

EFFECT OF PREDATOR REMOVAL ON GREATER SAGE-GROUSE
(CENTROCERCUS UROPHASIANUS) ECOLOGY IN THE BIGHORN
BASIN CONSERVATION AREA OF WYOMING

by

Elizabeth K. Orning

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

Julie K. Young
Major Professor

Frank P. Howe
Committee Member

Mary M. Conner
Committee Member

Mark R. McLellan
Vice President for Research and
Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2014

Copyright © Elizabeth K. Orning 2014

All Rights Reserved

ABSTRACT

Effect of Predator Removal on Greater Sage-grouse (*Centrocercus urophasianus*)

Ecology in the Bighorn Basin Conservation Area of Wyoming

by

Elizabeth K. Orning, Master of Science

Utah State University, 2014

Major Professor: Dr. Julie K. Young
Department: Wildland Resources

The decline of greater sage-grouse (*Centrocercus urophasianus*) populations across western North America has intensified conservation, research, and management efforts. Predator-prey interactions have been the focus of widespread scientific study, but little research has been conducted on the effects of predation and predator removal on sage-grouse ecology. This study had three main objectives: 1) identify the types of predators impacting hen survival and nest success, 2) compare the effect of predator removal on vital rates, and 3) evaluate habitat selection and movement. Over two years (2011-2012), an observational study and field experiment were used to test the effects of predation and predator removal on sage-grouse survival, nest success, and spatial ecology in Bighorn Basin, Wyoming. In year one, I quantified the impacts of predators on sage-grouse demographics and developed a basis for monitoring sage-grouse and predator populations. In year two, predator removal was modified to remove the primary nest and hen predator in this system: coyote (*Canis latrans*). I evaluated the impact of

anthropogenic features and management on sage-grouse home range size, seasonal movement, and habitat selection for potential behavioral responses. Resource selection functions (RSFs) were used to determine habitat selection and identify differences at multiple spatial extents (seasonal and annual scales). Hen survival was improved in sites treated with coyote removal over the nesting period ($P = 0.05$) but no improvement was seen in annual hen survival ($P = 0.19$). Observed nest success was higher at the site without coyote removal ($P < 0.0001$). RSF modeling showed sage-grouse to be sensitive to predator removal, avoiding areas close to roads, with high well density, and steep slopes. While this study suggests predator removal does not benefit observed nest success, provides only short-term enhancement to survival, and may disrupt habitat selection, potentially benefits to other life stages could exist and be detected with more time and monitoring. By taking an experimental approach to examining the effects of predation and predator removal, this study advances our knowledge of sage-grouse ecology by identifying changes in demographic vital rates and habitat selection, propagating the best management possible for sage-grouse populations.

(140 pages)

PUBLIC ABSTRACT

Effect of Predator Removal on Greater Sage-grouse (*Centrocercus urophasianus*)

Ecology in the Bighorn Basin Conservation Area of Wyoming

by

Elizabeth K. Orning

The decline of greater sage-grouse distribution and population densities across western North America has led conservation, research, and management objectives to focus efforts on understanding sage-grouse populations across their range. The purpose of this study was to gain a better understanding of direct and indirect predation effects on hen survival and nest success of sage-grouse. The project was conducted in Hot Springs and Park Counties in the Bighorn Basin of Wyoming. The study had three main objectives: 1) obtain and quantify the types and impacts of predators on sage-grouse hen survival and nest success, 2) compare the effect predator removals on hen survival and nest success, and 3) evaluate sage-grouse habitat selection and movement relative to predator removal.

In a two-year study (2011-2012) the effects of predation and predator removal on sage-grouse ecology were tested via a field experiment. Project costs to study sage-grouse from 1 April 2011 to 31 March 2013 were supported through funding for supplies and in-kind support worth \$225,000. Research was carried out by Utah State University and USDA-WS-National Wildlife Research Center-Predator Research Facility in cooperation with USDA-Wildlife Services, Meeteetse Conservation District, and

Wyoming Game and Fish. Survival of hens over the period removal occurred (nesting) was higher at sites with coyote removal, but not annually. No differences were detected in the survival rates of nests, but observed nest success was significantly higher at sites without coyote removal. Sage-grouse home range size, seasonal movement, and habitat selection were affected by management and anthropogenic features such that short-term alterations to management, like those associated with predator removal, appear to disturb sage-grouse behavior during critical life stages.

This research quantified the impacts of predators and predator removal on two important sage-grouse vital rates (hen survival and nest success), developed a framework for monitoring changes in both sage-grouse and predator populations, and evaluated the influences anthropogenic features and predator management can have on sage-grouse populations. This information will enhance sage-grouse conservation and management decisions.

ACKNOWLEDGMENTS

This project was a cooperative effort between many groups and agencies. Steve Jones and the Meeteetse Conservation District were important to the direction and success of this project through their facilitation of landowner contacts, logistical assistance, and engaging questions. Jim Perhinger and USDA-Wildlife Services NW District personnel were dedicated to the success of the project and were instrumental in implementing experimental design, capturing sage-grouse and providing field operational assistance. Eric Maringer, Gaston Aarts, and Wolbert van den Broek assisted with data collection. In addition, I thank Tim Woolley and the entire staff of the Wyoming Game and Fish Cody office, who provided not only support and immeasurable knowledge of wildlife, but accommodations, hospitality, and good neighborly banter. I thank Tom Easterly and Jerry Altermatt for their expertise on sage-grouse and habitat.

None of this would have been possible without my advisor, Dr. Julie Young. Julie's guidance, encouragement, and understanding were instrumental in my success. I thank her for believing in me and pushing me in all the right ways. A mentor to me in research, communication, and the epitome of a positive attitude, I will carry lessons learned from her throughout my career and life. I also want to recognize and thank my committee members, Drs. Mary Conner and Frank Howe, for their guidance and support throughout the entire process.

I give special thanks to my family, friends, and colleagues for their encouragement, moral support, and patience as I worked my way from field work to this final document. Special thanks to Linsey Blake, Megan Schwender, Cheyenne Burnett, Seth Dettenmaier, Tony Roberts, Kelly Goonan, Shannon Bardot, Kate Olson, Aimee

Tallian, Pete Mahoney, Michel Kohl, Sharon Poessel, and the most awesome Knitting group ever, for your friendship, open office doors, and invitations to play as hard as I work. I would like to pay special tribute to my amazing sister, Laura, for unshakable support through sometimes daily phone calls and multiple road/plane trips across the country while facing her own battle against breast cancer. You are my hero. Thanks also to my parents, Julie and Steve, for instilling in me a love of the natural world that inspired the passion to pursue a career in wildlife biology. Thanks to Grandmaster Yong Chin Pak, for being one of the greatest Martial Arts instructors in the world and teaching a dreamer how to turn desire and dedication into a path to reach my goals. I could not have completed this journey without all of your support and I will be forever grateful.

Research funding was provided by USDA-WS-NWRC, Utah State University, Meeteetse County Conservation District, USDA-Wildlife Services and contributions from Belden Ranch, Big Horn Basin Resource Conservation and Development Council, Powell-Clarks Fork, Shoshone, and Washakie County Conservation Districts, Legacy Reserves, LLC, Marathon Petroleum, Park County Farm Bureau, and V Ranch, with additional grant support through the Wyoming Animal Damage Management Board and in-kind contributions from Cody, Hot Springs, and South Big Horn Conservation Districts, Fidelity Exploration, Guardians of the Range, Big Horn, Hot Springs, Park and Washakie County Predator Management Districts, USDA NRCS, and USDI BLM.

Beth Orning

CONTENTS

	Page
ABSTRACT.....	iii
PUBLIC ABSTRACT.....	v
ACKNOWLEDGMENTS.....	vii
LIST OF TABLES.....	xii
LIST OF FIGURES.....	xiv
THESIS FORMAT.....	xv
CHAPTER	
1. INTRODUCTION.....	1
Purpose.....	6
Study Area.....	7
Literature Cited.....	8
2. COYOTE REMOVAL AS A TREATMENT TO INCREASE GREATER SAGE-GROUSE HEN SURVIVAL AND NEST SUCCESS.....	17
Abstract.....	17
Study Area.....	21
Methods.....	23
Experimental Design.....	23
Predator Removal.....	23
Field Monitoring and Surveys.....	24
Scent stations.....	24
Avian road transects.....	25
Point counts.....	25
Scat transects.....	26
Vegetation sampling.....	26
Hen survival.....	27
Nest survival & success.....	27
Statistical Analysis.....	29

Genetic Analysis..... 31

Results..... 31

 Baseline Data..... 31

 Predator surveys..... 31

 Hen survival..... 32

 Nest survival & success..... 33

 Experimental Data..... 34

 Coyote detection & removal..... 34

 Scent station surveys..... 35

 Avian point count surveys..... 36

 Vegetation surveys..... 36

 Hen survival..... 37

 Nest survival & success..... 38

 Discussion..... 39

 Management Implications..... 45

 Literature Cited..... 46

3. ANTHROPOGENIC INFLUENCES ON GREATER SAGE-GROUSE
SPACE USE AND HABITAT SELECTION..... 63

 Abstract..... 63

 Introduction..... 64

 Methods..... 67

 Study Area..... 67

 Field Procedures, Location Data, and Home Range Generation..... 69

 Landscape and Anthropogenic Variables..... 72

 Resource Selection Modeling..... 74

 Model Assessment..... 75

 Results..... 75

 Sage-Grouse Home Range Size and Seasonal Movement 76

 Resource Selection..... 77

 Annual..... 78

 Seasonal..... 79

 Discussion..... 80

 Literature Cited..... 86

4. CONCLUSION.....	107
APPENDICES.....	110
APPENDIX A.....	111
Chapter 2 Supplemental Material.....	112
APPENDIX B.....	116
Chapter 3 Supplemental Material.....	117

LIST OF TABLES

Table	Page
2.1 Sage-grouse hen survival estimates from Cox regression model for a predator study conducted over two years in the Bighorn Basin, Wyoming, USA, 2011 – 2012. As a pilot year, baseline data was collected in 2011. Experimental coyote removal was conducted in the second year (2012). In both years the Control site received no prescribed predator removal	56
2.2 Observed nest success estimates for sage-grouse based on daily survival rate (<i>dsr</i>) for two sites with different predator management in 2011 and three coyote removal treatment levels in 2012 in Bighorn Basin, Wyoming, USA.....	58
2.3 Capture, nesting, and survival data for VHF collared sage-grouse at three lek complexes with different levels of predator control in Bighorn Basin, Wyoming, USA (27 March – 31 August 2012).....	59
2.4 Means (SE) of vegetal variables measured at successful and unsuccessful greater sage-grouse nests ($n = 35$) in Bighorn Basin, Wyoming, USA, 2012.....	60
3.1 Variables fit to logistic models (GLMM) to predict habitat selection for greater sage-grouse (2011 – 2013) at annual or seasonal (breeding (March – May), brood (June – late August), seasonal (September – November)) time scales for Bighorn Basin, Wyoming, USA. Each annual logistic model was based on 6,309 used and 19,156 available points. Each seasonal logistic model was based on 5,713 used and 17, 139 available points.....	97
3.2 Average sage-grouse home range size over annual, breeding (March – May), brood rearing (June – August), and inter-seasonal (late August – early November) periods across three sites with varying levels of predator management and anthropogenic features. Fixed kernel density estimates (KDE) were used to generate 95% probability contours. Core use areas represent 25% density kernel areas. Total home ranges are 99% density kernel areas. Inter-seasonal ranges include multiple seasonal time frames as birds transitioned through areas during spring and fall. Asterisks identify significant ($\alpha = 0.10$) differences between sites.....	100
3.3 Average seasonal range distances between breeding, brood-rearing, and inter-seasonal use areas for GPS marked sage-grouse hens ($n = 12$) in Bighorn Basin, Wyoming, USA	101

- 3.4 Fit statistics for models incorporating anthropogenic, predator, habitat, terrain, and all variable (habitat+terrain+anthropogenic+predator) logistic mixed effect models explaining annual resource selection for sage-grouse in Bighorn Basin, Wyoming, USA 2011 – 2013. Each logistic model had random intercepts for individual bird ($n = 12$) and was based on 6,309 used and 19,156 available points. Models are ranked by the change in Akaike Information Criterion corrected for small sample size (ΔAIC_c) values. For each logistic model we report K (number of parameters in the model), LL (log-likelihood), and Akaike weights (w_i , the likelihood the model is the best of those evaluated)..... 102
- 3.5 Fit statistics for models incorporating anthropogenic, predator, habitat, terrain, and all variable (habitat+terrain+anthropogenic+predator) logistic mixed effect models explaining seasonal range resource selection for sage-grouse in Bighorn Basin, Wyoming, USA 2011 – 2013. Seasons were defined as breeding (March – May), brood (June – late August), inter-seasonal (September – November). Each logistic model had random intercepts for site ($n = 3$) and individual bird ($n = 12$), and was based on 5,713 used and 17, 139 available points. Models are ranked by the change in Akaike Information Criterion corrected for small sample size (ΔAIC_c) values. For each logistic model we report K (number of parameters in the model), LL (log-likelihood), and Akaike weights (w_i , the likelihood the model is the best of those evaluated)..... 104

LIST OF FIGURES

Figure	Page
2.1 Location of our study of coyote removal treatment effects on greater sage-grouse vital rates in the Bighorn Basin of Wyoming, USA 2011 – 2012. We implemented an experimental design at three sites to test the effects of no (Oregon Basin, control site), moderate (15 Mile), and high (Polecat Bench) coyote removal treatments on the observed nest success and hen survival of sage-grouse.....	61
2.2 Sage-grouse hen survival estimates (13 Apr 2011 – 1 Mar 2013) for the duration of a two year predator removal study in Bighorn Basin, Wyoming 2011 – 2012. We implemented an experimental design at three sites to test the effects of no (Oregon Basin, control site), moderate (15 Mile), and high (Polecat Bench) coyote removal treatments. Estimates are from Cox regression model for covariate effects of A) year of study, B) age of hen, and C) treatment.....	62
3.1 Location of our study of anthropogenic impacts on greater sage-grouse habitat selection and space use in Bighorn Basin, Wyoming, USA 2011 – 2013. We implemented resource selection modeling in conjunction with a predation study to evaluate the effects of anthropogenic features related to different levels of predator management at three sites with subsequent no (Oregon Basin), moderate (15 Mile), and high (Polecat Bench) predator management levels.....	106

THESIS FORMAT

Some chapters within this thesis have been formatted in the required style for journal submission. Chapter 1 is an overview of the entire thesis. Chapter 2 and 3 were written and formatted as individual manuscripts that will be submitted for publication in *The Journal of Wildlife Management* and *The Condor*, respectively. I am the first author on each manuscript within this thesis, but because this study was collaborative, Julie Young will be included in publications as a co-author and I used ‘we’ throughout Chapter 2 and 3. Supplemental material referred to in the text of Chapters 2 and 3 are available in the Appendix. Chapter 4 is a conclusion discussion of the entire thesis and returns to first person use of ‘I’ throughout.

CHAPTER 1

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) distribution and population densities have declined across western North America (Schroeder et al. 2004). The largest grouse species, sage-grouse once occupied 1,200,483km² of sagebrush habitat across 13 states in the U.S. and 3 provinces in Canada (Schroeder et al. 2004). The severity and extent of this decline have led to recent listing of sage-grouse under the Endangered Species Act of 1973 as warranted but currently precluded by species of higher concern (USFWS 2010). Extensive changes since European settlement have imperiled many sagebrush-steppe habitats through continuing fragmentation and degradation (Knick et al. 2003, Connelly et al. 2004), conversion to agriculture (Connelly et al. 2004), nonnative species invasion (Knick et al. 2003, Connelly et al. 2004), energy development (Braun et al. 2002, Lyon and Anderson 2003, Doherty et al. 2008), grazing pressure (Beck and Mitchell 2000, Crawford et al. 2004), and climate change (Nielson et al. 2005). Habitat loss and fragmentation (Braun 1998, Connelly et al. 2004), increasing natural disturbances like wildfire (Connelly and Braun 1997, Connelly et al. 2000), and anthropogenic disturbances influence both sagebrush communities and sage-grouse ecology (Smith et al. 2005, Walker et al. 2007, Aldridge et al. 2008, Blickley et al. 2012). No single factor has led to sage-grouse population declines.

Bird population declines are related to numerous factors. Habitat change in the form of degradation, fragmentation, or destruction is the most commonly cited explanation for bird population declines across the globe (Wilcove and Terborgh 1984,

Terborgh 1989). Predation is widely viewed to have shaped life histories and behaviors of birds (Côté and Sutherland 1997). Fluctuations in bird population sizes are a result of productivity, survival, and recruitment parameters (Crawford et al. 2004). The factors affecting these vital rates can vary with complex interactions between habitat loss and predation (Mezquida et al. 2006). Predation can exacerbate or dampen oscillations in abundance, and, in extreme cases, limit prey populations to the point of extinction (Mills 2007). With 40% of bird extinctions on islands attributed to predation from introduced predators (Estes et al. 2001), concern about predator impacts on bird populations is well founded.

Contrary to other upland game birds with a high reproductive strategy, including ring-necked pheasant (*Phasianus colchicus*), ruffed grouse (*Bonasa umbellus*), sharp-tailed grouse (*Tympanuchus phasianellus*), prairie chickens (*Tympanuchus cupido* and *pallidicinctus*), ptarmigan (*Lagopus* spp.), partridge (*Perdix* and *Alectoris* spp.), and quail (*Cyrtonyx*, *Colinus*, *Oreortyx* and *Callipepla* spp.), low reproductive rates in sage-grouse distinguish survival parameters as important contributors to population growth rates (Taylor et al. 2012). Sensitivity and elasticity analysis identified female survival as having the greatest impact on population growth rates, followed by chick survival and nest success (Walker et al. 2008, Dahlgren 2009, Taylor et al. 2012). These three parameters accounted for 73-75% of the variation in sage-grouse population growth rates (Taylor et al. 2012), suggesting management and conservation actions that simultaneously enhance these vital rates would produce the largest benefit for sage-grouse populations.

