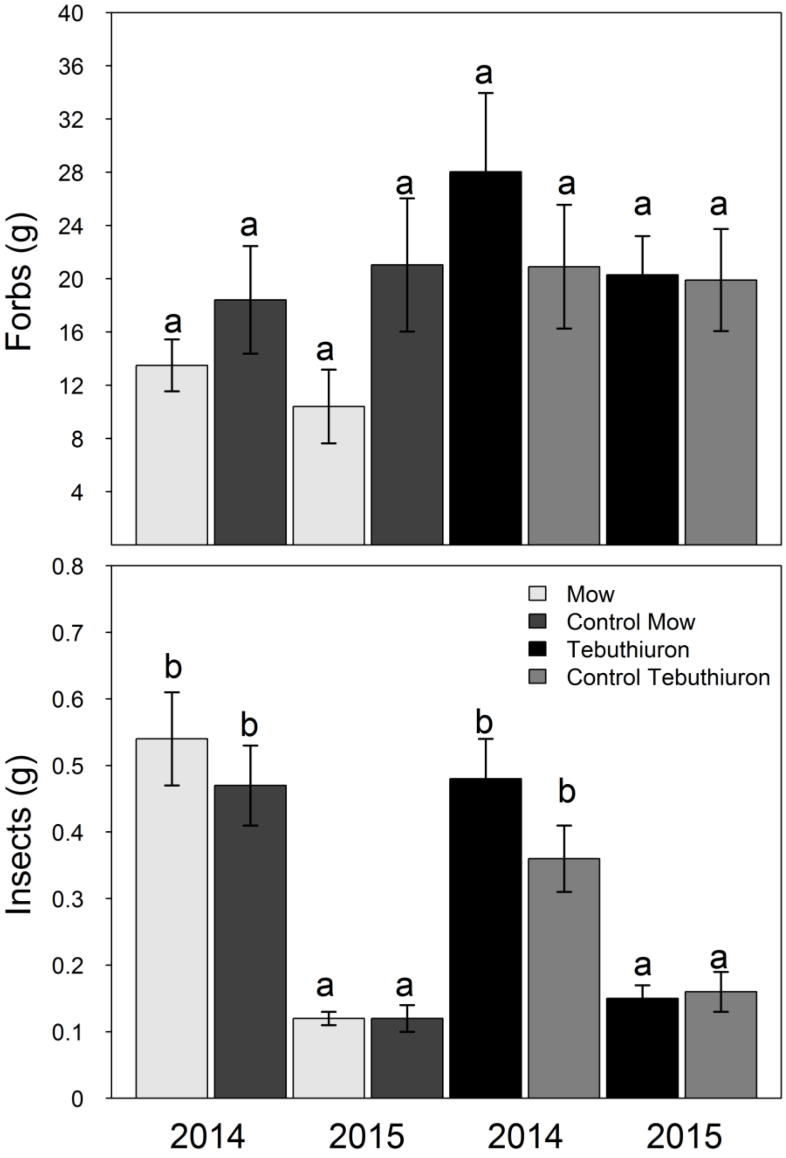


Figure 3**.** Mean forb and insect abundance (g dry mass; ± SE) at mowing, tebuthiuron, and un-treated locations sampled during 2014 and 2015, Jeffrey City study area, Wyoming, USA. Within each panel, means marked with the same letter are not different (Tukey's HSD test, P > 0.05).