The controlling of native predators to increase populations of game birds and mammals has a long history in the United States (Leopold 1933, Beasom 1974, Guthery and Beasom 1977, Potts 1986, Reynolds and Tapper 1996, Schroeder and Baydack 2001). The lowering of predator populations may also produce benefits to non-target birds as seen in nature reserves where the termination of predator removal resulted in increased predation rates on ground-nesting birds (Suarez et al. 1993). Predator management has been advocated as a large-scale conservation tool (Leopold 1933, Reynolds and Tapper 1996, Treves and Naughton-Treves 2005); however, recent studies (Frey et al. 2003, Smith et al. 2010, Ellis-Felege et al. 2012) and a meta-analysis on the effectiveness of predator removal to protect bird populations call into question the longevity of those effects (Côté and Sutherland 1997).

Potential indirect interactions resulting from predator removal can vary by system but have been hypothesized to include apparent competition (Holt 1977), exploitative competition (MacArthur and Levins 1967), and mesopredator release (Crooks and Soulé 1999, Prugh et al. 2009, Mezquida et al. 2006). While there is a growing body of evidence in support of mesopredator release across a diversity of ecosystems (Crooks and Soulé 1999, Berger et al. 2008, Prugh et al. 2009, Conner et al. 2010), two studies found less support for this dynamic in the tropics (Wright et al. 1994) and between raccoons (*Procyon lotor*) and coyotes in North America (Gehrt and Prange 2007). With a lack of studies that directly demonstrate these effects in upland game birds, it is possible predator management can increase bird populations. Other population factors, like emigration, could obscure results by detecting increases to overall meta-population size while local populations decline. Emigration effects such as these may be difficult to measure. In

addition, Côté and Sutherland (1997) suggested that the status of the prey population targeted for response might affect the magnitude of the effect predator removal produces, with stable or increasing populations responding positively and declining populations declining further.

Lethal coyote control programs across the western U.S. constitute an important management action to the livestock industry and big game management, but the effects on other wildlife populations, like sage-grouse, are largely unknown (Mezquida et al. 2006). Mezquida et al. (2006) posited that where sage-grouse, jackrabbit (*Lepus* spp.), golden eagle (*Aquila chrysaetos*), and coyote (*Canis latrans*) co-occur, sage-grouse populations have declined as a complex feedback from apparent competition shifts in alternate prey populations (jackrabbits) and exploitative competition through depressed sagebrush and forb forage availability, originating from changes in predator communities. Yet, in a meta-analysis, Côté and Sutherland (1997) found that predator removal did have a large, positive effect on the hatch success of target bird species as well as a large effect on post-breeding population size, but overall smaller effects were detected on the total population size of breeding birds. Furthermore, recent work by Fedy and Doherty (2011) found highly correlated population cycles over long time periods in Wyoming for sage-grouse and cottontail rabbits (*Sylvilagus* spp.), emphasizing the verity to which sage-grouse population dynamics and the observed declines include a multitude of complex direct and indirect interactions.

Efforts to assess and mitigate risks to sage-grouse populations have been initiated by local working groups, state and federal agencies, private landowners, and industry to improve population growth and habitat quality throughout their range (Connelly and

Braun 1997, Connelly et al. 2004, Aldridge et al. 2008). Protection and restoration of crucial breeding and brood areas has been the primary focus for managers as it relates to sage-grouse habitat requirements (Connelly et al. 2000, Holloran and Anderson 2005, Hagen et al. 2007). A majority of management plans focus recommendations on habitat restoration as the primary means to minimize predator-prey interactions (Braun 1998, Connelly et al. 2000, Coates and Delahanty 2004, Connelly et al. 2004). Human interference may also influence sage-grouse population declines by altering the dynamics of both predator-prey systems (i.e. altering predator community structure, densities, or distribution) and sage-grouse space use by disturbing or altering habitat selection during critical life stages of breeding (lek attendance and nesting), brood rearing, and migration (recruitment and overwinter survival). Tied up amongst these complex interactions is the association between disturbed or fragmented landscapes, lower breeding success commonly attributed to interactions with generalist predators, and predator community structure (Kurki et al. 2000, Coates and Delahanty 2004, 2010). While current management efforts indirectly address predation effects on nest success, and to some extent survival, by increasing concealment cover for nests, chicks, and adult birds, they may provide only limited success if large-scale factors associated with predator densities and landscape level disturbances are not considered (Coates and Delehanty 2004, Manzer and Hannon 2005, Mezquida et al. 2006, Aldridge et al. 2008, Blickley et al. 2012).

In light of recent studies emphasizing adult survival, specifically hen survival, as the most influential factor on population growth rates (Taylor et al. 2012), efforts to understand sage-grouse space use, habitat availability, and habitat selection over the course of all critical life stages has become increasingly important to conservation and

management objectives (Homer et al. 1993, Bruce et al. 2011, Fedy and Aldridge 2011, Dzialak et al. 2013). With the noted decline of sage-grouse, resource selection function (RSF) modeling has been used to examine applied ecology questions relating habitat selection and sage-grouse space use as it relates to critical breeding and nesting sites (Niemuth and Boyce 1995, Aldridge and Boyce 2007, Doherty et al. 2010, Aldridge et al. 2011, Dzialak et al. 2011), and more recently, selection effects on survival (Doherty et al. 2008, Carpenter et al. 2009, Dzialak et al. 2013). To date, few studies have used RSF modeling relative to measures of terrestrial predator communities or increased management to control and remove predators on sage-grouse habitat selection or space use. Notably, Manzer and Hannon (2005) recognized the importance of clarifying the associations between habitat, predators, and prey by relating nest success and corvid density as both important small and broad scale factors influencing breeding success. Resource use patterns are a direct influence of selection on survival and reproduction (Boyce and McDonald 1999), and thus identifying changes in these patterns as they relate to both habitat resources and anthropogenic activities are important components to management activities, like the application of predator removal, and overall conservation planning.

PURPOSE

The overall objective of my study was to evaluate the effect of predation and predator removal on sage-grouse survival, nest success, and space use. Understanding predation effects on sage-grouse will provide additional information beyond habitat improvements that could enhance sage-grouse management. Specifically, the objectives of my research were to 1) obtain and quantify data on the types and impacts of predators

on sage-grouse hen survival and nest success, 2) compare the effect of predator removals on hen survival and nest success, and 3) evaluate sage-grouse habitat selection and movement relative to predator removal activities. First, I evaluated variables known to be important to sage-grouse population growth and highly susceptible to changes in predation rates, survival, and nest success, in response to alterations in predator communities (Chapter 2). Secondly, I examined sage-grouse seasonal movement, habitat selection, and space use relative to anthropogenic features including intensified human presence for predator removal activities (Chapter 3). Finally, I drew conclusions from direct demographic and behavioral response to evaluate the overall effects of predation and predator removal on sage-grouse ecology in Bighorn Basin (Chapter 4).

STUDY AREA

The Bighorn Basin Conservation Area (BHB) of Wyoming holds an extant, relatively unstudied population of sage-grouse in the central portion of their historic range ideally suited to examine the effects of predators on sage-grouse ecology. Primary land uses in BHB include livestock grazing, dry land and irrigation crop production, oil and gas development, bentonite mining, urban and suburban developments, recreation, and wildlife habitat (Bighorn Basin Sage-grouse Working Group 2007). BHB is recognized to have a distinct subpopulation of sage-grouse with 258 known occupied lek sites, 69% of which fall on public lands (Connelly et al. 2004). While studies of sage-grouse populations in the eastern portion of BHB have recently been initiated (Hess 2011), grouse habitat selection, movements, and demographic data for populations in the western portion of the Basin have not been documented. USDA-Wildlife Services implements predator control in BHB in cooperation with private landowners and

stakeholders in response to livestock depredations, as well as with the Wyoming Game and Fish Department for the enhancement of ungulate game populations. The aggregation of these features makes BHB an ideal site to examine predation effects on sage-grouse demography and behavior in the form of a predator removal experiment.

LITERATURE CITED

- Aldridge, C.L., and M.S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17(2):508-526.
- Aldridge, C.L., S.E. Nielsen, H.L. Beyer, M.S. Boyce, J.W. Connelly, S.T. Knick, and M.A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions* 14:983-994.
- Aldridge, C.L., D.J. Saher, T.M. Childers, K.E. Stahlnecker, and Z.H. Bowen. 2011. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. *Journal of Wildlife Management* 76(2):391-406.
- Beasom, S.L. 1974. Intensive short-term predator removal as a game management tool. *Transactions of the North American Wildlife Conservation* 39:230-240.
- Beck, J.L., and D.L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. *Wildlife Society Bulletin* 28:993-1002.
- Berger, K.M., E.M. Gese, and J. Berger. 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* 89:818-828.
- Bighorn Basin Sage-grouse Working Group. 2007. Sage-grouse Conservation Plan for the Bighorn Basin, Wyoming. <<http://wgfd.wyo.gov/web2011/wildlife-1000817.aspx#>> Accessed 1 May 2011.

- Blickley, J.L., D. Blackwood, and G.L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. *Conservation Biology* 26:461-471.
- Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Tree* 14(7):268-272.
- Braun, C.E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association of State Fish and Wildlife Agencies* 78:139-156.
- Braun, C.E., O.O. Oedekoven, and C.L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. *Transactions of the North American Wildlife and Natural Resources Conference* 67: 334-349.
- Bruce, J.R., W.D. Robinson, S.L. Peterson, and R.F. Miller. 2011. Greater sage-grouse movements and habitat use during winter in central Oregon. *Western North American Naturalist* 71(3):418-424.
- Carpenter, J., C. Aldridge, and M.S. Boyce. 2009. Sage-grouse habitat selection during winter in Alberta. *Journal of Wildlife Management* 74(8):1806-1814.
- Coates, P.S., and D.J. Delehanty. 2004. The effects of raven removal on sage grouse nest success. Pages 17-20 *in* Proceedings from the 21st Vertebrate Pest Conference, University of California, Davis, CA, USA.
- Coates, P.S., and D.J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. *Journal of Wildlife Management* 74(2):240-248.

- 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., A.D. Apa, R.B. Smith, and K.P. Reese. 2000. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. *Wildlife Biology* 6(4):227-232.
- 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, Cheyenne, Wyoming.
- Conner, L.M., J.C. Rutledge, and L.L. Smith. 2010. Effects of mesopredators on nest survival of shrub-nesting songbirds. *Journal of Wildlife Management* 74:73-80.
- Côté, I.M., and W.J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11:395-405.
- Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosley, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C.S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2-19.
- Crooks, K.R., and M.E. Soulé. 1999. Mesopredator release and avifaunal extinction in a fragmented system. *Nature* 400:563-566.
- Dahlgren, D.K. 2009. Greater sage-grouse ecology, chick survival, and population dynamics, Parker Mountain, Utah. Dissertation, Utah State University, Logan, Utah, USA.

- 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(7):1544-1553.
- 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(1):187-195.
- Dzialak, M.R., C.V. Olson, S.M. Harju, S.L. Webb, J.P. Mudd, J.B. Winstead, and L.D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. *PLoS ONE* 6(10):e26273.
- 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(1):10-18.
- Ellis-Felege, S.N., M.J. Conroy, W.E. Palmer, and J.P. Carroll. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. *Journal of Applied Ecology* 49:661-669.
- Estes, J.A., K. Crooks, and R. Holt. 2001. Ecological role of predators. *Encyclopedia of Biodiversity*. Volume 4. Academic Press, New York, New York, USA.
- Fedy, B.C., and C.L. Aldridge. 2011. The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. *Journal of Wildlife Management* 75(5):1022-1033.

- Fedy, B.C., and K.E. Doherty. 2011. Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: greater sage-grouse and cottontail rabbits. *Oecologia* 165:915-924.
- Frey, S.N., S. Majors, M.R. Conover, T.A. Messmer, and D.L. Mitchell. 2003. Effect of predator control on ring-necked pheasant populations. *Wildlife Society Bulletin* 31(3):727-735.
- Gehrt, S.D., and S. Prange. 2007. Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. *Behavioral Ecology* 18:204-214.
- Guthery, F.S., and S.L. Beasom. 1977. Responses of game and nongame wildlife to predator control in south Texas. *Journal of Range Management* 30(6):404-409.
- Hagen, C.A., J.W. Connelly, and M.A. Schroeder. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. *Wildlife Biology* 13:42-50.
- Hess, J.E. 2011. Greater sage-grouse (*Centrocercus urophasianus*) habitat response to mowing and prescribed burning in Wyoming big sagebrush and the influence of disturbance factors on lek persistence in the Bighorn Basin, Wyoming. Master's Thesis, University of Wyoming, Laramie, Wyoming, USA.
- Holloran, M.J. and S.H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. *The Condor* 107(4):742-752.
- Holt, R.D. 1977. Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* 12:197-229.

- Homer, C.G., T.C. Edwards, R.D. Ramsey, and K.P. Price. 1993. Use of remote sensing methods in modeling sage grouse winter habitat. *Journal of Wildlife Management* 57(1):78-84.
- Knick, S.T., D.S. Dobkin, J.T. Rotenberry, M.A. Schroeder, W.M. Vander Haegen, and C. van Riper, III. 2003. Teetering on the edge of too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.
- Kurki, S., A. Nikula, P. Helle, and H. Linden. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* 81:1985-1997.
- Leopold, A. 1933. Predator Control. Pages 230-252 *in* Game management. 1946, Reprint. Charles Scribner's Sons, New York, New York and University of Wisconsin Press, Madison, Wisconsin, USA.
- Lyon, A.G., and S.H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486-491.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377-385.
- Manzer, L.D., and S.J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. *Journal of Wildlife Management* 69(1):110-123.
- Mezquida, E.T., S.J. Slater, and C.W. Benkman. 2006. Sage-grouse and indirect interactions: potential implications of coyote control on sage-grouse populations. *The Condor* 108:747-759.

- Mills, L.S. 2007. Predation and wildlife populations. Pages 159–175 *in* Conservation of Wildlife Populations: Demography, Genetics, and Management. Blackwell Publishing, Malden, Massachusetts, USA.
- Nielson, R.P., J.M. Lenihan, D. Bachet, and R.J. Drapek. 2005. Climate change implications for sagebrush ecosystems. Pages 145-159 *in* Transactions of the 70th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington, D.C., USA.
- Niemuth, N.D., and M.S. Boyce. 1995. Spatial and temporal patterns of predation of simulated sage grouse nests at high and low nest densities: an experimental study. *Canadian Journal of Zoology* 73:819-825.
- Potts, G.R. 1986. The partridge: pesticides, predation and conservation. Collins, London.
- Prugh, L.R., C.J. Stoner, C.W. Epps, W.T. Bean, W.J. Ripple, A.S. Laliberte, and J.S. Brashares. 2009. The rise of the mesopredator. *Bioscience* 59(9):779-791.
- Reynolds, J.C., and S.C. Tapper. 1996. Control of mammalian predators in game management and conservation. *Mammal Review* 26: 127-155.
- Schroeder, M.A., and R.K. Baydack. 2001. Predation and the management of prairie grouse. *Wildlife Society Bulletin* 29:24-32.
- 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.L. McCarthy, J.J. McCarthy, D.L. Mithchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage-grouse in North America. *The Condor* 106(6):363-376.

- Smith, J.T., L.D. Flake, K.F. Higgins, G.D. Kobringer, and C.G. Homer. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. *Western North America Naturalist* 65:310-320.
- Smith, R.K., A.S. Pullin, G.B. Stewart, and W.J. Sutherland. 2010. Effectiveness of predator removal for enhancing bird populations. *Conservation Biology* 24(3):820-829.
- Suarez, F., M. Yanes, J. Herranz, and J. Manrique. 1993. Nature reserves and the conservation of Iberian shrub steppe passerines-the paradox of nest predation. *Biological Conservation* 64:77-81.
- Taylor, R.L., B.L. Walker, D.E. Naugle, and L.S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* 76(2):336-347.
- Terborgh, J. 1989. *Where have all the birds gone? Essays on the biology and conservation of birds that migrate to the American tropics.* Princeton University Press, Princeton, New Jersey, USA.
- Treves, A. ,and L. Naughton-Treves. 2005. Evaluating lethal control in the management of human-wildlife conflict. Pages 86-106, *in* R. Woodroffe, S. Thrigood, and A. Rabinowitz editors. *People and wildlife: conflict or co-existence?* Cambridge University Press, New York, New York, USA.
- USFWS. 2010. Endangered and Threatened Wildlife and Plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 50 CFR Part 17 [FWS-RS-ES-2010-00189].

Walker, B.L., D.E. Naugle, and K.E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management* 71:2644-2654.

Walker, B.L., D.E. Naugle, and K.E. Doherty. 2008. Greater sage-grouse population response to habitat loss and coal-bed natural gas development. *Journal of Wildlife Management* 71:2644-2654.

Wilcove, D.S., and J.W. Terborgh. 1984. Patterns of population decline in birds. *American Birds* 38:10-13.

Wright, S.J., M.E. Gompper, and B. Deleon. 1994. Are large predators keystone species in Neotropical forests? The evidence from Borro Colorado Island. *Oikos* 71:279-294.

CHAPTER 2

COYOTE REMOVAL AS A TREATMENT TO INCREASE GREATER SAGE-
GROUSE HEN SURVIVAL AND NEST SUCCESS**ABSTRACT**

Greater sage-grouse (*Centrocercus urophasianus*) are in decline across western North America and predators are the primary cause of nest failure. In a two-year study (2011-2012) we tested the direct and indirect effects of predation on sage-grouse ecology. We modified the existing framework from predator removal efforts in accordance with wildlife damage management in Hot Springs and Park Counties to identify and measure predation effects on sage-grouse survival and nest success in the Bighorn Basin, Wyoming, USA. We hypothesized that the removal of primary predators would increase nest success and hen survival during the time period treatment was applied, but that annual survival would remain constant. We used VHF radio telemetry to monitor hen survival, confirm nesting, and track brood movements post-hatch. We used infrared trail cameras to monitor and document nest predation and novel lab forensic genetic analysis of egg remains to identify depredating species. Scent stations, avian point counts, and non-invasive genetic analysis were used to estimate predator occupancy and describe coyote populations. Significant differences were detected in hen survival between control, moderate, and high removal sites over the nesting period ($\beta = -1.22$, $SE = 0.64$, $P = 0.05$) but not on annual hen survival ($\beta = -0.53$, $SE = 0.41$, $P = 0.19$). No differences were detected in the daily survival rates of nests ($\beta = -0.56$, $SE = 0.62$, $P = 0.18$) between predator removal sites, but observed nest success was significantly higher at the experimental control site than sites treated with coyote removal ($t = 6.53$, $df = 22$, $P <$

0.0001). We conclude that the application of coyote removal as a treatment during the nesting period improved survival during that phase of a hen's life but fitness benefits did not translate into higher annual survival. We also conclude that removing the primary nest predator identified within this system (coyote) did not improve observed nest success. We quantified the impacts of predators on two important sage-grouse vital rates, conducted a field experiment to understand these impacts, and developed a framework for monitoring changes in both sage-grouse and predator populations that will enhance management decisions.

Habitat change in the form of degradation, fragmentation, or destruction is a common explanation for bird population declines (Wilcove and Terborgh 1984, Terborgh 1989). However, predation is widely viewed to have shaped life histories and behaviors of birds (Côté and Sutherland 1997). Fluctuations in sizes of bird populations are a result of reproductive productivity, survival, and recruitment (Crawford et al. 2004). The factors affecting those vital rates can vary with complex interactions between habitat loss and predation (Mezquida et al. 2006). Predation can cause either exacerbated or dampened oscillations in abundance, or, in extreme cases, limit prey populations to the point of extinction (Mills 2007). With 40% of the extinctions of birds on islands ascribed to predation impacts from introduced predators (Estes et al. 2001), concern about predator impacts on bird populations is well founded. There has been an overall declining trend in bird species with high susceptibility to nest predation (i.e. ground nesting birds) which supports the hypothesis that nest predation has increased over the last several decades and is a factor causing long-term declines in populations of ground nesting birds (Rogers and Caro 1998). Tied up amongst these complex interactions is the association

between disturbed or fragmented landscapes, lower breeding success commonly attributed to interactions with generalist predators, and predator community structure (Kurki et al. 2000, Coates and Delahanty 2004, 2010).

Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) distribution and population densities have declined across western North America and now occupy 56% of their historic range (Schroeder et al. 2004). The severity and extent of this decline have led to recent listing of sage-grouse under the Endangered Species Act of 1973 as warranted but precluded by species of higher concern (USFWS 2010). Low reproductive rates in sage-grouse differentiate this species from other grouse and survival parameters have been indicated as more important contributors to population growth rates (Taylor et al. 2012). Female survival, chick survival, and nest success accounted for 73-75% of the variation in sage-grouse population growth rates (Taylor et al. 2012), suggesting management and conservation actions that simultaneously improve these vital rates would produce the largest benefit for sage-grouse populations.

Several species have been documented as predators of sage-grouse and their nests, including golden eagle (*Aquila chrysaetos*), coyote (*Canis latrans*), American badger (*Taxidea taxus*), common raven (*Corvus corax*), black-billed magpie (*Pica hudsonia*), long-tailed weasel (*Mustela frenata*), striped skunk (*Mephitis mephitis*), northern harrier (*Circus cyaneus*) and other raptors (Boyko et al. 2004, Coates et al. 2008, Dahlgren 2009). Gregg et al. (1994, 2009) attributed declining abundance of sage-grouse to impaired productivity from excessive nest predation as well as reduced recruitment due to poor quality habitat. While vegetation structure and habitat characteristics can effect nest predation, chick survival, and nest placement (Gregg et al. 1994, 2009, Coates et al.

2008, Conover et al. 2010), habitat quality mitigation without assessment of predator-prey and community effects may fail to improve sage-grouse populations.

A majority of management plans focus recommendations on habitat restoration as the primary means to minimize predator-prey interactions (Braun 1998, Connelly et al. 2000, Coates and Delahanty 2004, Connelly et al. 2004). While these efforts indirectly address predation effects on nest success, and to some extent survival by increasing concealment cover for nests, chicks, and adult birds, they may provide only limited success if large-scale factors associated with predator densities are not considered (Coates and Delehanty 2004, Manzer and Hannon 2005, Mezquida et al. 2006). Human interference may influence the dynamics of predator-prey systems and affect population declines by altering predator community structure and distribution, which could potentially increase predation rates on birds (Greenwood et al. 1995) or result in compensatory shifts in the causes of mortality (Sedinger et al. 2009) and nest loss (Ellis-Felege et al. 2012).

Lethal coyote control programs across the west constitute a management action of substantial importance to the livestock industry and big game management but the effects on other wildlife populations is largely unknown (Mezquida et al. 2006). The controlling of native predators to increase populations of game birds and mammals has a long history in the United States (Leopold 1933, Beasom 1974, Guthery and Beasom 1977, Potts 1986, Reynolds and Tapper 1996, Schroeder and Baydack 2001). Predator management has been advocated as a conservation tool (Leopold 1933, Reynolds and Tapper 1996, Treves and Naughton-Treves 2005); however, the longevity of predator removal effects to protect bird populations has been questioned (Côté and Sutherland 1997, Frey et al.

2003, Smith et al. 2010, Ellis-Felege et al. 2012). Potential indirect interactions resulting from predator removal have been hypothesized to include apparent competition (Holt 1977), exploitative competition (MacArthur and Levins 1967), and mesopredator release (Mezquida et al. 2006). Côté and Sutherland (1997) found that predator removal had a large, positive effect on the hatch success and post-breeding population size of target bird species but an overall smaller effect was detected on the total population size of breeding birds.

The overall goal of our study was to evaluate the effect of predation on sage-grouse survival and nest success in the Bighorn Basin of Wyoming, USA. Our objectives were to obtain and quantify data on the types and impacts of predators on sage-grouse and to compare the effect of the removal of a key predator, the coyote, on hen survival and nest success. Our primary research questions were: 1) what predators are affecting sage-grouse nest success and survival in Bighorn Basin?, and 2) does the removal of a key predator improve hen survival or nest success? Understanding predation effects on sage-grouse will provide managers and conservationists with additional information beyond habitat improvements that could enhance sage-grouse management.

STUDY AREA

During 2011 and 2012, we studied predation of sage-grouse hens and nests in the northwest portion of Bighorn Basin, Wyoming (Fig. 2.1). Bighorn Basin is a semi-arid, plateau, intermontane basin located in north-central Wyoming that encompasses 32,000 km² of Bighorn, Hot Springs, Park, and Washakie Counties. The study area included 504 km² of Bighorn Basin, and we conducted the study at three lek complexes: Oregon Basin (44° 22.45 N, 108° 48.17 W), 15 Mile (44° 10.89 N, 108°44.38 W), and Polecat Bench

(44° 57.00 N, 108° 45.54 W). Average valley elevation was 1,524 m and the area was composed of badland topography, intermittent buttes, and big sagebrush communities. Average maximum and minimum temperature during the study period (March to September) was 25.7° C and -0.4° C, respectively, in 2011 and 29.7° C and 0.1° C in 2012. Total precipitation during the study period was 14.7 cm in 2011 and 19.5 cm in 2012 (Fales Fock, WY, USA; <http://www.raws.dri.edu/cgi-bin/rawMAIN.pl?wyWFAL>).

Bighorn Basin is composed of mostly public land managed by the Bureau of Land Management (40%), Forest Service (25%), state (5%), other federal agencies (>1%; Bureau of Reclamation, National Park Service, Department of Defense), and private land (25%) (Sage-grouse Conservation Plan for the Bighorn Basin, WY 2007). Land uses in sagebrush areas included livestock grazing, wildlife habitat, dry-land and irrigated crop production, recreation, bentonite mining, and oil and gas extraction. Common plants included shrubs, such as Wyoming big sagebrush (*Artemisia tridentate*), basin big sagebrush (*A.t. vaseyana*), greasewood (*Sarcobatus vermiculatus*), and rabbitbrush (*Chrysothamnus viscidiflorus* and *Ericameria nauseosa*); forbs such as globemallow (*Sphaeralcea spp.*), milkvetch (*Astragalus spp.*), fringed sagewort (*A. frigida*), phlox (*Phlox spp.*), and common pepperweed (*Lepidium densiflorum*); perennial grasses such as blue-bunch wheatgrass (*Pseudoroegneria spicata*), blue grama (*Bouteloua gracilis*) and needle and thread (*Hesperostipa comate*); and invasive species such as cheatgrass (*Bromus tectorum*), knapweed (*Centaurea spp.*) and toadflax (*Linaria spp.*). Detailed descriptions of vegetative characteristics for Bighorn Basin can be found in Hess and Beck (2012).

METHODS

Experimental Design

In 2011, we collected baseline information about predators of sage-grouse hens and nests at two sites in the northwest portion of Bighorn Basin: Oregon Basin and Polecat Bench. The two sites used in 2011 differed in predator management. Oregon Basin served as an experimental control site representative of areas with no predator removal, and Polecat Bench served as a representative area where predator removals occurred regularly as part of management plans for other species. Using information learned in 2011, in 2012 we added a third site and implemented an experimental predator removal design (Fig. 2.1) to test the effects of no (Oregon Basin), moderate (15 Mile), and high (Polecat Bench) coyote removal treatments on the hen survival and nest success of sage-grouse.

Predator Removal

Coyote and other predator removals were carried out by USDA-APHIS Wildlife Services (WS) as part of regular management activities in both years and as experimental treatment in year two in 15 Mile and Polecat Bench. Removal methods included aerial gunning, snare and leg-hold trap, den gassing, and opportunistic shooting. Sites received year-round predator management for domestic livestock depredation and agriculture damage at Polecat Bench (hereafter high treatment site) in both years and for mule deer fawn (*Odocoileus hemionus*) production at 15 Mile (hereafter moderate treatment site) in the second year. The high treatment site was classified as such because the treatment was carried out in areas sage-grouse were nesting in and was in addition to regular predator management activities, whereas the moderate treatment site received predator removal as

applied for ungulate management purposes. Targeted coyote removal actions to measure changes in sage-grouse vital rates were carried out from 14 March – 15 June 2012 on the high treatment site. No predator removal occurred at Oregon Basin (hereafter, control site) and it served as the experimental control for the study in both years. To measure coyote control the location of each removed coyote was recorded and genetic samples were collected; incidentally identified coyote mortalities from the experimental control site were also recorded and genetically sampled.

Field Monitoring and Surveys

We used ArcGIS (version 10.0, Esri, Redland, CA) to create survey grids for each site. A 3 x 3 km grid size and 3-km sampling interval were selected based on minimum territory sizes of the smallest potential terrestrial predators on the landscape (<1-3 km² for striped skunk (*Mephitis mephitis*; Bixler and Gittleman 1999), 2.7-6.2 km² for badger (*Taxidea taxus*; Linzey 1978, Sullivan 1996) and 1-3 km² for raccoon (*Procyon lotor*; Tesky 1995)). To survey for both terrestrial and avian predators relative to sage-grouse nesting habitat we incorporated observed average nest distances from leks through a system of 7-km lek, and 3-km nest buffers overlaid with the sampling grid which covered all buffered areas at each site. We generated random points (ETGeowizards plugin tool, version 10.2, www.ion-ko.com) within grid cells to serve as the start point for scat transect and point count surveys. Predator surveys were conducted once in 2011 and twice, pre- and post-treatment, in 2012.

Scent stations.— In both years, we conducted scent station surveys to detect the presence of terrestrial predators and alternative prey (lagomorphs) across sites. Following Roughton and Sweeney (1982) we systematically set stations along roads, two-tracks,

and game trails spaced at 3-km intervals within each survey grid. Each station consisted of a 1-m circle of finely sifted dirt cleared of any vegetation. We pre-set stations a minimum of 4 days prior to addition of scent to discourage predator avoidance of freshly disturbed soil (Windberg 1996). On or after the fourth pre-set day, we placed fatty-acid scent (FAS) in a 15.25-cm hole at the center of the station and covered it with a plug of dry grass. We checked scent stations daily for 10 nights and visits were recorded to species.

Avian road transects.— In 2011, two transects were established per site within the survey grids (55 km of road per site). We ran transects twice between 13 July – 10 August at two time intervals: morning and mid-day. Counts were made by one observer from a vehicle starting approximately one hour after sunrise (morning interval) or after 1100 hours (mid-day interval). At each raptor sighting, we stopped the vehicle and recorded species, activity (perched or flying), radial direction, distance (using rangefinders), and major land use (Andersen et al. 1979, Anderson et al. 1985, Fuller et al. 1987, Williams et al. 2000).

Point counts.— In 2012, we conducted point counts for raptors (hen and chick predators) and Corvidae (nest predators). Point count locations were randomly generated within each survey grid and sampled three times (Ralph et al. 1995). Each point count was conducted for 10 min in which the observer recorded all individual raptors and corvids observed. We used a laser rangefinder to record distance to birds. Counts were conducted between 30 min after sunrise and completed within four hrs. We suspended counts if wind speeds exceeded 15 mph or during inclement weather that could impair avian detection (e.g., heavy rain, fog, snow).

Scat transects.— In 2012, points generated for point counts served as start points for 1.5-km transects to collect coyote scat. A random number generator was used to select a transect bearing (between 0-359 degrees). Each transect was cleared of all scat on day zero and subsequently double sampled (transects walked in both directions) a total of four times at a 4-day interval between sampling. Each transect required 20 days to sample and we used an average of 30 days to complete all transects at each site. In most cases, transects were sampled by one observer over the entire collection period with no more than two observers sampling any one transect. Hand-held Global Positioning System (Garmin International, Olathe, Kansas, USA) units were used to plot and navigate transects. A portion of each scat observed within 3 m of a transect was collected, stored in paper envelopes, and stored at -20°C until extraction. Transects were not sampled when inclement weather impaired observer detection of scat (i.e. snow).

Vegetation sampling.— In 2012, we evaluated vegetation in June and July at nest sites following Connelly et al. (2003) and a modified University of Wyoming GRSG Microhabitat Protocol (2008). Vegetation sampling occurred on average 41 days (range 1 – 84 days) post-hatch or fail event and sampling duration was 30 days. Shrub (sagebrush) canopy cover was measured using line-intercept (Canfield 1941) along two perpendicular 30-m transects that intersected the nest. Orientation of transects was fixed to cardinal directions. Herbaceous cover was measured within a 20 x 50 cm quadrat using the Daubenmire (1959) canopy cover method at 0 (transect intersection at nest bowl), 1, 3, 7.5, and 12.5 m along each 15-m portion of the 30-m transect (17 points at each microsite). Herbaceous categories included grass cover, food, and non-food forb cover. We also estimated bare soil, cactus, cryptobiotic crust, and litter cover. Grasses were

grouped and classified as annual, perennial, and residual (previous year's dead growth). A modified 6 cover class system was used to convert categorical estimates of cover as percentages: 1 = 0 – 1%, 2 = 1.1 – 5%, 3 = 5.1 – 25%, 4 = 25.1 – 50%, 5 = 50.1 – 75%, 6 = 75.1 – 100%. We averaged height and converted cover estimates from the 17 points to derive a single estimate for each vegetative variable per nest microsite. We measured visual obstruction for the nest and microsite (30 x 30 m area around nest) using a robel pole (Robel et al. 1970) placed directly in the nest bowl and averaged measurements from 5, 10, and 15 m on each transect. We also recorded vegetal characteristics of the nest shrub including species, height, maximum and perpendicular width, vigor (proportion of dominant nest shrub alive), branch density, and the total number of shrubs obscuring the nest bowl.

Hen survival.— During March and April of both years, we captured female sage-grouse on leks using rocket nets (Giesen et al. 1982). Hens were fitted with VHF necklace style transmitters (Advanced Telemetry Systems Inc [ATS], Isanti, Minnesota) and were classified as yearling (first breeding season) or adult (\geq second breeding season) based on wing primary morphology (Eng 1955). Transmitters weighed 22 g and had a battery life expectancy of 869 days. We monitored hens for survival using hand-held receivers and vehicle mounted whip or Yagi antennas every 48-72 hrs from the time of capture through the end of the brood-rearing season (August). Hen mortalities were investigated by WS personnel within 72 hrs of signal detection to determine cause-specific mortality.

Nest survival & success.— After obtaining three consecutive locations of a radio marked hen in one area we located nests as described by Holloran et al. (2005) and

placed infrared Bushnell Trophy Cam trail cameras (Bushnell Outdoor Products, Overland Park, Kansas, USA) 3-5 m from the nest's entrance or exit. Cameras were mounted on 1-m rebar stakes on average 41 cm above the ground and were concealed using sagebrush to camouflage and prevent use as a perch. We wore rubber boots to minimize human scent and did not approach nests if avian predators were visible when cameras were initially set or to replace batteries and memory cards.