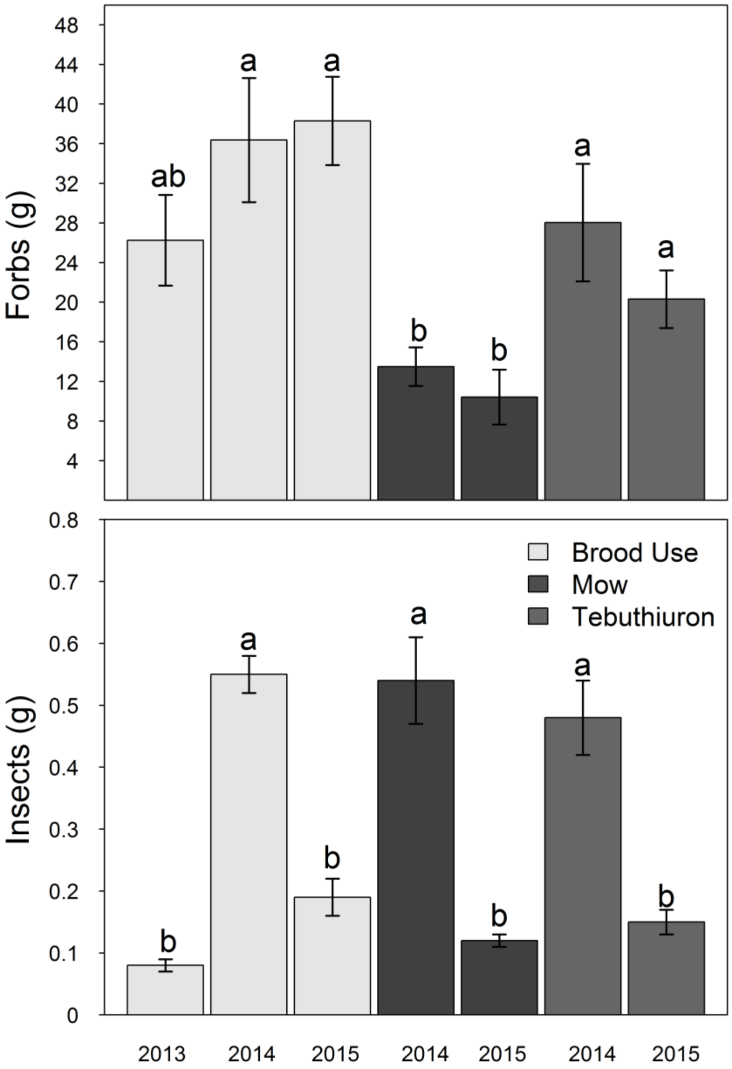


Figure 4. Mean forb and insect abundance (grams dry mass; ± SE) at locations used by brood-rearing females (2013–2015) in Bighorn Basin and Jeffrey City, and habitats treated with mowing and tebuthiuron (2014–2015) in Jeffrey City (only), Wyoming, USA. Within each panel, means marked with the same letter are not different (Tukey's HSD test, $P > 0.05$).

APPENDIX A: Jeffrey City Sagebrush Treatment Study Design

To capture the effects of treatments on brood-rearing habitat we employed a use-availability design to evaluate early brood-rearing sage-grouse habitat selection (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We identified resource use as locations obtained from relocations of radio-collared sage-grouse during 2011 and 2012 and pooled locations across individuals to represent a population level response (a Type 1 Design; Manly et al. 2002, Thomas and Taylor 2006). We generated 5-times the number of use locations across the study area to represent available habitat. Available locations were randomly located across a 100% minimum convex polygon generated from sage-grouse use locations during the early brood-rearing period (first 2 weeks following nest hatch; Thompson et al. 2006). We used Northwest Gap Analysis (2009) to constrain random locations to sagebrush habitats by excluding areas that were inappropriate to be considered as available habitat such as exposed rock, open water, and stands of conifer. We down weighted available units to account for over representation bias (Aldridge and Boyce 2007, Carpenter et al. 2010).

We considered a suite of predictor variables on the basis of *a priori* information from previous landscape-scale research on early brood-rearing habitat (Homer et al. 1993, Aldridge and Boyce 2007, Doherty et al. 2008, Carpenter et al. 2010, Doherty et al. 2010, Kirol et al. 2015; Table 1). These variables encompassed environmental categories that were evaluated at 3 spatial scales around used and available points: 0.283-km radii (0.25-km^2), 0.564-km radii (1.00-km^2), and 1.260-km radii (4.99-km^2). Spatial scales were based on previous research documenting relationships between landscape features and sage-grouse selection at those scales (Aldridge and Boyce 2007, Berry and Eng 1985, Doherty et al. 2010, Holloran and Anderson 2005).

We used remotely sensed sagebrush products (Homer et al. 2012; Table 1), to estimate percentage canopy cover of sagebrush (all *Artemisia* spp. combined), big sagebrush (*A. tridentata* species), Wyoming big sagebrush (*A.t. wyomingensis*), shrubs (all species), herbaceous cover, bare ground, and litter. We calculated the mean estimated percent cover and the standard deviation for each variable across the 3 spatial scales. Standard deviation was used as a proxy for habitat diversity or heterogeneity (Kastdalen et al. 2003, Carpenter et al. 2010). We assessed quadratic relationships to evaluate potential nonlinearities in mean percent cover estimates of all sagebrush and shrub categories (i.e., potential selection for intermediate landscape features; Dzialak et al. 2013). In addition, we calculated estimated mean and standard deviation of shrub height (all species; Homer et al. 2012).

We used a 10-m digital elevation map (DEM; USGS 2011) to calculate slope, aspect and elevation. We used these estimates to determine a Vector Ruggedness Measure (VRM). VRM uses the variation in slope and aspect to create a single measure of terrain ruggedness (Sappington et al. 2007). VRM values were calculated using a 3 x 3 cell format (Sappington et al. 2007). We rescaled VRM values by multiplying the original values by 1000 for ease of interpretation. In addition, we generated a Normalized Difference Vegetation Index (NDVI; measure of surface greenness) from National Agriculture Imagery Program (NAIP) color aerial imagery (U.S. Department of Agriculture [USDA] 2010).

Statistical Methods

We computed a Pearson's correlation matrix to test for multicollinearity among predictor variables and omitted one of each correlated variable when correlation coefficients $|r|$ were ≥ 0.7. We inspected tolerance (t) values and removed one of the correlated variables when $|t| \leq 0.40$

(Allison 2009, SAS Institute 2011). We checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($0.3 \leq |r| \leq 0.7$). Undetected correlations between variables may cause instability in the signs of coefficients and also result in inflated standard errors (Doherty 2008). If variables were correlated, the variable with the lowest AIC score was retained. We did not permit correlated variables to compete in the same model at any level of model selection.

We used a 2nd-order Akaike's Information Criterion adjusted for small sample sizes (AICc) to assess model support (Burnham and Anderson 2002). For all scale-dependent variables, we examined the 3 spatial scales (described above) to determine the scale that was most correlated to sage-grouse early brood selection by testing each variable scale individually and comparing AICc scores (Arnold 2010, Carpenter et al. 2010, Doherty et al. 2010). For each variable we retained the scale with the lowest AICc score corresponding to the greatest predictive potential (Burnham and Anderson 2002). After the selection of the most appropriate scale, we removed unsupported variables based on whether 85% confidence intervals (CIs) around odds ratios included 1 (Hosmer and Lemeshow 2000, Arnold 2010). An odds ratio of 1 indicates no significant difference between used and available habitat units (Hosmer and Lemeshow 2000). We used variable screening to remove unsupported predictor variables, thereby reducing the likelihood of over fitting models in our model selection process (Burnham and Anderson 2002, Arnold 2010).

We used a sequential model selection approach (Arnold 2010) by evaluating the relative importance of predictor variables for selection. We explored all variable combinations (Burnham and Anderson 2002). We considered models with AICc scores in the range of 0–7 units (Burnham and Anderson 2002) to be competitive with the top model. We assessed variable importance by summing Akaike model weights across models that included the variable of interest (Arnold 2010). When a single top model was not apparent based on AICc scores (≤7 units considered competitive) we used multi-model inference to calculate final parameter coefficients, 95% confidence intervals, and odds ratios. We determined confidence sets for those models where Akaike weights (w_i) were within 10% of the top model (Burnham and Anderson 2002). At the final level of model selection, we further filtered variables with poor support for a true statistical difference between groups that had odds ratios with 95% CIs that overlapped 1 (Hosmer and Lemeshow 2000). We performed a 5-fold cross validation to evaluate the predictive performance of our top model (Boyce et al. 2002). We conducted all statistical analyses with Statistical Analysis Software (SAS), version 9.3 (SAS Institute 2011).

We mapped our final resource selection model with 30-m pixel resolution across the study area. For interpretation, the final resource selection function (RSF) was mapped with values rescaled between 0 and 1 (linear stretch; DeCesare et al. 2012) where 1 represents the highest and 0 represents the lowest predicted relative probability of selection. We distributed our predicted probabilities into 4 quartiles on the basis of percentile breaks in predicted probabilities (Sawyer et al. 2006). Areas of high relative probability of selection (highest 25% of predicted probabilities for summer resource selection) were assigned a value of 4, moderate-high (51 to 75% predicted probabilities for summer resource selection) a value of 3, moderate-low (26 to 50% predicted probabilities for summer resource selection) a value of 2, and low (lowest 25% of predicted probabilities for summer resource selection) a value of 1.

Results

Seventeen models, which included 6 predictor variables at 2 spatial scales, made up our candidate set for early brood-rearing habitat selection. At the 0.25-km^2 (0.283 km radius) scale shrub height was negatively correlated with selection and shrub cover was positively correlated with selection. NDVI and variability in shrub cover were positive predictors of selection when averaged across 4.99-km^2 (1.260-km radii). In contrast, variability (as measured by standard deviation) in Wyoming big sagebrush was a strong negative predictor of selection at the 4.99-km^2 scale. Because our candidate set contained more than one model, we performed model averaging to estimate parameter coefficients, 95% confidence intervals, and odds ratios for all variables contained within the candidate set.

Model averaging indicated that the 95% confidence interval for the odds ratios of distance to water, shrub height, and variability of shrub height overlapped 1 and were therefore considered uninformative predictors of habitat selection. Our best approximating model of sage-grouse early brood-rearing habitat consisted of shrub cover (0.283 radius), NDVI (1.260 km radius) and variability in Wyoming big sagebrush cover (1.260 km radius; Table 2). Cross-validation indicated that our best model was a strong positive predictor of sage-grouse early brood-rearing habitat use ($r_s = 0.96$, P = 0.001, n = 10).

Through the process of developing a RSF (Figure 1) and retaining the 2 highest predicted relative probability bins we overlaid clusters of early brood-rearing locations that were spatially separated across our study area and located 6 spatially separated project treatment locations (2 mowing, 2 tebuthiuron, and 2 reference sites). Mowing treatment study areas were 50.0 km^2 and 33.8 km^2, tebuthiuron treatment study areas were 24.9 km^2 and 44.8 km^2, and reference study areas were 61.1 km^2 and 16.5 km^2, respectively. This was attributed to the spatial arrangement of leks that were chosen for capture because females occupied habitats in the relative vicinity of the lek in which they were bred, but also the habitat conditions present in those locations that were being used. Because of the relatively high site fidelity of sage-grouse across years (Berry and Eng 1985, Dunn and Braun 1985, Fischer et al. 1993, Holloran and Anderson 2005, this study) clusters of sage-grouse use locations during the early brood-rearing period were deemed appropriate for outlining treatment areas. This ensured that 1) locations were in suitable sage-grouse habitat in a location that we could test for a response to sagebrush treatments, and 2) grouse have occurred in and likely will occur in these locations in the future. Each location was buffered by the mean distance between nest and the week 2 early brood-rearing locations (1048 m). Then we generated a 100% minimum convex polygon around buffered locations that were within similar clusters of use locations.