We continued to monitor hens via telemetry to confirm their location on nests from a distance ≥ 50 m and obtained visual confirmation when camera memory cards were changed every 7 days. Cameras were used until nests hatched or failed. Cameras were used for an additional two weeks on any nest where the hen was depredated during incubation to monitor and document post-mortem nest predation events. Minimum clutch sizes were determined opportunistically if a hen was away from the nest, inadvertently flushed while maintaining cameras, from depredated egg remains, or after hatching. All nests were categorized as successful (≥ 1 egg hatched) or unsuccessful (Rearden 1951). Hatch dates were determined by telemetry, nest camera evidence, or calculated based on an average incubation time of 27 days from nest initiation dates (Schroeder et al. 1999). Nest predators were determined by tracks, scat, and nest camera photographic evidence. We conducted additional lab DNA analysis when egg remains were available in 2012. Opportunistic counts of chicks were recorded throughout the brooding season and we conducted a spotlight count 35 days post-hatch (based on chick independence approximately ≥ 5 weeks of age; Hannon and Martin 2006). Chick survival was calculated as a percentage of chicks that survived to 35 days from hatch date and minimum clutch size.

Statistical Analyses

Occupancy rates were estimated for terrestrial predators from presence-absence scent station survey data and for avian predators from point count data using occupancy models in Program MARK. Predators were modeled on a species basis with two exceptions in avian predators where species were classified into 1) medium raptor spp. (red-tailed hawk and northern harrier), and 2) other Corvid spp. (pinyon jay (*Gymnorhinus cyanocephalus*), American crow (*Corvus brachyrhynchos*), and black-billed magpie (*Pica hudsonia*)).

We used Cox proportional hazard models in program R (R Development Team 2008) to analyze covariates and produce survival estimates of sage-grouse hens (Fox 2002). To estimate the effect of coyote removal on survival, we adjusted for other possible explanatory variables by including age, season, and year covariates to models. We excluded three hens from survival analysis in 2011 because one hen moved outside of the study site (> 19 km), one hen died within 72 hrs of capture, and a radio collar slipped off one hen. Four hens were excluded from analysis in 2012 because one hen moved outside of the study site (> 19 km), one hen moved out of the capture treatment site into an area of another treatment, one hen died within 72 hrs of capture, and contact was lost with one hen in May resulting in an unknown fate.

Nest models were used in Program MARK (version 6.1, White and Burnham 1999) to obtain daily survival rates (*d_{sr}*) and model nest survival based on hen age, site (treatment), and vegetation covariate effects. Subsequently, we obtained and report an unbiased measure of observed nest success as a function of the *d_{sr}* using,

$$\widehat{NS} = dsr^t$$

where t is the time required in days for a nest to hatch from initiation through incubation to hatch (37 days). To account for parameters that are a function of other parameters (NS as a function of dsr), we followed Seber (1982) and used the DELTA method to calculate variances and 95% confidence intervals for observed nest success,

$$\widehat{var}(NS) = \left(\frac{\partial NS}{\partial dsr}\right)^2 \times \widehat{var}(dsr),$$

where $\left(\frac{\partial NS}{\partial dsr}\right) = t \times dsr^{t-1}$, and $\widehat{var}(dsr) = (SE_{dsr})^2$, and a confidence interval following,

$$CI = \widehat{NS} \pm 1.96(\sqrt{\widehat{var}(NS)})$$

In addition to using nest models to evaluate coyote removal effects on dsr at treatment sites, traditional hypothesis tests (t -tests) were used to evaluate differences in observed nest success between sites in 2012. We tested for differences in nest vegetative characteristics between successful and unsuccessful nests both within a given site and among treatments using analysis of variance (ANOVA). Significant interactions were then added to nest models in MARK to eliminate “noise” from differences in vegetation that may mask nest survival effects from experimental coyote removal treatments. We defined statistically significant differences at $P \leq 0.10$.

We used an information theoretic approach and Akaike’s information criterion corrected for small sample sizes (AIC_c) to evaluate model fit (Burnham and Anderson 2002). We selected the model with the smallest AIC_c value as the best-fitting model, and used the difference in AIC_c (ΔAIC_c) and Akaike weights (w_i) to assess the strength of evidence in favor of each model (Burnham and Anderson 2002).

Genetic Analysis

Predator DNA was isolated, amplified, and sequenced from egg shell remains following protocols outlined in Hopken et al. (in prep). Species identification of DNA sequences were performed using BLAST (National Center for Biotechnology, <http://www.ncbi.nlm.nih.gov>; Bensen et al. 2011). Consensus multilocus genotypes were generated for each scat sample using the program GIMLET (Valiere 2002) to identify matching genotypes among samples. Samples with genotypes for at least 6 loci were retained in the dataset and loci without 3 matching genotypes were scored as missing data. Only unique multilocus genotypes were included in subsequent analyses of basic population genetic parameters for the overall dataset.

RESULTS

Baseline data

Twenty-five hens were captured from four leks in Bighorn Basin in spring 2011. Ten birds were radio marked from the predator management site and 15 birds were marked from the experimental control site. A disproportionate number of yearlings (hens at first breeding season) were captured (7 adults, 18 yearlings).

Predator surveys.— In 2011, the most common predators detected at scent stations were coyotes, followed by red fox (*Vulpes vulpes*) and raccoon. Other terrestrial predators detected from surveys include bobcat (*Lynx rufus*), badger, striped skunk, and weasel (Mustelidae). Scent stations detected seven species of terrestrial predators and two species of lagomorphs (black-tailed jackrabbit (*Lepus spp.*) and cottontail (*Sylvilagus spp.*)). Only four predator species and combined lagomorphs were detected at sufficient levels to model occupancy. No differences were observed in occupancy rates between the

experimental control and predator managed site for fox ($\psi_{\text{all}} = 0.13$, SE = 0.06, 95% CI = 0.05, 0.30), skunk ($\psi_{\text{all}} = 0.12$, SE = 0.11, 95% CI = 0.02, 0.49), badgers ($\psi_{\text{all}} = 0.12$, SE = 0.10, 95% CI = 0.02, 0.47), or lagomorphs ($\psi_{\text{all}} = 0.74$, SE = 0.13, 95% CI = 0.44, 0.92), but coyote occupancy appeared higher in the control site than the predator managed site ($\psi_{\text{Control}} = 0.83$, SE = 0.24, 95% CI = 0.14, 0.99; $\psi_{\text{Predator managed}} = 0.27$, SE = 0.14, 95% CI = 0.08, 0.62).

We documented six raptor species in the two lek complexes surveyed. The most commonly detected raptor, American kestrel (*Falco sparverius*), was also the least likely to have direct predation effects on sage-grouse. Kestrels mainly prey on invertebrates, small mammals, and reptiles (Smallwood and Bird 2002). Red-tailed hawk (*Buteo jamaicensis*) and golden eagles were detected at all sites but at insufficient levels to obtain density estimates from transect data.

Hen survival.— Eleven of 25 hens survived (44%) to 31 December 2011 in the two study sites (predator management site = 6, control site = 5). Coyotes ($n = 5$) and ravens ($n = 2$) were observed to be the primary predators of nests, while coyotes ($n = 5$) were observed to be the primary predators of sage-grouse hens. Other hen losses were attributed to badgers ($n = 2$), golden eagles ($n = 1$), unidentified raptor ($n = 1$), bodily trauma of undetermined origin ($n = 1$), unknown predators ($n = 2$), and unknown cause of death ($n = 1$). Although non-significant, a negative site effect ($\beta = -0.84$, SE = 0.67, $P = 0.21$) on hen survival was observed, with higher hen survival in the predator managed site than at the control site (Table 2.1). Age was not observed to be a significant factor in hen survival ($\beta = 0.09$, SE = 0.61, $P = 0.88$). Sixty percent of collared hens in the control site and 30% of hens at the predator management site died. One hen slipped her collar and

was classified as fate unknown. Of the mortalities documented, 2 hens died before nesting, 4 during the nesting period, and 7 after nesting when hens and broods had moved out of brood and nesting areas.

Nest survival & success.— We documented 22 hens as initiating nests between 28 April – 16 June 2011. There were 24 nests, including two second nest attempts. Two hens were documented as re-nesting after predation of first nests in the control site. We did not document any third nest attempts in 2011. Two hens died before nesting and we were unable to locate and track one hen after capture to obtain nesting information.

Fifty-four percent of nests documented in 2011 were depredated, including second nest attempts. Individual area nest predation was 46% in the control site and 66% in the predator management site. Nest losses due to abandonment or hen mortalities during the nesting season accounted for 22% and 20% of nest failures in the control and predator management site, respectively. We set trail cameras on 21 nests and documented 11 complete nest predations and two partial nest predations. The most common nest predators identified were coyotes. However, five nest predation events were categorized as unknown due to insufficient evidence to indicate a predator species. One nest loss occurred before trail camera placement at the nest site and no discernible sign could be identified. Two unknown losses were due to a lack of photos on the trail cameras set at the nests where thick sage cover and camera placement at only an entrance or exit resulted in the failure to document a nest predator. One camera failed to take pictures after camouflaging material blocked the sensor, and one nest was not investigated after the hen moved off nest within 1-2 days of visual confirmation of nest initiation.

No significant differences were observed in the *dsm* rates ($\beta = -0.51$, $SE = 0.74$, $P = 0.25$) of nests between the control and predator managed site in the pilot year, but significant differences were detected in observed nest success between the control site and the site with predator management. Higher nest success was associated with the control site ($t = 2.45$, $P = 0.02$, Table 2.2). Eight hens successfully hatched nests with mean clutch sizes of six and seven eggs for the control and predator managed sites, respectively. Chick survival to 35 days was 44% for the control site and 40% for the predator managed site.

Experiment data

We captured and radio collared 44 additional hens from three lek complexes in Bighorn Basin in 2012. We supplemented tags deployed in 2011 with 14 more VHF collars in the control site (five collars remained from 2011), 16 in the moderate treatment site, and 14 in the high treatment site (6 collars remaining from 2011) for a total of 55 marked hens (Table 2.3). Hens were intensely monitored during breeding, nesting and brood-rearing between 14 March – 31 August 2012 and weekly through 1 March 2013. Thirty-nine radio-marked hens were alive and being monitored at the end of the brood rearing season in 2012. More adult than yearling hens were captured and monitored in the second year (36 adults, 20 yearlings).

Coyote detection & removal.— We collected 69 coyote scats from transects across sites ($n_{\text{Control}} = 33$, $n_{\text{Moderate}} = 11$, $n_{\text{High}} = 25$); 43 scats were collected during the pre-treatment survey period ($n_{\text{Control}} = 20$, $n_{\text{Moderate}} = 4$, $n_{\text{High}} = 19$) and 26 scats were collected during the post-treatment period ($n_{\text{Control}} = 13$, $n_{\text{Moderate}} = 7$, $n_{\text{High}} = 6$). Fifteen percent of scat samples amplified to yield individual coyote genotypes; 93% of tissue samples from

removed coyotes amplified to produce genotypes (one sample failed in both the control and moderate sites). We had only one recapture in the high treatment site from transect sampling. Six unique coyote genotypes were identified from scat in the control site (3 pre- and 3 post-treatment). Four coyotes were incidentally removed from the experimental control site via road kills (all young of the year, <6 mo), but tissue samples from three of these individuals did not match scat samples from transects (the fourth sample failed to amplify). WS removed 27 coyotes from treatment sites. Nine coyotes were removed by WS from the moderate treatment site during the nesting period. We identified two coyote genotypes from scat in the moderate treatment site (none in pre- and 2 in post-treatment); none matched the genotypes of removed coyotes. WS removed 18 coyotes over the treatment season from the high treatment site, 13 during the nesting period. We identified two individual coyotes from scat in the high treatment site (two in pre- and none in post-treatment); only one matched the genotypes of removed coyotes.

Scent station surveys.— In 2012, we documented 563 visits to scent stations across sites over 11,902 trap nights, including 47 predators (excluding domestic dog, *Canis lupus familiaris*) and 58 lagomorphs visits in 2012. The most commonly detected predator species was coyote, followed by red fox, badger, and bobcat (S1, available online at www.onlinelibrary.wiley.com). Striped skunk, raccoon, weasel, domestic dog, domestic cat (*Felis catus*), and two species of lagomorph (black-tailed jackrabbit and cottontail) were also detected on scent station surveys.

Only three of the 11 species detected at scent stations were detected at sufficient levels to model occupancy (coyote, bobcat, and lagomorph spp.) as opposed to the five species modeled in 2011. Lagomorphs were the only species with enough detections in

both pre- and post-treatment survey periods to obtain occupancy estimates for each period. There were no differences observed in lagomorph occupancy between treatment sites, but model results suggest there were differences in rates between sampling periods ($\psi_{\text{pre}} = 0.35$, SE = 0.08, 95% CI = 0.21, 0.52; $\psi_{\text{post}} = 0.53$, SE = 0.12, CI = 0.30, 0.75; $\psi_{\text{all}} = 0.58$, SE = 0.09, CI = 0.41, 0.79). No differences were observed in occupancy estimates between treatment sites for coyote ($\psi_{\text{all}} = 0.52$, SE = 0.15, CI = 0.25, 0.78) or bobcat ($\psi_{\text{all}} = 0.18$, SE = 0.16, CI = 0.03, 0.65).

Avian point count surveys.— Six species of raptors and four species of Corvidae were detected on point counts (see Table S2, available online at www.onlinelibrary.wiley.com). No differences were observed in avian predator occupancy rates across sites for golden eagle ($\psi_{\text{all}} = 0.89$, SE = 0.19, CI = 0.16, 0.99), medium raptors ($\psi_{\text{all}} = 0.68$, SE = 0.25, CI = 0.18, 0.95), or other nest depredating species. Raven ($\psi_{\text{pre}} = 0.94$, SE = 0.06, 95% CI = 0.68, 0.99; $\psi_{\text{post}} = 0.65$, SE = 0.17, CI = 0.30, 0.89; $\psi_{\text{all}} = 0.93$, SE = 0.05, CI = 0.74, 0.98) occupancy rates were 1.4 times higher during the pre-treatment period while other corvid spp. ($\psi_{\text{pre}} = 0.44$, SE = 0.11, 95% CI = 0.25, 0.64; $\psi_{\text{post}} = 0.41$, SE = 0.18, CI = 0.14, 0.75; $\psi_{\text{all}} = 0.58$, SE = 0.10, CI = 0.37, 0.76) occupancy rates remained the same during pre- and post-treatment surveys. We were not able to obtain pre-treatment occupancy estimates for golden eagle or the medium raptor spp. group due to low detection numbers and lack of model convergence.

Vegetation surveys. — We collected vegetation information on the herbaceous and shrub cover features at all 35 nests detected across sites (Table 2.4 and S3, available online at www.onlinelibrary.wiley.com). Only non-food forb cover ($F = 4.03$, $P = 0.03$) and total herbaceous cover ($F = 3.60$, $P = 0.04$) differed among treatment sites but when

modeled on nest fate did not have a significant effect on success or failure (non-food forb cover, $F = 0.69$, $P = 0.41$; total herbaceous cover, $F = 0.37$, $P = 0.54$). When modeled with site, these features were not observed to impact nest fate ($P = 0.41$, and $P = 0.54$, respectively) and were excluded from nest models in MARK. Nest shrub heights were not different among sites, but had a significant effect on nest fate ($F = 3.22$, $P = 0.08$) and were included in nest survival modeling. However, nest shrub height did not place in top models in MARK. Based on ANOVA testing, other vegetation features measured were not significantly different between sites nor had an effect on nest fate and were not incorporated in nest survival models in MARK.

Hen survival.— Seventeen hens died during the 2012 study period. Of the 7 hen mortalities in the control site, 4 were depredated by unidentified raptors, one by a coyote, one by an unidentified canid, and one cause of death was unknown. Of the 5 hen mortalities in the moderate treatment site, 2 were depredated by unidentified raptors, one by a golden eagle, and one was killed by a hay swather. One hen from the moderate treatment site died within three days of capture, suggesting the hen died while still adjusting to telemetry equipment. Of the 5 hen mortalities in the high treatment site, one hen was depredated by a coyote, one by an unidentified raptor, and 3 causes of death were unknown.

Survival of hens varied across sites and a treatment effect was detected over the nesting period ($\beta = -1.22$, $SE = 0.64$, $P = 0.05$). Hens in the high treatment site were 1.36 times more likely to survive the nesting period than hens from the experimental control site (Table 2.1). Age was not observed to be a significant factor in hen survival during the treatment period ($\beta = 0.39$, $SE = 0.69$, $P = 0.57$). After the nesting season treatment

period, there was no significant difference in annual survival of hens between years ($\beta = -0.49$, $SE = 0.41$, $P = 0.23$), between yearlings and adults ($\beta = 0.49$, $SE = 0.38$, $P = 0.20$), or between experimental control and combined treatment sites (30 Mar 2012 – 1 Mar 2013, $\beta = -0.53$, $SE = 0.41$, $P = 0.19$; Fig. 2). Additionally, the proportion of marked hens that survived in the high treatment site was 1% higher than 2011 (67%, 6 of 9 hens), when 46 coyotes were removed over the year, to 2012 (68%, 13 of 19 hens), when 63 coyotes were removed in 6 months.

Nest survival & success.— We documented 34 hens to have initiated nests between 13 April – 18 May 2012 across the three treatment sites in Bighorn Basin. Two hens attempted second nests after one hen (experimental control site) abandoned a nest in response to camera placement and another hen (high treatment site) lost a nest to raven predation. We set trail cameras on 34 nests ($n_{\text{Control}} = 10$, $n_{\text{Moderate}} = 10$, $n_{\text{High}} = 14$) and observed 15 nest predations (Table 2.3). Of the nest failures ($n = 3$) in the experimental control site, one nest was depredated by a fox, one by a striped skunk, and the third was lost due to abandonment after nest camera placement. All the nest failures ($n = 4$) in the moderate treatment site were caused by predation with 3 nests depredated by coyotes and the fourth by ravens. Of the nest failures ($n = 10$) in the high treatment site, 3 were depredated by coyotes, 3 by ravens, and one was abandoned after camera placement. Cameras successfully identified depredating species for 9 nest predation events; lab forensics additionally identified species for three predation events not captured by cameras and confirmed photo evidence for 2 documented predations. Trail cameras, sign, and lab forensics failed to identify depredating species for 3 nests (high treatment). Mean 35-day brood size was 2 chicks at all sites. However, 5 of the 7 successful nests in the

control site could not be counted at the allotted time due to 1) the hen dying before the count, thus brood fate was unknown ($n = 2$), and 2) landowner restrictions prohibiting access to perform counts ($n = 3$).