We restricted potential treatment areas to locations falling in the two highest predicted probability bins. We removed from consideration locations of cultural significance, such as historical trails, and locations where long-term rangeland monitoring takes place (BLM Lander Field Office). Following the Wyoming Game and Fish Department (WGFD) Protocols for Treating Sagebrush for the Benefit of Sage-Grouse in Core Areas (WGFD 2011) we buffered known leks within the study area by 0.97- km (2.96-km^2) and removed locations closer than 0.97 km to leks from treatment consideration.

We followed the State of Wyoming Executive Order 2011-5 guidelines detailing sage-grouse Core Area protection within Core Areas to calculate the maximum allowable disturbance by means of a Density/Disturbance Calculation Tool (DDCT) for our proposed project areas (State of Wyoming 2011). Stipulations for the DDCT are found in the Wyoming Game and Fish

Department protocols for treating sagebrush (WGFD 2011). We digitized existing disturbance using NAIP imagery (NAIP 2009). Disturbance included any human alterations such as roads, energy infrastructure, and human dwellings. We used geographic information predictor variables from our best approximating models to further refine suitable treatment locations within overall project locations. We removed locations when shrub cover was less than 2 standard deviations of the mean grouse use location (7.9% as computed from Homer et al. 2012 data layer) so we would not treat locations containing sparse shrub cover. We considered treatment locations as suitable if they were in areas greater than 100 m from water, less than 15% slope, and had VRM values no greater than two standard deviations above the mean grouse use location. Removing steep slopes and high ruggedness (VRM) was a precautionary measure to ensure accessibility and equipment operator safety during treatment. Within the 4 treatment areas, we generated n = 4-5 ~2.59-km2 polygons that were used to demarcate locations for treatment in each of the 4 treatment sites (Figure 2).

We treated sagebrush (Spike® 20P [active ingredient, tebuthiuron] and mechanical mowing in early brood-rearing habitat during winter and spring 2014. We used female early brood-rearing locations and areas that were predicted to have high early brood-rearing occurrence to identify 4 treatment locations (2 tebuthiuron and 2 mowing treatments) and 2 reference locations. Treatments followed guidelines of the Wyoming Game and Fish Department Protocols for Treating Sagebrush to be consistent with Wyoming Executive Order 2011-5; Greater Sage-Grouse Core Area Protection (WGFD 2011). The only exception to the WGFD protocols was that instead of grazing rest for 2 growing seasons after treatments, we installed exclosures to measure post-treatment vegetative response in the absence of grazing. This was necessitated by the fact that only 1 allotment in the 6 study areas had cross fencing and a rotational grazing system–the remaining 5 study areas occurred in areas with season-long continuous grazing–thus, making evaluations of ungrazed post treatment vegetation responses impossible without exclosures. Therefore, B and A Leasing of Greybull, Wyoming installed 12, 30 m x 60 m exclosures in mowed sites and 12, 30 m x 80 m exclosures in tebuthiuron-treated sites (exclosures constructed in herbicide-treated areas were larger to account for potential herbicide leaching into the untreated side) to serve as controls for livestock grazing. The general design of these exclosures was to exclude a 30 x 30 m (0.22 ac) area of untreated sagebrush with an adjoining 30 x 30 m area excluding livestock grazing in treated sagebrush. The size of these exclosures permit us to evaluate vegetation and ground cover characteristics within an area equivalent to the size of plots used to assess sage-grouse microhabitat selection at nesting and brood-rearing locations. During January and February 2014, the Wyoming Game and Fish Department and the University of Wyoming mowed approximately 489 ha (1,208 ac) of sagebrush habitats across 2 mowing treatment areas (Figure 3). Tebuthiuron application occurred in early May 2014 (Figure 4). We contracted with Ag Flyers, Inc. of Torrington, Wyoming to apply 1.12 kg/ha (0.22 kg/ha active ingredient), anticipating a 50% kill rate of sagebrush, to 6.1 km2 (1,500 ac) across 2 study areas. Exclosures were erected in May 2014 following treatments.

LITERATURE CITED

Aldridge, C.L., and M.S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat based approach for endangered greater sage-grouse. Ecological Applications 17:508-526

Allison, P.D. 2009. Logistic regression using SAS: theory and application. Eighth edition. SAS Institute Incorporated. Cary, North Carolina, USA.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178.

Berry, J.D., and R.L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. Journal of Wildlife Management 49:1175-1178.

Boyce, M.S., P.R. Vernier, S.E. Nielson, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281-300.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Carpenter, J., C. Aldridge, and M.S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806-1814.

DeCesare, N.J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G.J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K.G. Smith, L.E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions Ecological Applications 22:1068-1083.

Doherty, K.E. 2008. Sage-grouse and energy development: integrating science with conservation planning to reduce impacts. Dissertation, University of Montana, Missoula, 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, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Dunn, P.O., and C.E. Braun. 1985. Natal dispersal and lek fidelity of sage-grouse. Auk 102:621-627.

Dzialak, M.R., S.L. Webb, S.M. Harju, C.V. Olson, J.B. Winstead, and L.D. Hayden-Wing. 2013. Greater sage-grouse and severe winter conditions: identifying habitat for conservation. Rangeland Ecology and Management 66:10-18.

Fischer, R.A., A.D. Apa, W.L. Wakkinen, K.P. Reese, and J.W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038-1041.

Holloran, M.J. and S.H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Homer, C.G., C.L. Aldridge, D.K. Meyer, and S.J. Schell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. Journal of Applied Earth Observations and Geoinformation 14:233-244.

Homer, C.J., T.C. Edwards, Jr., D.R. Ramsey, and K.P. Price. 1993. Use of remote sensing methods in modeling sage grouse winter habitat. Journal of Wildlife Management 57:78-84.

Hosmer, D.W., and S. Lemeshow. 1999. Applied survival analysis: regression modeling of time to event data. John Wiley and Sons, New York, New York, USA.

Johnson, C.J., S.E. Nielsen, E.H. Merrill, T.L. McDonald, and M.S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347-357.

Kastdalen, L., H. C., Pedersen, F., Gunnar, and H. P. Andreassen. 2003. Combining resource selection functions and distance sampling: an example with willow ptarmigan. Pages 52–59 *in* S. Huzurbazar eds. Resource Selection Methods and Application. Western EcoSystems Technology, Incorporated, Cheyenne, Wyoming, USA.

Kirol, C.P., J.L. Beck, S.V. Huzurbazar, M.J. Holloran, and S.N. Miller. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:968-990.

Manly, B.F., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London.

Northwest GAP Analysis Project. 2009. Land cover data (Gap Analysis Program Northwest) 30 m for Wyoming. Sanborn Map, Portland, Oregon, USA.

Sappington, M.J., K.M. Longshore, and D.B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:419-1426.

SAS Institute. 2011. SAS/STAT user’s guide. Release 9.3. SAS Institute, Cary, North Carolina, USA.

Sawyer, H., R.M. Nielson, F. Lindzey, and L.L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396-403.

State of Wyoming. 2011. State of Wyoming Executive Department, Executive Order 2011-5, Greater sage-grouse core area protection. Cheyenne, WY, USA; Office of the Governor of Wyoming. 18p.

Thomas, D.L., and E.J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 71:1410-1426.

Thompson, K.M., M.J. Holloran, S.J. Slater, J.L. Kuipers, and S.H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. Western North American Naturalist 66:332-342.

U.S. Department of Agriculture. 2010. 2009 NAIP survey: summary report. Farm Service Agency, Aerial Photography Field Office, Salt Lake City, Utah, USA.

U.S. Geological Survey. 2011. Seamless Data Warehouse. http://seamless.usgs.gov/\

Table 1. Variables used in the model selection analysis evaluating greater sage-grouse early brood-rearing habitat selection in Fremont and Natrona counties, Wyoming, USA, 2011 and 2012.

Variable names	Description
Bsage†	Mean big sagebrush (*Artemisia tridentata*) cover (%; Homer et al. 2012)
Bsagesd	Standard deviation of big sagebrush cover (%; Homer et al. 2012)
DEM	Digital elevation model to calculate aspect, slope, and elevation(USGS 2011)
NDVI	Normalized Difference Vegetation Index (NAIP imagery; USDA 2010)
Sage†	Mean sagebrush (all *Artemisia* spp.) cover (%; Homer et al. 2012)
Sagesd	Standard deviation of sagebrush cover (%; Homer et al. 2012)
Shrub†	Mean shrub cover (%; Homer et al. 2012)
Shrubsd	Standard deviation of shrub cover (%; Homer et al. 2012)
Shrubhgt	Mean shrub height (cm; Homer et al. 2012)
Shrubhgtsd	Standard deviation of shrub height (cm; Homer et al. 2012)
VRM	Mean topographic roughness (vector roughness measure [VRM; Sappington et al. 2007])
Wysage†	Mean Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) cover (%; Homer et al. 2012)
Wysagesd	Standard deviation of Wyoming big sagebrush cover (%; Homer et al. 2012)

†Quadratic transformation assessed

Table 2. Parameter estimates, variable importance values, and odds ratios for variables that were included in top models(s) depicting sage-grouse early brood-rearing habitat selection in Fremont and Natrona counties, Wyoming, USA, 2011 and 2012.

Parameter	Estimate	95% CI		Variable importance	Odds ratio	95% CI	
		Lower	Upper			Lower	Upper
Intercept	-4.260	-6.991	-1.527				
NDVI1260	0.016	0.006	0.025	0.923	1.016	1.006	1.026
Shrub283	0.096	0.013	0.178	0.702	1.100	1.013	1.195
WY1260SD	-0.4921	-0.855	-0.129	0.824	0.611	0.425	0.879