We did not find differences in *d_{sr}* for nests between the sites ($\beta = -0.56$, SE = 0.62, $P = 0.18$, Table 2.2). Comparisons of observed nest success showed higher success in the experimental control site than both the moderate ($t = 2.53$, $P = 0.02$) and high ($t = 6.53$, $P \leq 0.001$, Table 2.2) treatment sites, as well as higher nest success in the moderate treatment site compared to the high treatment site ($t = 3.22$, $P = 0.004$).

DISCUSSION

In 2011 we identified coyotes as the species most responsible for nest predations and hen mortalities. Coyote occupancy was four times higher in the experimental control site than the predator managed site, while only a small number of raptors were detected on road transects and other predator occupancy (red fox, bobcat, and skunk) was relatively low (< 15% sites occupied). Although not significant, in the baseline data collection year hen survival was higher at the site where predators were managed. Unexpectedly, observed nest success was higher at the control site where no predator management occurred. Together, these data suggested the removal of coyotes could produce measurable changes to important sage-grouse vital rates. Thus, we designed year two to evaluate coyotes but also control for other factors affecting survival and nest success.

In 2012, when experimental coyote removal was applied, we observed that survival of hens varied across sites, with higher survival of hens during the nesting period in areas where coyote removals occurred. While treatment enhanced hen

survival by 1.36 times during the nesting period, the relatively short time period that survival was examined and the small observed effect may have influenced our results. Power analysis based on published literature was performed before the study and indicated a sample size of 20 birds per site would allow detection of treatment effects. Because we observed higher survival for hens in Bighorn Basin than expected, a larger sample size of birds per treatment level would have been necessary to detect differences in survival. We also observed a shift in the leading predator responsible for hen mortalities at all sites from coyote to raptors. Compensatory predator guild shifts in cause-specific mortality have been observed in response to predator removal in other vital rates (nest success) for northern bobwhite (*Colinus virginianus*, Ellis-Felege et al. 2012), establishing the potential for a similar relationship between survival and predator removal in our system with sage-grouse. Continued monitoring in Bighorn Basin and a higher sample size of cause-specific mortality events are necessary to further examine this multi-predator-prey relationship.

Although we observed nest success to be higher at the experimental control site than both the moderate and high treatment site, no effective differences could be detected in the daily survival rate of sage-grouse nests in response to experimental removal of coyotes. There were small differences in *d_{sr}*, so a very large treatment effect would have been necessary to distinguish differences between sites based on coyote removal. As a field experiment, we designed our treatment levels to augment and work with existing removal management scenarios; subsequently the number of coyotes removed from an area and the response in nest success are relative to coyote population density at those sites (i.e. high removal treatments might not be high

compared to coyote density). Further, observed nest success was already different between sites, 18% higher in the experimental control site in 2011, where no predator management occurred, affecting the magnitude of change possible in *d_{sr}* and our ability to detect that response. Nest shrub height was observed to have a small effect on nest fate, but when included in estimation of nest *d_{sr}* did not explain enough variation to place in top models and thus produced little effect on observed nest success as part of the assessment of coyote removal treatment impacts on our study in Bighorn Basin.

Annual variation in sage-grouse nest success is well documented (LaMontagne et al. 2002, Crawford et al. 2004, Fedy and Doherty 2011, Taylor et al. 2012) and may explain some of the variability we observed. On the surface, the higher nest success observed in the control site falls in line with expectations from mesopredator release theory, which states that the increased presence of an apex predator should decrease negative nest impacts by suppressing mesopredator populations (Rogers and Caro 1998). If mesopredator release were occurring in response to coyote removal, we would expect to see a positive correlation between nest predation and mesopredator populations (i.e. higher nest losses from predators other than coyote at removal sites). While we observed the opposite in Bighorn Basin, if there was a delay of mesopredator response to removals or if removal levels were not high enough to result in release, we would have been unable to detect those changes over our time scale. Further, the small number of nests lost to predators in the control site, where predators were not managed, were from mammalian predators other than coyote, whereas both treatment sites had an equal number of nests depredated by coyote, ravens, and unknown predators. Inter-guild compensatory shifts in nest predators has been observed in other galliformes as a

result of predator removal (Ellis-Felege et al. 2012), suggesting an important indirect effect that encourages further examination in this relationship and system. Continued monitoring and experimental manipulation in Bighorn Basin and a higher sample size of cause-specific nest loss would enhance understanding of this complex relationship.

We were unable to model terrestrial predator occupancy pre- and post-treatment due to low species detection numbers during either one or both survey periods. Although no differences in site occupancy were detected, modeling of coyote occupancy showed differences in detection probabilities between sites, with lower detection probabilities observed at the two sites with coyote removal. In addition, there was a shift in the detection of other mammalian predators to the extent that the three mesopredator species detected in 2011 were not detected at levels sufficient to model occupancy in 2012. This type of detection effect has been hypothesized as a potential behavioral response in mesopredator populations (vs. direct suppression through killing) to apex predator removal (Rogers and Caro 1998). The variability between 2011 and 2012 occupancy estimates for coyote appear to show lower rates in the control site and higher rates in the high treatment site. This may be associated with the effects of on-going predator removal at both the high and moderate treatment sites for livestock and game management purposes. The question of whether these sites have historically higher predator populations resulting in more WS removal activities, or if the sites are used by livestock and game species and subsequently compel predator management could have implications for our results by contextualizing the inherent survival and nest success risks sage-grouse at those sites must tolerate. Additionally, if there is a time-lag to the way in which predator populations are responding to disturbance and exploitation

(Rogers and Caro 1998), only continued assessment of the predator community and subsequent changes in sage-grouse vital rates would identify such a trend. Differences in cause-specific hen and nest predators, and whether there were differences in the associated densities of depredating species, would have furthered our understanding of these results by enhancing our ability to address the question of how both coyote and other predator populations change in response to removal efforts.

We observed no differences in occupancy rates between sites for lagomorphs and the estimates suggest the rate differences observed from pre- and post-surveys reflect differences in the detection of lagomorphs based on seasonal movements, avoidance from disturbance, or some unidentified source of influence on detection. It was noteworthy that there were no site differences in lagomorph occupancy during any sample period in 2012, suggesting alternative prey for coyotes were similarly available across all sites. High annual variation of both prey and predator populations are well documented (Estes 1996, Fedy and Doherty 2011), but we observed consistent lagomorph occupancy in all sites and only a slight decrease in occupancy rates from 2011 to 2012. Fedy and Doherty (2011) found highly correlated cycles (population indices) in sage-grouse and cottontails in Wyoming and concluded neither direct competition nor prey-switching were factors in their observations adding support to our results.

We observed yearly differences in annual survival to have an almost equivalent effect on the survival of sage-grouse hens as the application of the coyote removal treatment during nesting. Further, the additional number of coyotes removed from the high treatment site between study years yielded little enhancement to the proportion of

hens surviving. Annual variation in sage-grouse vital rates, including survival, is common across their range (LaMontagne et al. 2002, Crawford et al. 2004, Taylor et al. 2012), and it is therefore unclear if the effect we observed was from coyote removal treatment, or whether coyote removal could produce an effect on long-term survival and population growth rates. Additionally, compensatory effects could negate the observed higher survival response during nesting as sage-grouse move seasonally, which would produce minimal changes to annual survival.

Our results support emerging evidence that predator removal to protect bird populations may be effective on a short-term basis. Even though we examined effects of predator removal on two of the three most important sage-grouse vital rates, neither a large nor annual benefit were observed in the Bighorn Basin system. We did not observe evidence of mesopredator release or other potential indirect interactions resulting from coyote removal. However, the potential for cyclical or time lag effects (Rogers and Caro 1998, Crawford et al. 2004) was not addressable within the two years the study was conducted. If mesopredator densities were higher in response to coyote removal we would have expected to have seen consequential shifts in hen and nest predators to the “released” species at the most heavily treated sites. Interestingly, we did observe a shift from coyote-dominated nest predations to equal numbers of coyote and raven predations. Whether there is a direct relationship between coyote and raven populations that could explain this shift, or whether the change in nest predator was truly compensatory, as identified in other predator guilds (Ellis-Felege et al. 2012), is unclear. It is possible anthropogenic influences through altered predator community structure and distribution could be a factor for this system and understanding the way predator-prey relationships

are determined by human land use is critical (Moss et al. 2010). By conducting our study in Bighorn Basin, we could examine the question of predator effects on sage-grouse ecology using a fairly stable population with as close a historical predator-prey dynamic as possible, providing a baseline to examine predation impacts in other sage-grouse systems. The decline of sage-grouse invariably includes a multitude of complex interactions (Crawford et al. 2004, Moss et al. 2010, Hagen 2011). Habitat degradation, fragmentation and destruction are identified factors impacting sage-grouse populations (Crawford et al. 2004, Schroeder et al. 2004). We examined predation effects in a core sage-grouse population, constraining the application of information based on our results to well-established populations with similar limiting factors. The question of whether predation is an exacerbating secondary factor will be population specific, and predation may vary spatially and temporally within a given population. Identifying the role predation plays in a specific population's system is imperative to test and understand in order to provide the most effective management.

MANAGEMENT IMPLICATIONS

Management of sage-grouse populations and their habitat involves a complex variety of relationships to understand, assess, and manage. Solutions to address declining sage-grouse numbers must consider the multitude of influential factors affecting sage-grouse ecology (livestock grazing, fire regime, disease, predation, oil and gas development). Our results suggest the application of coyote removal during the nesting period improves survival during that phase of a hen's life but that those fitness benefits do not translate into higher annual survival. We also observed that removing the primary nest predator identified within this system (coyote) did not benefit observed nest success.

Compensatory shifts in nest predators (coyotes to ravens), natural annual variation, or predator density factors may be causing the observed results in Bighorn Basin.

Conducting experimental predator removals over multiple years and with higher sample sizes may result in an observable pattern (cycles, density-dependence, etc.). It is also possible that removal of key predators during other life stages (chicks) or time periods (overwinter) may produce meaningful results to increase sage-grouse populations through enhanced chick survival and recruitment, the other major component in sage-grouse population growth. Beyond retrospective evaluation, we conducted a field experiment to understand predation impacts with targeted manipulation of predators and definitive results. Our research has provided information quantifying the impacts of predators on two important sage-grouse vital rates (hen survival and nest success) and developed a framework for monitoring changes in both sage-grouse and predator populations that will enhance management decisions in Bighorn Basin. Continued efforts and time are needed to determine if management actions produce measureable changes in the context of other environmental and habitat fluctuations inherent in natural systems.

LITERATURE CITED

- Anderson, D.E., O.J. Rongstad, and W.R. Mytton. 1985. Line transect analysis of raptor abundance along roads. *Wildlife Society Bulletin* 13:533-539.
- Beasom, S.L. 1974. Intensive short-term predator removal as a game management tool. *Transactions of the North American Wildlife Conservation* 39:230-240.
- Anderson, D.R., J.L. Laake, B.R. Crain, and K.P. Burnham. 1979. Guidelines for line transect sampling of biological populations. *Journal of Wildlife Management* 43: 70-78.

- Bensen, D.A., I Karsch-Mizrachi, and K. Clark. 2011. GenBank. Nucleic Acids Research 1-6.
- Bixler, A., and J. L. Gittleman. 1999. Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). *Journal of Zoology* 251:525-533.
- Boyko, A.R., R.M. Gibson, and J.R. Lucas. 2004. How predation risk affects the temporal dynamics of avian leks: greater sage grouse versus golden eagles. *The American Naturalist* 163:154-165.
- Braun, C.E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association of State Fish and Wildlife Agencies* 78:139-156.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388-394.
- Coates, P.S., and D.J. Delehanty. 2004. The effects of raven removal on sage grouse nest success. Pages 17-20 *in* *Proceedings of the 21st Vertebrate Pest Conference*, University of California, Davis, USA.
- Coates, P.S., and D.J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. *Journal of Wildlife Management* 74:240-248.
- Coates, P.S., J.W. Connelly, and D.J. Delehanty. 2008. Predators of greater sage-grouse nests identified by video monitoring. *Journal of Field Ornithology* 79:421-428.

- Connelly, J.W., A.D. Apa, R.B. Smith, and K.P. Reese. 2000. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. *Wildlife Biology* 6:227-232.
- 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, Cheyenne, Wyoming, USA.
- Connelly, J.W., K.P. Reese, and M.A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. Station Bulletin 80 (October 2003). College of Natural Resources Experiment Station, University of Idaho, Moscow, USA.
- Conover, M.R., J.S. Borgo, R.E. Dritz, J.B. Dinkins, and D.K. Dahlgren. 2010. Greater sage-grouse select nest sites to avoid visual predators but not olfactory predators. *The Condor* 112:331-336.
- Côté, I.M., and W.J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11:395-405.
- Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosley, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C.S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2-19.
- Dahlgren, D.K. 2009. Greater sage-grouse ecology, chick survival, and population dynamics, Parker Mountain, Utah. Dissertation, Utah State University, Logan, Utah, USA.
- Daubenmire, R.F. 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33:224-227.

- Ellis-Felege, S.N., M.J. Conroy, W.E. Palmer, and J.P. Carroll. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. *Journal of Applied Ecology* 49:661-669.
- Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. *Journal of Wildlife Management* 19:267-272.
- Estes, J.A. 1996. Predators and ecosystem management. *Wildlife Society Bulletin* 24:390-396.
- Estes, J.A., K. Crooks, and R. Holt. 2001. Ecological role of predators. *Encyclopedia of Biodiversity*. Volume 4. Academic Press, New York, New York, USA.
- Fedy, B.C., and K.E. Doherty. 2011. Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: greater sage-grouse and cottontail rabbits. *Oecologia* 165:915-924.
- Fox, J. 2002. Cox proportional-hazards regression for survival data. Appendix to An R and S-PLUS Companion to Applied Regression. <<http://cran.r-project.org/doc/contrib/Fox-Companion/appendix-cox-regression.pdf>>
- Frey, S.N., S. Majors, M.R. Conover, T.A. Messmer, and D.L. Mitchell. 2003. Effect of predator control on ring-necked pheasant populations. *Wildlife Society Bulletin* 31:727-735.
- Fuller, M.R., and J.A. Mosher. 1987. Raptor survey techniques. Pages 37 – 65 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird, editors. Raptor management techniques manual. National Wildlife Federation, Washington, D.C., USA.

- Giesen, K.M., T.J. Schoenberg, and C.E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- Greenwood, R.J., A.B. Sargent, D.H. Johnson, L.M. Cowardin, and T.L. Shaffer. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. *Wildlife Monographs* 128:1-57.
- 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., J.A. Crawford, M.S. Drut, and A.K. DeLong. 1994. Vegetational cover and predation of sage-grouse nests in Oregon. *Journal of Wildlife Management* 58:162-166.
- Guthery, F.S., and S.L. Beasom. 1977. Responses of game and nongame wildlife to predator control in south Texas. *Journal of Range Management* 30:404-409.
- Hagen, C.A. 2011. Predation of greater sage-grouse: facts, process, and effects. *Studies in Avian Biology* 38:95-100.
- Hannon, S.J., and K. Martin. 2006. Ecology of juvenile grouse during the transition to adulthood. *Journal of Zoology* 269:422-433.
- 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.
- Holloran, M.J., and S.H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. *The Condor* 107:742-752.
- Holt, R.D. 1977. Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* 12:197-229.

- Kurki, S., A. Nikula, P. Helle, and H. Linden. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* 81:1985-1997.
- LaMontagne, J.M., R.L. Irvine, and E.E. Crone. 2002. Spatial patterns of population regulation in sage grouse population viability analysis. *Journal of Animal Ecology* 71:672-682.
- Leopold, A. 1933. Predator Control. Pages 230-252 *in* Game management. 1946, Reprint. Charles Scribner's Sons, New York, New York and University of Wisconsin Press, Madison, Wisconsin, USA.
- Lindzey, F. G. 1978. Movement patterns of badgers in northwestern Utah. *Journal of Wildlife Management* 42: 418–422.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377-385.
- Manzer, L.D., and S.J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. *Journal of Wildlife Management* 69:110-123.
- Mezquida, E.T., S.J. Slater, and C.W. Benkman. 2006. Sage-grouse and indirect interactions: potential implications of coyote control on sage-grouse populations. *The Condor* 108:747-759.
- Mills, L.S. 2007. Predation and wildlife populations. Pages 159-175 *in* Conservation of wildlife populations. Blackwell Publishing, Malden, Massachusetts, USA.
- Moss, R., I. Storch, and M. Muller. 2010. Trends in grouse research. *Wildlife Biology* 16:1-11.

- Potts, G.R. 1986. The partridge: pesticides, predation and conservation. Collins, London, UK.
- Ralph, J.C., S. Droege, and J.R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. USDA Forest Service, General Technical Report. PSW-GTR-149.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <<http://www.R-project.org>>
- Rearden, J.D. 1951. Identification of waterfowl nest predators. *Journal of Wildlife Management* 15:386-395.
- Reynolds, J.C., and S.C. Tapper. 1996. Control of mammalian predators in game management and conservation. *Mammal Review* 26: 127-155.
- Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.
- Rogers, C.M., and M.J. Caro. 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. *Oecologia* 116:227-233.
- Roughton, R.D., and M.W. Sweeney. 1982. Refinements in scent-station methodology for assessing trends in carnivore populations. *Journal of Wildlife Management* 46:217-229.
- Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, PA. Deibert, S.C. Gardner, M.A. Hilliard, G.D. Kobriger, S.M. McAdam, C.L. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J.