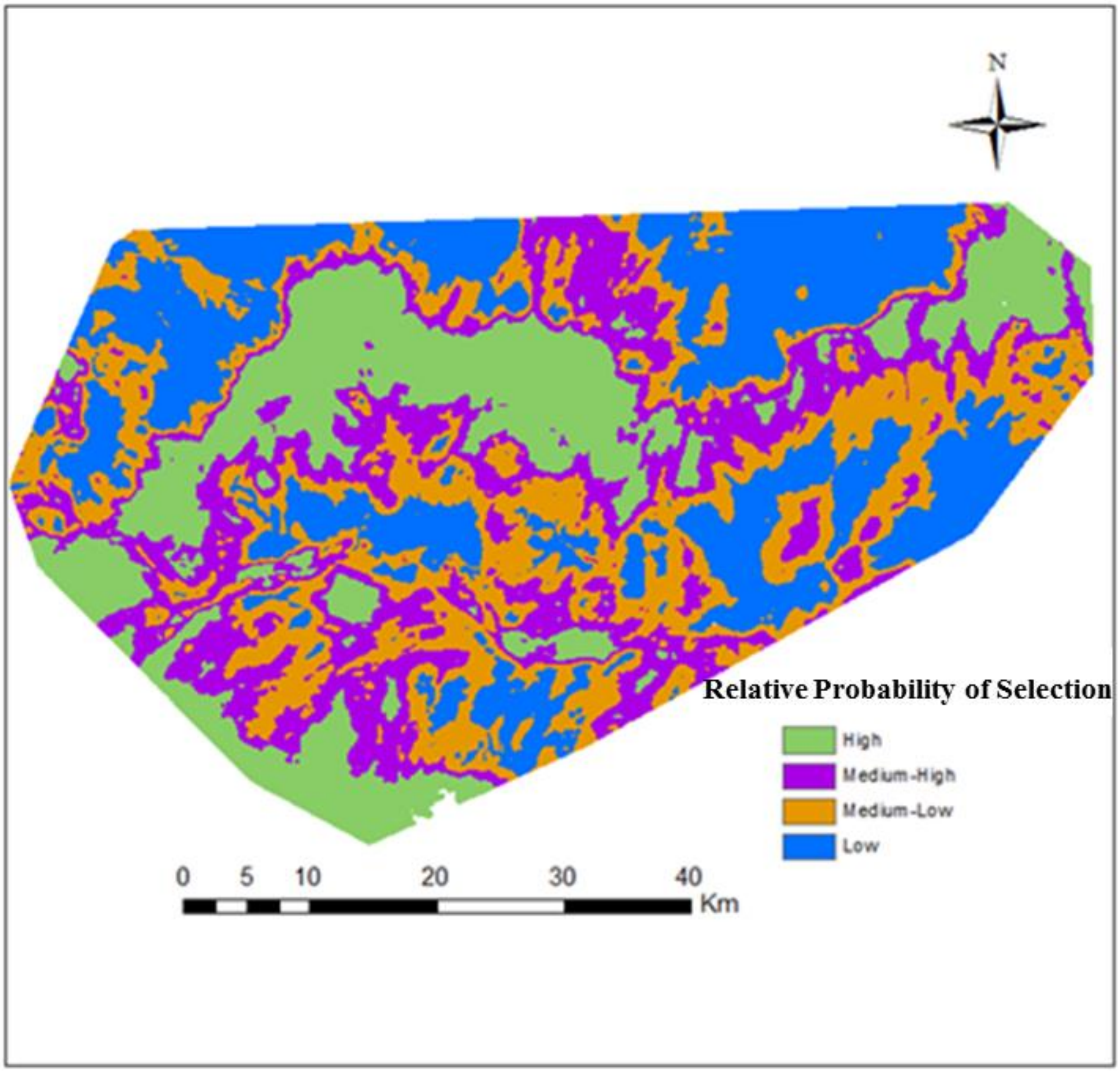


Figure 1. Predicted relative probability of sage-grouse early brood-rearing habitat selection in Fremont and Natrona counties, Wyoming, summers 2011 and 2012.

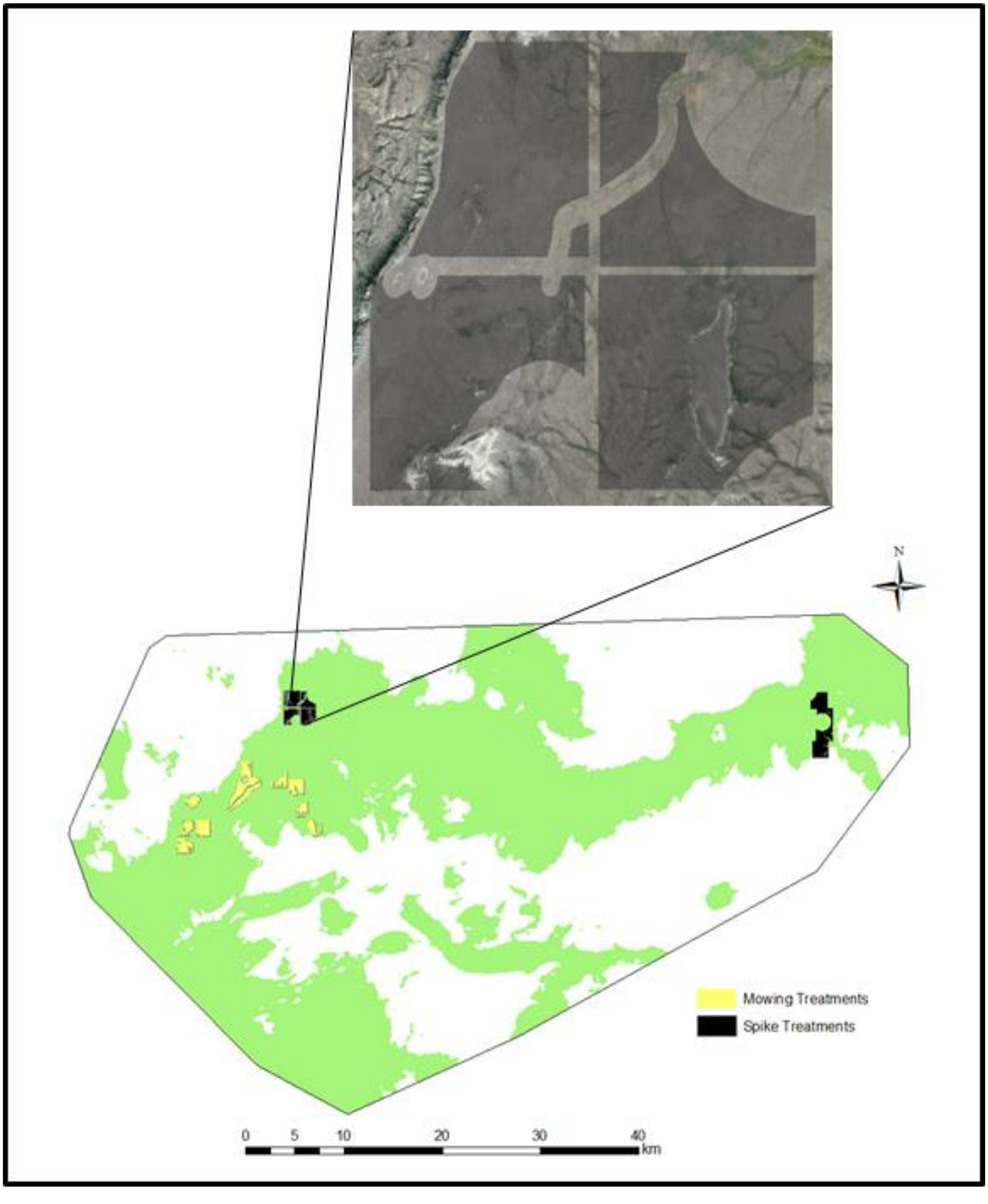
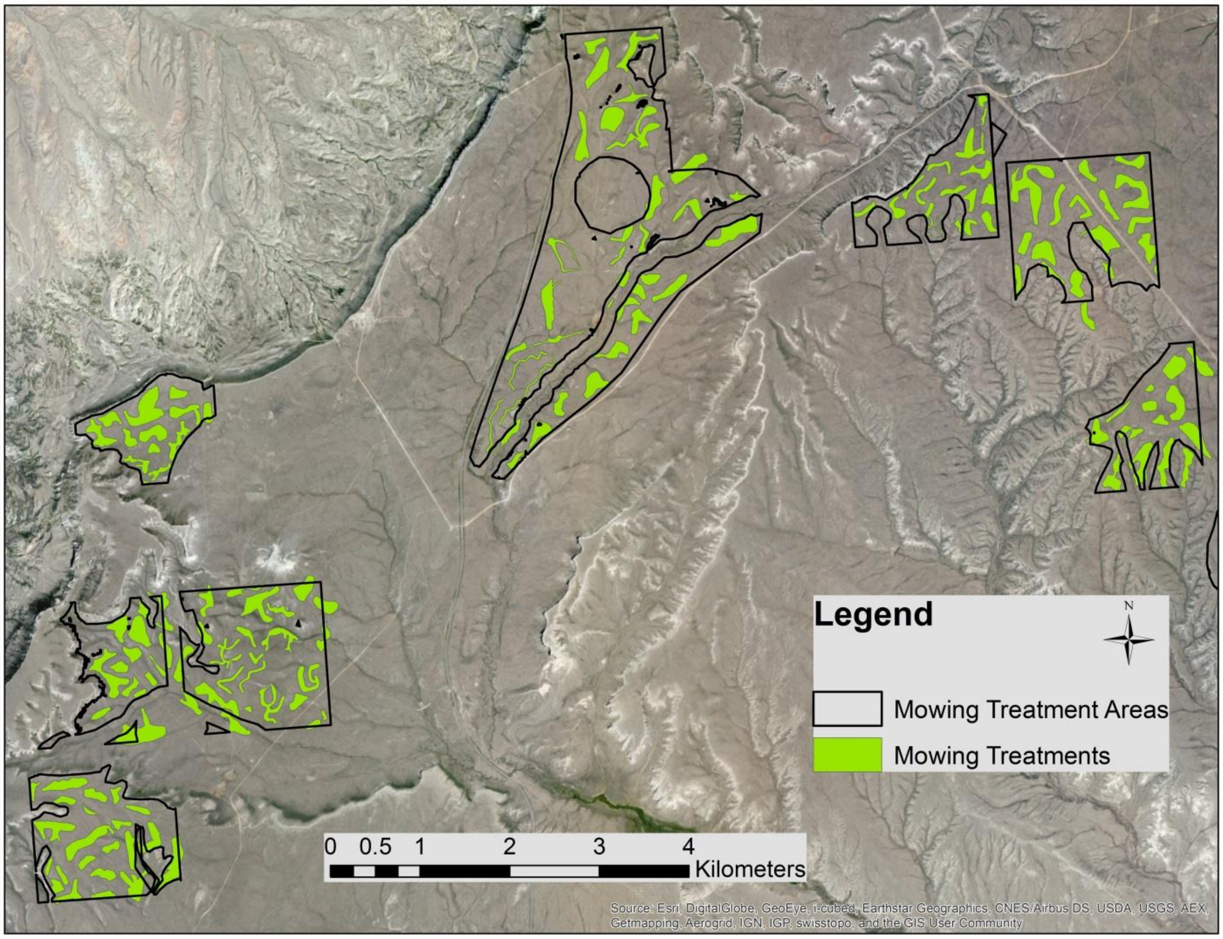