- Stiver. 2004. Distribution of sage-grouse in North America. *The Condor* 106:363-376.
- Schroeder, M.A., and R.K. Baydack. 2001. Predation and the management of prairie grouse. *Wildlife Society Bulletin* 29:24-32.
- Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 in A. Poole and F. Gill, editors. *The birds of North America*, no. 425. The Birds of North America, Philadelphia, Pennsylvania, USA.
- Seber, G.A. 1982. Estimation of animal abundance and related parameters. Second edition. MacMillan, New York, New York, USA.
- Sedinger, J.S., G.C. White, S. Espinosa, E.T. Partee, and C.E. Braun. 2009. Assessing compensatory versus additive harvest mortality: an example using greater sage-grouse. *Journal of Wildlife Management* 74:326-332.
- Smallwood, J. A., and D. M. Bird. 2002. American Kestrel (*Falco sparverius*). In A. Poole and F. Gill, editors. *The birds of North America*, no. 602. The Birds of North America, Philadelphia, Pennsylvania, USA.
<<http://bna.birds.cornell.edu/bna/species/602>>. Accessed 15 Sept 2011.
- Smith, R.K., A.S. Pullin, G.B. Stewart, and W.J. Sutherland. 2010. Effectiveness of predator removal for enhancing bird populations. *Conservation Biology* 24:820-829.
- Sullivan, J. 1996. *Taxidea taxus*. In, Fire effects information system [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. <<http://www.fs.fed.us/database/feis/>>

- Taylor, R.L., B.L. Walker, D.E. Naugle, and L.S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* 76:336-347.
- Terborgh, J. 1989. *Where have all the birds gone? Essays on the biology and conservation of birds that migrate to the American tropics*. Princeton University Press, Princeton, New Jersey, USA.
- Tesky, J. L. 1995. *Procyon lotor*. In, *Fire Effects Information System* [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <<http://www.fs.fed.us/database/feis/>>
- Treves, A., and L. Naughton-Treves. 2005. Evaluating lethal control in the management of human-wildlife conflict. Pages 86-106 in R. Woodroffe, S. Thrigood, and A. Rabinowitz, editors. *People and wildlife: conflict or co-existence?* Cambridge University Press, New York, New York, USA.
- USFWS. 2010. Endangered and Threatened Wildlife and Plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 50 CFR Part 17 [FWS-RS-ES-2010-00189].
- Valiere, N. 2002. GIMLET: a computer program for analyzing genetic individual identification data. *Molecular Ecology Notes* 2:477-379.
- White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement), 120-138.
- Wilcove, D.S., and J.W. Terborgh. 1984. Patterns of population decline in birds. *American Birds* 38:10-13.

Williams, C.K., R.D. Applegate, R.S. Lutz, and D.H. Rusch. 2000. A comparison of raptor densities and habitat use in Kansas cropland and rangeland ecosystems.

Journal of Raptor Research 34:203-209.

Windberg, L.A. 1996. Coyote responses to visual and olfactory stimuli related to familiarity with an area. *Canadian Journal of Zoology* 74:2248-2253.

Table 2.1. Sage-grouse hen survival estimates from Cox regression model for a predator study conducted over two years in the Bighorn Basin, Wyoming, USA, 2011 – 2012. As a pilot year, baseline data was collected in 2011. Experimental coyote removal was conducted in the second year (2012). In both years the Control site received no prescribed predator removal.

Site	<i>n</i>	Hen survival	SE	95% CI
Year one – 2011 ^a				
Control	14	0.36	0.13	0.18, 0.72
Predator managed	8	0.64	0.16	0.39, 1.00
Year two – 2012 ^b				
Control	17	0.66	0.11	0.47, 0.92
Moderate treatment	15	0.87	0.09	0.71, 1.00
High treatment	19	0.90	0.07	0.77, 1.00
Coyote removal treatment ^c	34	0.88	0.03	0.89, 1.00
Overall ^d				
2011	22	0.47	0.10	0.30, 0.72
2012	51	0.63	0.07	0.51, 0.78
Adult ^e	36	0.57	0.08	0.43, 0.76
Yearling ^e	20	0.72	0.08	0.58, 0.90
Control site ^e	17	0.52	0.11	0.34, 0.80
Moderate treatment ^e	15	0.66	0.12	0.47, 0.94
High treatment ^e	19	0.71	0.10	0.55, 0.94
Coyote removal treatment ^{b,e}	34	0.69	0.10	0.64, 1.00

^a Baseline data, survival for 6 months (13 Apr – 1 Oct)

^b Experimental coyote removal treatment, survival for 2.5 months over the nest period (27 Mar – 15 Jun)

^c Moderate and high coyote treatment levels combined

^d Survival for study duration (13 Apr 2011 – 1 Mar 2013)

^e Estimates from experimental coyote removal in 2012 only

Table 2.2. Observed nest success estimates for sage-grouse based on the daily survival rate (d_{sr}) for two sites with different predator management in 2011 and three coyote removal treatment levels in 2012 in Bighorn Basin, Wyoming, USA.

Site	n	Nest success ^a	Var ^b	95% CI ^c	d_{sr}	SE	95% CI
2011							
Control	13	0.39	0.03	0.33, 0.45	0.98	0.01	0.94, 0.99
Predator management	9	0.21	0.04	0.13, 0.29	0.96	0.02	0.88, 0.99
2012							
Control	9	0.65	0.07	0.51, 0.79	0.99	0.01	0.96, 0.99
Moderate treatment	15	0.43	0.06	0.31, 0.55	0.98	0.01	0.94, 0.99
High treatment	10	0.23	0.03	0.17, 0.29	0.96	0.01	0.92, 0.98

^a Observed nest success = d_{sr}^t , where $t = 37$ (laying + incubation)

^b $\widehat{var}(NS) = \partial NS / \partial d_{sr} \times \widehat{var}(d_{sr})$, where $\partial NS / \partial d_{sr} = t \times d_{sr}^{t-1}$ and $\widehat{var}(d_{sr}) = (SE_{d_{sr}})^2$

^c $CI = \widehat{NS} \pm 1.96(\sqrt{\widehat{var}(NS)})$

Table 2.3. Capture, nesting, and survival data for VHF collared sage-grouse at three lek complexes with different levels of predator control in Bighorn Basin, Wyoming, USA (27 March – 31 August 2012).

	Control	Moderate Treatment	High Treatment
# VHF radio-collars deployed	19	16	20
# Coyotes removed	4 ^a	9	18
# Nests	10 ^b	10	15 ^b
Clutch size (\bar{x})	7	7	6
Nest predations	0.20 (2 ^b)	0.40 (4)	0.53 (8 ^b)
Other losses (abandon)	0.01 (1)	0	0.01 (1)
Brood size ^c	7	5	6
Hen mortalities	0.36 (7)	0.31 (5)	0.25 (5)
Fate unknown	0.05 (1)	0	0.05 (1)
% Predations (of failed nests)	67	100	90

^a Road killed, all < 6 mo

^b Includes second nest attempts

^c Average initial size determined at hatch

Table 2.4. Means (SE) of vegetal variables measured at successful and unsuccessful greater sage-grouse nests ($n = 35$) in Bighorn Basin, Wyoming, USA, 2012.

Variable	Successful		Unsuccessful	
	nests		nests	
	Mean	SE	Mean	SE
Visual obstruction (at nest)	2.25	0.92	2.73	1.21
Visual obstruction (at microsite)	0.91	0.43	0.94	0.32
Total shrub canopy cover (%)	14.14	7.08	14.81	5.20
Sagebrush canopy cover (%)	12.65	7.02	13.02	5.52
Nest shrub height (cm)	50.67	7.78	55.59	8.44
Shrub height (cm)	34.60	10.39	34.87	5.27
Annual grass cover (%)	3.09	7.45	1.74	4.85
Perennial grass cover (%)	7.38	6.85	5.14	2.27
Residual grass cover (%)	23.25	21.73	15.08	6.26
Total grass cover (%)	33.71	9.00	21.96	7.51
Food-forb cover (%)	1.31	1.87	1.00	1.30
Non-food forb cover (%)	3.03	4.54	1.28	1.50
Total herbaceous cover (%)	4.35	6.08	2.28	2.40
Bare soil cover (%)	19.97	14.64	16.50	5.32
Cactus cover (%)	1.74	1.96	0.96	1.55
Crypto biotic crust cover (%)	5.29	4.78	4.94	1.88
Gravel rock cover (%)	10.79	15.00	8.78	9.84
Litter cover (%)	32.70	22.78	28.71	8.57

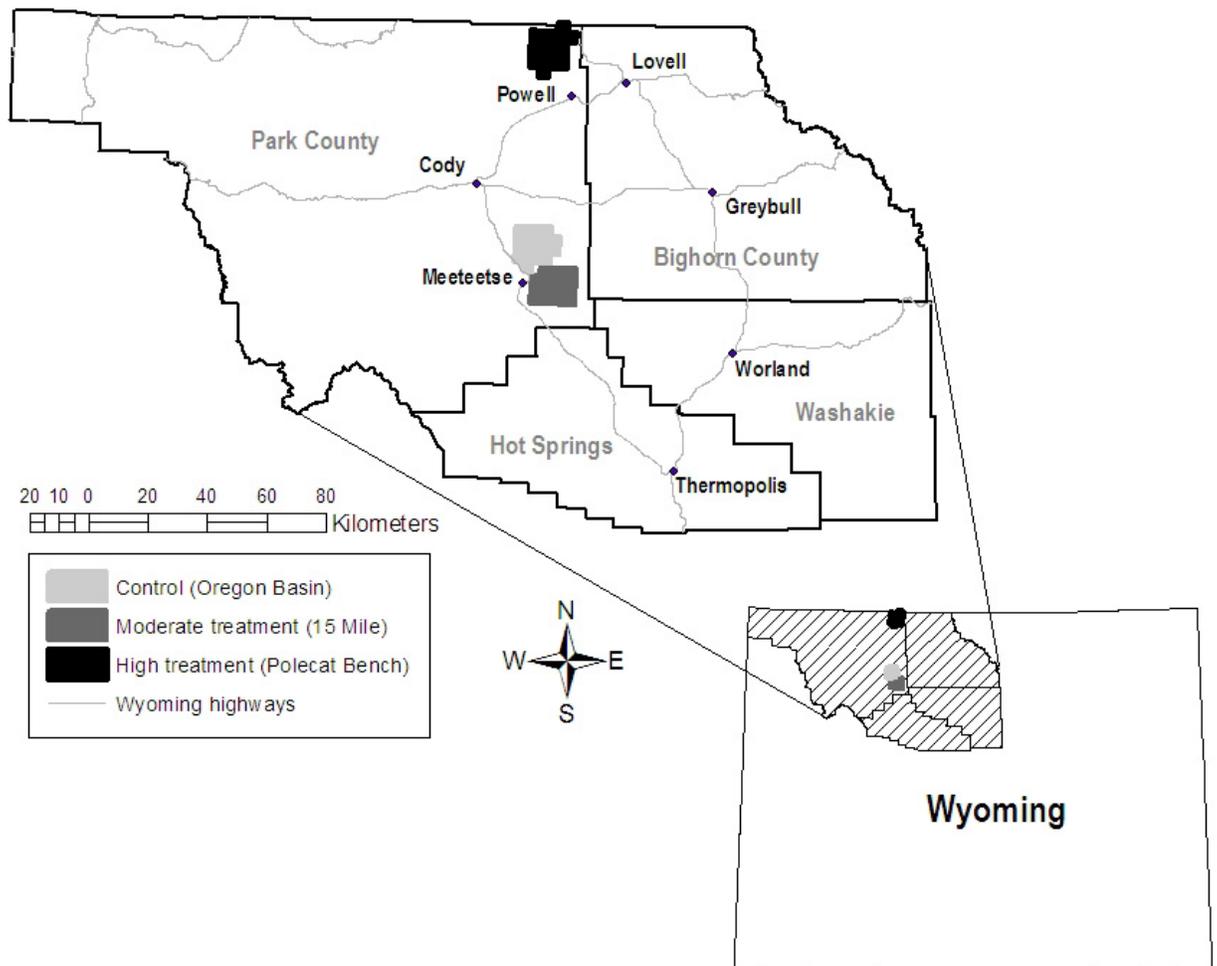


Figure 2.1. Location of our study of coyote removal treatment effects on greater sage-grouse vital rates in the Bighorn Basin of Wyoming, USA 2011 – 2012. We implemented an experimental design at three sites to test the effects of no (Oregon Basin, control site), moderate (15 Mile), and high (Polecat Bench) coyote removal treatments on the observed nest success and hen survival of sage-grouse.

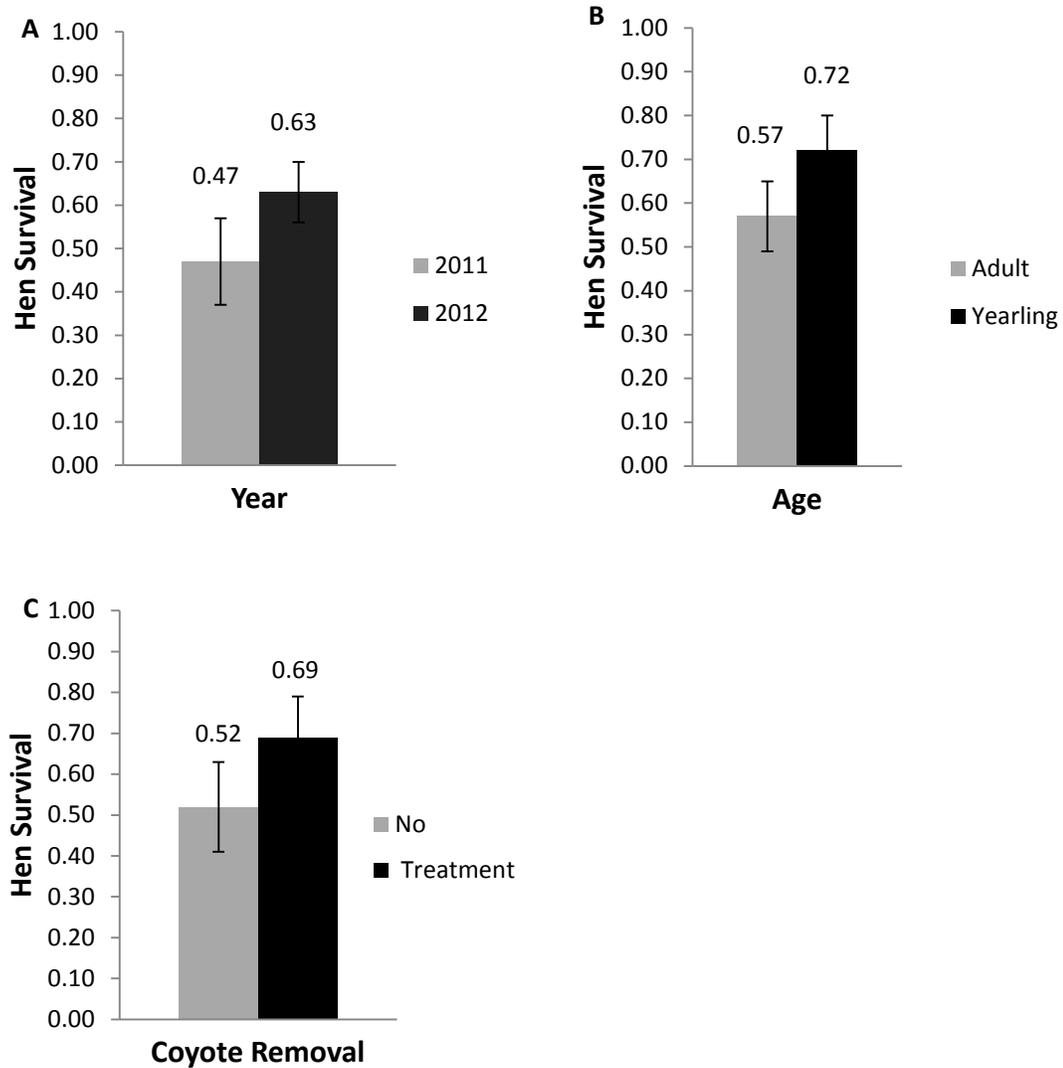


Figure 2.2. Sage-grouse hen survival estimates (13 Apr 2011 – 1 Mar 2013) for the duration of a two year predator removal study in Bighorn Basin, Wyoming 2011 – 2012. We implemented an experimental design at three sites to test the effects of no (Oregon Basin, control site), moderate (15 Mile), and high (Polecat Bench) coyote removal treatments. Estimates are from Cox regression model for covariate effects of A) year of study, B) age of hen, and C) treatment.