Figure 2. Polygons used to demarcate locations for treatment in each of the 4 treatment sites. This excerpt is from one tebuthiuron treatment in the northwest portion of the study area.



Source: Esri, DigitalGlobe, GeoEye, i-cubed, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 3. Mowed sagebrush habitat configuration in mowed polygons at two mowing treatment areas. Approximately 489 ha (1,208 ac) of sagebrush habitats were mowed across two study areas during January and February 2014.

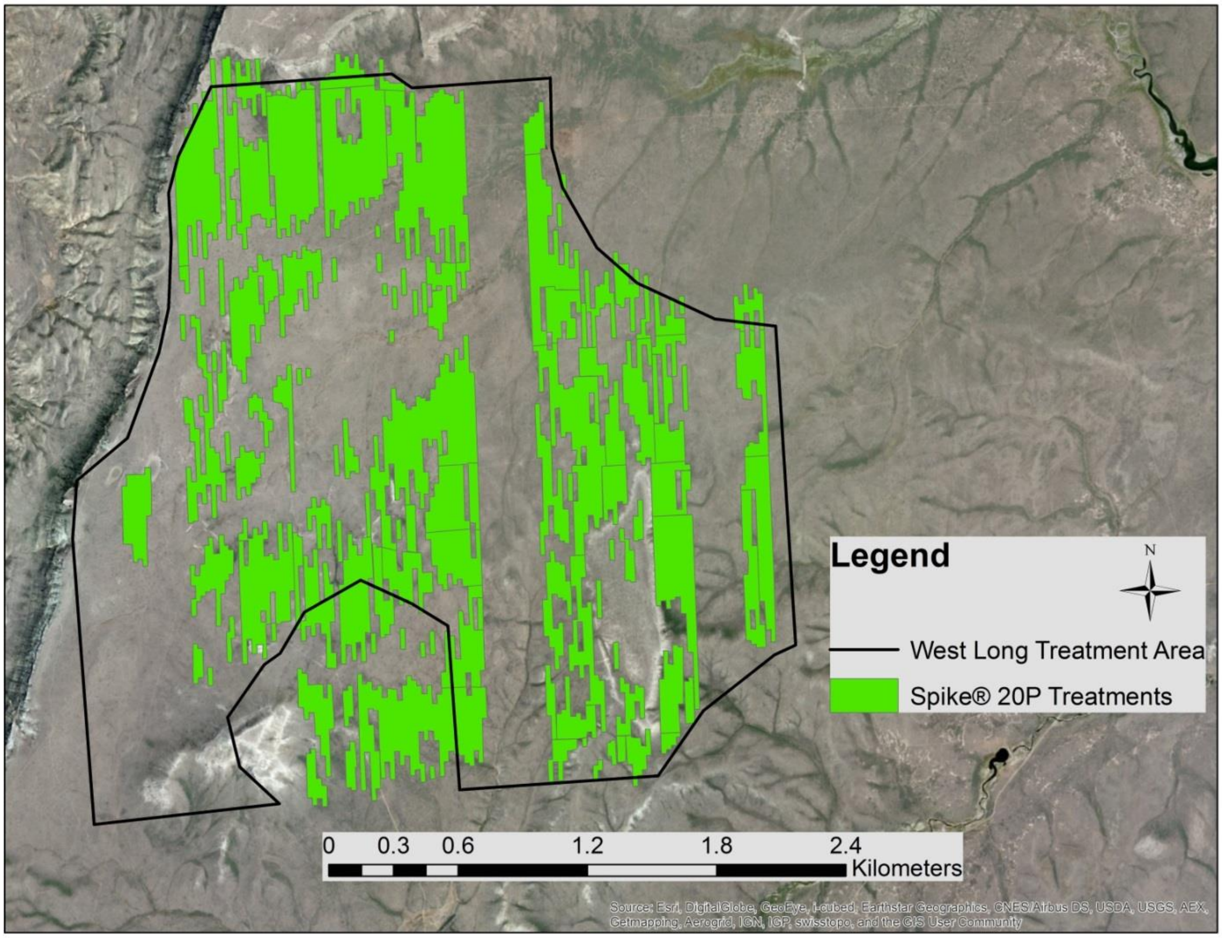


Figure 4. Arrangement of sagebrush habitats treated with tebuthiuron at one treatment area. Approximately 607 ha (1,500 ac) of sagebrush habitats were treated with tebuthiuron across two study areas during May 2014.