CHAPTER 3

ANTHROPOGENIC INFLUENCES ON GREATER SAGE-GROUSE SPACE USE
AND HABITAT SELECTION

Abstract. Greater sage-grouse (*Centrocercus urophasianus*) is a species in decline across western North America. Identification of management strategies to enhance sage-grouse populations is imperative to reduce further declines. We evaluated the impact of anthropogenic features associated with predator management and other plausible human influences on sage-grouse space use and habitat selection. Home range size, seasonal movement timing, and inter-seasonal distances traveled were examined as potential behavioral responses to different levels of predator management. We developed measures of relative predation risk and avoidance using distance to known coyote den and nest predation events, location points for removed coyotes, and coyote presence-absence (scat, tracks, trail camera images) data collected as part of a simultaneous sage-grouse predation study in Bighorn Basin. We hypothesized that sage-grouse would select resources similarly between sites with differing short-term management (i.e. predator removal), but respond strongly to other human features (e.g. oil/gas development, urbanization). We used logistic regression-based resource selection functions (RSFs) to determine habitat selection and identify differences in use at multiple spatial extents (seasonal and annual ranges). We observed larger home range sizes during critical life stages (brood rearing) but overall smaller annual core (25% density kernel) area size with higher levels of predator management. We observed higher proportions (%) of sage-grouse making inter-seasonal movements and longer distances traveled with higher levels of predator management. Our models showed sage-grouse selected areas with higher

sagebrush and with access to water. We also observed sage-grouse to be sensitive to predator removal management but also avoided areas close to roads, with high well density, and steep slopes. We conclude short-term intensifications of management can disrupt sage-grouse during critical life stages (avoidance during breeding and brood periods), but potentially benefit other stages (selection during inter-seasonal use periods). Our resulting models improve our understanding of how anthropogenic features impact sage-grouse across multiple spatial and temporal extents. The use of models that incorporate unique variables associated with predator management and other anthropogenic features show promise for identifying changes in home range size, seasonal use patterns, and habitat selection as they relate to both habitat resources and proposed management.

INTRODUCTION

The largest grouse species in North America, Greater Sage-Grouse (*Centrocercus urophasianus*, hereafter sage-grouse) had at one time occupied 1,200,483km² of sagebrush habitat across 13 western states in the U.S. and three provinces in Canada (Schroeder et al. 2004). Habitat loss and fragmentation (Braun 1998, Connelly et al. 2004), increasing natural disturbances like wildfire (Connelly and Braun 1997, Connelly et al. 2000), and anthropogenic disturbances influence sagebrush communities and sage-grouse ecology (Smith et al. 2005, Walker et al. 2007, Aldridge et al. 2008, Blickley et al. 2012). As a sagebrush obligate species, sage-grouse distribution and population density declines across western North America are related to many of the factors affecting sagebrush-steppe communities (Braun et al. 2002, Knick et al. 2003, Connelly et al. 2004, Nielson et al. 2005). Occupying 56% of their historic range (Schroeder et al. 2004),

the severity and extent of this decline have led to recent listing of sage-grouse under the Endangered Species Act of 1973 as warranted, but are currently precluded by species of higher conservation concern (USFWS 2010).

No single factor has led to sage-grouse population declines, but unintentional stressors or disturbance that result from anthropogenic activities have been shown to impact sage-grouse populations (Johnson et al. 2011, Blickley et al. 2012, Hess and Beck 2012*b*). Anthropogenic disturbance comes from a variety of long- and short-term human activities including agricultural development (Smith et al. 2005, Walker et al. 2007, Aldridge et al. 2008), historical livestock activities (Beck and Mitchell 2000, Crawford et al. 2004), urbanization (Braun 1998), energy development (Lyon and Anderson 2003, Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008), prescribed fire (Connelly and Braun 1997, Nell et al. 2000, Hess and Beck 2012*a*), higher OHV (off highway vehicle) presence or use (Blickley et al. 2012), and greater human presence for management purposes like predator removal (Chapter 2).

Management plans for sage-grouse often focus on habitat restoration as the primary means to mitigate reductions in habitat quality and quantity as well as to minimize predator impacts (Braun 1998, Connelly et al. 2000, Coates and Delahanty 2004, Connelly et al. 2004). These efforts may provide only limited success if anthropogenic factors operating at larger spatial scales are not considered (Coates and Delahanty 2004, Manzer and Hannon 2005, Mezquida et al. 2006). Human interference may influence sage-grouse population declines by altering the dynamics of both predator-prey systems (i.e. altering predator community structure, densities, or distribution) and sage-grouse by disturbing or altering space use (e.g. habitat selection, home range,

seasonal use patterns) during critical life stages of breeding (lek attendance and nesting), brood rearing, and overwinter survival. Changes in these behaviors could subsequently increase predation rates on birds and their nests (Greenwood et al. 1995) or alter causes of individual mortality (Sedinger et al. 2009) and nest loss (Ellis-Felege et al. 2012).

Protection and restoration of crucial breeding and brood rearing areas have been the primary focus for managers across their range as they are strongly linked to specific, known habitat requirements of the sage-grouse (Connelly et al. 2000, Holloran and Anderson 2005, Hagen et al. 2007). Efforts to understand sage-grouse space use, habitat selection, and habitat availability throughout all life stages have become increasingly important to conservation and management objectives (Homer et al. 1993, Bruce et al. 2011, Fedy and Aldridge 2011, Dzialak et al. 2011, 2013). Resource selection functions (RSFs) are fundamental tools frequently used to test the influence of landscape-level characteristics on animal habitat selection and the space use (Boyce and McDonald 1999, Manly et al. 2002). To date, few studies have used RSF modeling to evaluate the influence of predator communities and predator control on sage-grouse habitat selection. Importantly, resource use patterns directly influence survival and reproduction (Boyce and McDonald 1999). Thus, identifying changes in these patterns as they relate to both habitat resources and anthropogenic activities are important components to management and conservation planning.

We sought to evaluate the influence of anthropogenic activities on sage-grouse space use and habitat selection in the Bighorn Basin of Wyoming, USA. Our objectives were to quantify sage-grouse home range size, document the presence and nature of seasonal movement patterns, and to compare habitat selection of sage-grouse between

sites with differing levels of predator management. Our primary research questions were:

- 1) what are the home range sizes and habitat selection of sage-grouse in Bighorn Basin;
- 2) does the timing of seasonal movements change relative to predator management; and
- 3) does sage-grouse space use or habitat selection change relative to predator management or other anthropogenic features. Understanding anthropogenic effects on sage-grouse habitat selection and space use will provide managers and conservationists with information to aid habitat improvement efforts and enhance sage-grouse management.

METHODS

Study Area

During 2011 and 2012, we studied sage-grouse space use in the northwest portion of Bighorn Basin, Wyoming (Fig. 3.1). Bighorn Basin is a semi-arid, intermontane basin located in north-central Wyoming plateau that encompasses 32,000 km² of Bighorn, Hot Springs, Park, and Washakie Counties. The study area included 504 km² of Bighorn Basin and was carried out at three lek complexes: Oregon Basin (44° 22.45 N, 108° 48.17 W), 15 Mile (44° 10.89 N, 108° 44.38 W), and Polecat Bench (44° 57.00 N, 108° 45.54 W). Average valley elevation was 1,524 m and the area was composed of badland, intermittent buttes, and big sagebrush communities. Average maximum and minimum temperature during the study period (March to September) was 25.7° C and -0.4° C, respectively in 2011 and 29.7° C and 0.1° C in 2012. Total precipitation during the study period was 14.7 cm in 2011 and 19.5 cm in 2012 (Fales Fock, WY, USA; <http://www.raws.dri.edu>). Bighorn Basin is composed of mostly public land managed by the Bureau of Land Management (40%), Forest Service (25%), state (5%), and other

federal agencies (>1%; Bureau of Reclamation, National Park Service, Department of Defense), as well as some private land (25%) (Sage-grouse Conservation Plan for the Bighorn Basin, WY 2007). Land uses in sagebrush areas included livestock grazing, wildlife habitat, dry-land and irrigated crop production, recreation, bentonite mining, and oil and gas extraction. Common plants included shrubs, such as Wyoming big sagebrush (*Artemisia tridentate*), basin big sagebrush (*A.t. vaseyana*), greasewood (*Sarcobatus vermiculatus*), and rabbitbrush (*Chrysothamnus viscidiflorus* and *Ericameria nauseosa*); forbs such as globemallow (*Sphaeralcea spp.*), milkvetch (*Astragalus spp.*), fringed sagewort (*A. frigida*), phlox (*Phlox spp.*), and common pepperweed (*Lepidium densiflorum*); perennial grasses such as blue-bunch wheatgrass (*Pseudoroegneria spicata*), blue grama (*Bouteloua gracilis*) and needle and thread (*Hesperostipa comate*); and invasive species such as cheatgrass (*Bromus tectorum*), knapweed (*Centaurea spp.*) and toadflax (*Linaria spp.*). Detailed descriptions of vegetative characteristics for Bighorn Basin can be found in Hess and Beck (2012a).

Coyote and other predators were removed at two sites by USDA-APHIS Wildlife Services as part of regular management activities for livestock and wild ungulates during both years of the study, as well as for protecting sage-grouse nesting areas at one of these two sites in 2012 (Chapter 2). Removal methods included aerial gunning, snare and leg-hold trapping, den gassing, and opportunistic shooting. Removal areas received year-round predator management for domestic livestock depredation and agriculture damage (Polecat Bench, hereafter high management) and for mule deer fawn (*Odocoileus hemionus*) production (Fifteen Mile, hereafter moderate management). In addition to these ongoing predator removal activities, at the high management site in 2012, coyotes

(*Canis latrans*) were lethally removed near sage-grouse nests. The moderate management site received no additional predator removal. The high management site was classified as such because the additional predator removal was part of an experimental treatment that was specific to areas sage-grouse were nesting in and was not part of regular predator management, whereas the moderate management site received predator removal as applied for regular ungulate management purposes. Targeted coyote removals and the associated higher management occurred between 14 March – 15 June 2012. No predator removal occurred at Oregon Basin (hereafter, control site). The location of each removed coyote was recorded for all sites, including incidentally identified mortalities from the control site (i.e. road kills).

Field Procedures, Location Data, and Home Range Generation

In 2011-2012, we captured female sage-grouse using rocket nets on three lek complexes (6 leks) in March and April and hoop net and spotlight techniques in post-brood flock areas in September (Giesen et al. 1982). Leks were targeted for capture based on sufficient male/female lek attendance to minimize rocket use to no more than two launches per lek (i.e. 10-20 hens in attendance). Hens were fitted with either VHF necklace-style transmitters (Advanced Telemetry Systems Inc. [ATS], Isanti, Minnesota) or ARGOS/GPS solar PTT packs (PTT-100, Microwave Telemetry, Columbia, MD, USA) using a rump mount (Dzialak et al. 2012). Hens were weighed and classified as a yearling (first breeding season) or an adult (\geq second breeding season) based on wing primary shape (Eng 1955). GPS transmitters weighed 30 g and were fitted to hens weighing more than 1300 g. GPS packs were programmed to record a location every three hours during fall and spring at 12:00, 15:00 and 18:00 hrs (15 September – 15

November , 22 March – 30 April), every two hours during winter at 13:00 and 17:00 hrs (15 November – 2 January), and every hour during the nest, brood, and seasonal from 12:00 – 18:00 hrs (1 May – 14 September). VHF transmitters weighed 22 g and had a battery life expectancy of 869 days. We monitored VHF marked hens using hand-held receivers and vehicle mounted whip or Yagi antennas every 48-72 hours from the time of capture through the end of the brood-rearing season (August) to document survival, identify nest sites, and track seasonal movement timing. We obtained ≥ 3 sequential bearings within 15 min for each triangulation of a hen and collected locations twice per week. Opportunistic visuals and homing to within 50 m of marked animals were also used as part of the VHF data set. We obtained location estimates for VHF triangulation data from program LOCATE III (version 3.34, Pacer Computing, Tatamagouche, NS, Canada) using maximum likelihood estimation (MLE). To screen precision in triangulation estimates, error polygons (Heezen and Tester 1967) and a 900-m threshold were used as retention criteria. VHF-marked birds were not located over the entire annual period, thus information from this data set was only used in the calculation of the proportion of birds making inter-seasonal movements.

Home range is a commonly used measure of animal space use across multiple taxa including sage-grouse (Musil et al. 1993, Drut et al. 1994, Connelly et al. 2000), allowing the evaluation of changes in use over temporal and spatial scales (White and Garrott 1990). Currently, minimum convex polygon (MCP) is the most common method used to report sage-grouse home range (Drut et al. 1994, Sveum et al. 1998, Connelly et al. 2000, Aldridge and Boyce 2007, Dzialak et al. 2012), but identifying fine-scale changes in space use, and subsequent resource selection, with this broad-scale estimator

could be problematic (Garshelis 2000). Powell (2000) advocated kernel density estimates (KDE) as the best estimator available for home range estimation and this technique is well represented in the home range estimation of other taxa (Seaman 1993, Stahlecker and Smith 1993, Nielsen and Woolf 2001, Hebblewhite and Merrill 2007, Berger et al. 2008), yet seldom used to evaluate sage-grouse or other grouse home ranges (see Burnett 2012 and Whitaker et al. 2007 for exceptions). Given the scope of our interests, we decided to use KDE estimates for later steps in resource selection modeling, but report average MCP ranges as well.

We obtained both MCP and annual fixed KDE home ranges for GPS-marked sage-grouse using Geospatial Modelling Environment (GME version 7.2.0, Beyer 2012) in program R (R Development Team 2008). Home ranges were only generated for GPS-marked birds with ≥ 10 locations over annual ($n = 12$) and seasonal periods. We excluded birds from seasonal range estimation when this criterion was not met. We generated KDEs with 95% probability contours using a 30-m cell size and the PLUGIN bandwidth (smoothing factor). Total home ranges are the 99% density kernel areas and represent the maximum range used by a given bird. We defined core areas by the 25% density kernel contour (i.e. higher density of use like nesting).

We generated movement step lengths for GPS-marked birds which were used to calculate a measure of average daily, monthly, and yearly movements. Because we were interested in selection differences at a finer scale than a migratory/non-migratory classification (Connelly et al. 2000), we classified the occurrence of seasonal movements if either of two criteria were met: 1) ≥ 5 km movement occurred, or 2) identifiable shifts in location area habitat features occurred (e.g. a hen moved from a sagebrush bench down

in elevation to a riparian/agriculture habitat). Seasonal KDE ranges were generated for birds that showed inter-seasonal movement behavior. We defined seasonal ranges biologically (i.e. a general time frame and adjusted depending on individual bird movement patterns) as breeding (March – May), brood (June – August), and inter-seasonal (September – November). We calculated the inter-seasonal movement distances for GPS marked birds as the distance between 25th percentile core area centroid points and averaged distances within sites. We used analysis of variance (ANOVA) to evaluate differences in home range size and seasonal distances traveled.

Landscape and Anthropogenic Variables

We developed and examined a suite of variables at 30-m² resolution in a Geographic Information System (ArcGIS, version 10.0, ESRI, Redland, CA). We included *a priori* model variables comprising habitat and terrain characteristics identified as important to sage-grouse occurrence and fitness as well as features influenced by humans (Table 3.1, Aldridge and Boyce 2007, Doherty et al. 2008). We separated variables into four classes for modeling and analysis: 1) habitat features, 2) terrain features, 3) anthropogenic features, and 4) predator features. Habitat features included the Euclidean distance (km) to nearest streams, stream density, sagebrush density (USGS, Hanser 2006), and the major land cover vegetation classes from Gap Analysis Program (GAP; USGS-2006 National Land Cover Database land cover map, NASA LP DAAC). We reclassified and reduced the ten GAP NLCD cover classes to seven by condensing introduced/semi-natural, nonvascular/sparse, recently disturbed, developed/other human use into one Disturbed/Developed class. We retained six GAP vegetation classes including Forest, Shrub/Grassland, Semi-Desert, High Montane, Agriculture, and Open

Water classes (Table 3.1). Distance to nearest streams was calculated as the shortest distance to the nearest major river or stream (range 0 – 35.2 km). Terrain features included elevation (USGS National Elevation Dataset 30-m Digital Elevation Model (DEM)), slope, and Compound Topographic Index (CTI, Gessler et al. 1995). Slope, the average change in vertical elevation per unit of horizontal distance, was calculated as a measure of topographic steepness using Spatial Analyst and the 30-m DEM. CTI is a function of both slope and upstream contributing area and has been used as a surrogate for soil moisture and vegetation productivity in previous sage-grouse resource selection modeling (Aldridge et al. 2007, Aldridge et al. 2011). Anthropogenic features included Euclidean distance (km) to roads and oil well sites and kernel density estimates of well sites. In addition, we incorporated a measure related to predator removal management using Euclidean distance (km) to location points for removed coyotes. For predator features we developed measures of relative predation risk using Euclidean distance (km) to known coyote hen and nest predation events and coyote presence-absence (scat, tracks, trail camera photographs) data collected as part of a predation study in Bighorn Basin (Chapter 2). The distance to nearest roads (range 0 – 33.3 km) was calculated as the shortest distance between each raster grid cell and the nearest road. All distance metrics were standardized to km and analyzed as a continuous variable. Stream density was derived from water polyline features (Wyoming Game and Fish Department). Well density was derived from well pad point features (USGS, Hanser 2007) and converted to a raster using a kernel density estimate in GME. All raster layer covariate inputs were constructed at a 30-m resolution with the exception of sagebrush density (USGS, Hanser 2006), which was an 18-km scaled density proportion at a 540-m resolution.

Resource Selection Modeling

We used a resource selection function framework with a use-availability design to compare sage-grouse space use among sites and across seasons. We defined used points by location points for GPS-marked birds and developed RSF models at second (landscape) and third (within-season range areas) order scales (Johnson 1980). We incorporated a random effect for individual (second and third order models), and site (third order models), to account for differences in the number of locations per individual and unknown variability in selection among individuals and selection among sites, allowing for population level inference (Manly et al. 2002). We screened variables for collinearity before modeling by calculating Pearson's correlation and variance inflation (variance inflation factor, VIF) between variables and using $|r| \geq 0.70$ and $VIF \geq 10$, respectively, as thresholds for removing a covariate (Hosmer and Lemeshow 2000). If variables were highly correlated, we retained one that best reflected selection based on sage-grouse biology and peer-reviewed literature. Availability was established by generating and distributing random available locations at a 3:1 available to used ratio within individual annual (second order available points, $n = 19,156$) and seasonal (third order available points, $n = 17,139$) KDE home ranges for GPS-marked hens. Candidate models were generalized linear mixed-effect models (GLMM) with a random intercept for each individual (landscape model) and site (seasonal model) allowing the assessment of covariate differences among birds and between sites (Hebblewhite and Merrill 2008, Bolker et al. 2009). We generated models using the lme4 package (Bates et al. 2011) in program R.

Model Assessment

We used a hierarchical model selection framework to evaluate sage-grouse habitat selection by identifying the spatial scale at which anthropogenic and habitat features affect space use. We used Akaike's information criterion corrected for small sample sizes (AIC_c) to evaluate relative model fit (Burnham and Anderson 2002). We selected the model with the lowest AIC_c value as the best-fitting model, and used the difference in AIC_c (ΔAIC_c) and Akaike weights (w_i) to assess the strength of evidence in favor of each model within the model set (Burnham and Anderson 2002). We followed the convention that models with $\Delta_i \leq 2$ were competitive with the top model (Burnham and Anderson 2002, Arnold 2010). We identified the top model(s) within each habitat, terrain, predator, and anthropogenic class and allowed models to compete across categories to see if the additional information improved model fit. After selecting a top model we used P -values to derive inference across sites and among seasons from parameters in the top model. We did not use VHF location data as part of the RSF use data set to control for the lack of adequate precision in triangulation location estimates (White and Garrot 1990) and to avoid ambiguous habitat selection results because location data was biased toward the quantity of GPS data.

RESULTS

We obtained 6,309 GPS telemetry locations (September 2011 – March 2013) and 474 VHF telemetry locations (April – August 2011, 2012) of sage-grouse from 57 individuals. Location points per site were relatively equal for GPS-marked hens ($n_{\text{control}} = 1906$, $n_{\text{moderate}} = 2167$, $n_{\text{high}} = 2234$), but biased towards the two sites that had marked hens in both years in the VHF data set ($n_{\text{control}} = 161$, $n_{\text{moderate}} = 43$, $n_{\text{high}} = 260$). Average

daily (control = 46.31 m, SD = 114.66; moderate = 94.57 m, SD = 660.96; high = 81.12 m, SD = 266.73, $P \leq 0.001$), monthly (control = 1.39 km, SD = 3.44; moderate = 2.84 km, SD = 19.83; high = 2.43 km, SD = 8.00, $P \leq 0.001$), and annual (control = 16.67 km, SD = 41.28; moderate = 34.05 km, SD = 237.95; high = 29.20 km, SD = 96.02, $P \leq 0.001$) movement distances were longer with higher levels of predator management. Nest distances were on average within 6 km of leks, similar to other sage-grouse populations (5-8 km, Holloran et al. 2005). However, the site with high management had the longest lek-to-nesting distance observed in the study, 18.2 km, and four hens nested > 10 km from respective capture leks. Conversely, one hen in the control site nested 16.9 km from the capture lek.

Sage-Grouse Home Range Size and Seasonal Movement

Annual home range ($P = 0.04$) and inter-seasonal ($P \leq 0.001$) range sizes (99% kernel areas) were negatively associated with predator management (25% kernel area, Table 3.2). Core range sizes were also negatively associated with predator management over annual ($P = 0.08$) and inter-seasonal ($P = 0.001$) periods. There were no differences in core area size during the brood period between the control and predator managed sites ($P = 0.70$). Total brood range sizes were $3.27 \pm 2.68 \text{ km}^2$ in the moderate management site, and $1.24 \pm 0.74 \text{ km}^2$ in the high management site during the brood phase. Though total brood range sizes were largest in the control site ($2.56 \pm 2.77 \text{ km}^2$), they were not statistically different between sites ($P = 0.67$).

Seasonal movement occurred between 24 Jun – 30 Jul in 2011 with the median dispersal date being 12 Jul, and between 8 May – 9 Jul in 2012 with a median dispersal date of 13 Jun. Timing of dispersal to brood (> 5-km from nesting) and inter-seasonal use

areas varied between years by almost a month with sage-grouse moving on average 24 days earlier in 2012 than was observed in 2011 ($n = 8$, $SD = 9.17$, range 8 – 34 days). Sage-grouse moved on average 21 days earlier in the control site and on average 29 days earlier in the high management site in 2012. Data were not available for 2011 in the moderate management site for comparison.

Far more than half of marked birds showed evidence of inter-seasonal movement (92%). The proportion of birds making inter-seasonal movements was not consistent across sites; 66% of marked control site birds showed inter-seasonal movement, whereas 81% of moderate management site birds and 80% of high management site birds were moving inter-seasonally. Average distances between seasonal ranges were longer in both the moderate ($P = 0.02$) and high ($P = 0.16$) management sites compared to the control site (Table 3.3). Inter-seasonal movements from breeding to brood ranges were shorter in the control site compared to moderate and high management sites. Similarly, distances were also shorter from breeding to inter-seasonal ranges (i.e. some birds transitioned directly to secondary areas during nesting periods, presumably after failed nest attempts) between the control and predator managed sites. However, the average distances traveled were shortest in the high management site when birds were moving from brood to inter-seasonal ranges (Table 3.3).

Resource Selection

Covariates comprising top second (annual) and third (seasonal) order models were identical (Table 3.4 and 3.5). However, the sign and magnitude of covariate effects varied between spatial scales, among sites, and across seasons (Tables S1, S2, and S3 Appendix B). For example, sage-grouse selected areas with higher sage density on both seasonal

and annual scales, but closer examination within seasons, showed sage-grouse strongly select for dense sage during breeding, as would be expected during nesting, but strongly avoided dense sage during brood rearing. This avoidance could be to increase insect and forb forage availability for chicks (Crawford et al. 2004), or to reduce negative associations with dense sage (less escape routes, increased predation risk for flight-limited chicks; Weibe and Martin 1998, Aldridge and Boyce 2007). As another example, in annual ranges sage-grouse selected areas in proximity to wells at control and moderate sites, but avoided areas close to wells in the high management site, suggestive of sage-grouse sensitivity to this feature at this site.

Annual

Resource selection by sage-grouse over annual home ranges was different among sites, but only significantly different between the control site and the high management site ($P < 0.0005$, see Table S1 and S2, Appendix B). Distance to coyote removal, distance to well sites, CTI, and forest vegetation showed no significant trends in predicting annual resource selection by sage-grouse in Bighorn Basin. Grouse avoided areas with higher well density, higher elevations, and steeper slopes, as well as disturbed/developed and semi-desert (i.e. sagebrush) vegetation classes (relative to shrub/grassland). Specifically, holding other variables constant, the odds of use by sage-grouse were lowered 8% for each 100 m gained in elevation. Further, each 0.25% rise gained in slope, the average change in elevation per unit horizontal distance, reduced the odds of use by 90%. In addition, grouse selected areas away from coyote predation, known coyote presence, and roads. Sage-grouse selected agricultural lands over shrub/grasslands. A quadratic response was observed for the distance to water with sage-grouse avoiding areas further

from water and selecting areas with higher stream density. Sage-grouse also selected areas with higher sagebrush density.

Site-specific RSF modeling (see Table S2, Appendix B) showed differences in selection among sites occurred in a number of variables including proximity to coyote presence and coyote removal, distance to wells, elevation, and use of forest and agricultural lands. Sage-grouse consistently avoided areas with steep slopes across all sites, but selected for higher elevations in the control and high management site and lower elevations in the moderate management site. In effect, holding other variables constant, for each 100 m gained in elevation the odds of use by sage-grouse were 95% and 65% higher at the control and high management sites respectively, but 45% lower in the moderate management site. Sage-grouse selected areas away from roads in the moderate and high management sites, but not in the control site. Conversely, closer proximity to wells was selected for in the control and moderate management site, whereas sage-grouse avoided (selected further distances from) wells in the high management site.

Seasonal

Resource selection by sage-grouse varied seasonally among all biological seasons ($P \leq 0.02$, see Table S1 and S3, Appendix B). Distance to coyote predation and coyote removal, CTI, elevation, and forest and disturbed/developed lands showed no significant trends in predicting seasonal resource selection by sage-grouse in Bighorn Basin.

Avoidance occurred with respect to well density, steeper slopes, and proximity to roads and wells. Specifically, each 0.25% rise gained in slope reduced the odds of sage-grouse use by 98%. Sage-grouse also avoided semi-desert (encompassing sagebrush) and

agriculture vegetation classes relative to shrub/grassland. A quadratic response was observed for the distance to water with sage-grouse avoiding areas further from water and selecting areas with higher stream density. Expectedly, sage-grouse seasonally selected areas with higher sagebrush density.

Season-specific RSF modeling revealed differences in selection between seasons occurred in a number of variables, including proximity to coyote predation and coyote removal, distance to wells, sage density, and elevation (see Table S2, Appendix B). Sage-grouse consistently selected for areas further from coyote removal during breeding and brood periods and but not during inter-seasonal periods. Areas further from wells were selected for in breeding and inter-seasonal use, but grouse selected for areas close to wells during the brood rearing season. Well density was a feature significantly avoided only during the breeding period. While sage-grouse avoided areas closer to roads during the brood season (expected based on annual landscape trends), areas close to roads were selected during periods of inter-seasonal movement. Dense sage was strongly selected for during breeding, but strongly avoided during the brood period.

DISCUSSION

Increasing natural and anthropogenic disturbances leading to continued habitat loss and fragmentation affect not only sagebrush-steppe communities but the behavior and ecology of sagebrush dependent species like greater sage-grouse (Connelly and Braun 1997, Connelly et al. 2004, Walker et al. 2007, Aldridge et al. 2008). Our findings support emerging evidence (Crawford et al. 2004, Blickley et al. 2012, Hess and Beck 2012*b*) on the disturbance effects of anthropogenic features and demonstrate the impact activities like predator management can have on the behavioral and spatial ecology of

sage-grouse. Our results suggest sage-grouse in Bighorn Basin are restricting their overall range use in response to anthropogenic features while simultaneously requiring larger areas to meet specific life-stage requirements (e.g. human use + poor quality habitat/habitat fragmentation). Larger home range sizes during critical life stages (brood rearing), but overall reduced annual core area size with higher predator management supports the manifestation of altered behavioral patterns in response to long and short-term anthropogenic features.

Evidence of a behavioral response was apparent with higher proportions of birds showing inter-seasonal movement behavior and longer distances traveled relative to a higher level of predator management. While we observed a clear shift in the timing of inter-seasonal movements between years, we lacked sufficient multi-year data within each site to evaluate if the observed shift was in response to higher short-term management or a response to natural climate and environmental variation (i.e. drought response, Fischer and Reese 1996). For instance, the spring of 2011 was colder, had more rainfall, and had longer persisting snow. Whereas the spring of 2012 had little remaining snow from winter, warmer temperatures, and less rainfall, drying out nest and brood areas earlier. This annual weather variation between the two study years might account for some of the differences in the timing of seasonal movements that we observed. However, sage-grouse habitat use is influenced by landscape-scale factors (Doherty et al. 2008) and disturbance from human activity has been linked to avoidance of wintering habitats (Doherty et al. 2008), longer nest distances from leks (Lyon and Anderson 2003), and lek abandonment (Holloran 2005, Hess and Beck 2012*b*, Blickley et al. 2012), demonstrating

a sensitivity to human uses that suggests alterations in the timing of inter-seasonal movements could also be in response to predator management.

On an annual basis, sage-grouse demonstrated strong selection for areas with higher sagebrush density, proximity to water and lower elevations as would be expected given their strong dependence on sagebrush-steppe habitat at each life stage (i.e. shrubs for nesting, cover for broods, primary forage overwinter). Notably, sage-grouse avoided areas with higher well density and in close proximity to roads suggesting short-term human activities (like the higher management level involved for predator removal) might not be as disturbing as persistent activities from other anthropogenic features (e.g. noise from oil machinery and vehicles). For example, it may be that roads are not a problem, but persistent human presence or noise (Blickley et al. 2012) from cars and equipment disturbs sage-grouse. Also noteworthy over the annual period is the avoidance of all other vegetation classes relative to shrub/grasslands, including the cover class containing sagebrush, in favor of agricultural lands. It was evident when examined at finer site and season levels that a more complex relationship existed. For example, agricultural lands were strongly avoided in the moderate management site, but selected for in the high management site. There was no trend in the control site. While sage-grouse are known to forage in agriculture fields (Patterson 1952), and it is possible sage-grouse have adapted to make use of agricultural lands during some life stages (early brood, Burnett 2012), Aldridge and Boyce (2007) state they do not typically occur in landscapes heavily dominated by agriculture over all life-stages of an annual period. Cultivated lands directly remove habitats from use. Thus, it is possible avoidance of agriculture at the control site was strong enough to functionally remove that habitat patch from available

use (Aldridge and Boyce 2007) and would have been underrepresented in our logistic models.

Similar to annual selection preferences, inter-seasonally, sage-grouse strongly selected for areas with higher sagebrush and stream density, and close proximity to water. In addition, sage-grouse avoided areas close to roads, with high well density, and steep slopes. The shift in vegetation class preference between seasonal and annual selection was likely a function of prediction scale differences, following Johnson's (1980) perception that animals select resources by first choosing larger home ranges or areas that meet an animal's general needs (landscape scale), and subsequently select finer scale attributes necessary for more specific life stage requirements (seasonal scale). Hence, despite some variables having landscape-scale influences, nested seasonal scale selection likely drives some variables more strongly than others within each level (nesting, brood, inter-seasonal movement). For example, sage-grouse selecting for areas close to coyote predation while avoiding proximity to removal locations during the breeding and brood season, and then selected areas close to removals during inter-seasonal movement. This information suggests different behavioral responses depending on life stages such that increased management for predator removal may be disturbing during courtship and nesting, but perhaps enhance other life stages (i.e. benefit chick survival, recruitment, or overwinter survival). Based on our landscape scale assessment and between-site variable coefficient comparisons, we determined that the level of disruption a given anthropogenic features poses is highly variable and site specific.

Sage-grouse are clearly sensitive to proximity to roads and well density across both fine-scale seasonal and landscape level spatial extents. The issue is complicated by

the variability in the magnitude and direction of these effects across sites and among seasons. One possible explanation is that this may reflect a behavioral response to a disturbing feature (Forman and Alexander 1998) through tolerance of road presence while maintaining avoidance of the activities roads facilitate (human traffic, OHV use, predator travel routes, etc.). Alternatively, because anthropogenic disturbance can have accumulating effects (Johnson et al. 2011), sage-grouse sensitivity to predator management may contain a functional threshold, which once surpassed produces observable behavioral shifts in selection and space use. We did not directly measure human use or differences in the amount of traffic between sites, so it is unclear if discrepancies between selection and avoidance of roads is related to use (e.g. if use was low at our study sites compared to road use in other studies). Similar to previous research, we observed sage-grouse avoided areas with greater density of well sites (Aldridge and Boyce 2007) at both annual (second order) and seasonal (third order) scales, with particular avoidance during breeding.

We quantified sage-grouse home range size and habitat selection in Bighorn Basin at two spatial scales by examining space use over annual (landscape scale) and seasonal (patch scale) time periods. We produced a framework for examining resource selection between sites with differing levels of predator management, and among biologically important seasons, providing managers with valuable information to enhance the management of sage-grouse populations. By conducting our study in Bighorn Basin simultaneous to a predator removal experiment examining vital rate responses, we could examine the question of whether intensifications in management and human presence impacted sage-grouse behavior (home range, seasonal movement, and habitat selection).

As a baseline component for determining habitat use, home range has important considerations for resource selection modeling. We observed a negative association between annual home range size and predator management. Congruently, Whitaker et al. (2007) identified home range reductions when human disturbance was reduced (hunting closure) for ruffed grouse (*Bonasa umbellus*), suggesting that alterations in home range size can be relative to human factors beyond just resource availability or limitation. We also observed substantively less variation in brood range size in the high management site compared to the relatively equal variation in both the moderate and control sites. While variation could have been influenced by our small sample size, site sample sizes were nearly equivalent. Alternative to expected inverse relationships to resource availability, it is possible the observed smaller ranges and low variability were indicative of disturbing activity restricting habitat availability. It follows that the identification of factors associated with variation in home range size could help identify resource limitations or disruptive activity (Whitaker et al. 2007).

Our models should be seen as a preliminary tool to understand the impacts predator management can have on sage-grouse and can be used to inform management and conservation decisions in Bighorn Basin. Our development of models that incorporated unique variables associated with anthropogenic features in conjunction with a predator removal experiment (Chapter 2) shows promise for integrating a more complete understanding of the impacts a recommended management action can have on sage-grouse populations. Though our focal species for this study was the sage-grouse, application of our modeling concept could enhance the management of other rare and declining galliformes. For example, Pitman et al. (2005) reported that anthropogenic

features were important in determining nest site selection by lesser prairie-chicken (*Tympanuchus pallidicinctus*) and that nest success was best predicted by the interaction of nest site vegetation and distance to anthropogenic features. We posit that expanding current habitat selection modeling to incorporate different temporal and spatial scale anthropogenic features coupled with predator population metrics could provide insight into the management of other declining species like lesser prairie-chicken. This approach allows meaningful identification of those variables beyond habitat characteristics most strongly associated with resource selection.

Sage-grouse declines invariably include a multitude of complex interactions (Crawford et al. 2004, Moss et al. 2004, Hagen 2011). The impacts anthropogenic features and higher levels of predator management produce will be population specific and, based on our findings, vary within a given population spatially and temporally across sage-grouse life stages. Thus identifying changes in behavior as they relate to both habitat resources and human activities is imperative to test and understand to propagate the most effective management for a specific population's system. Management actions must consider crucial habitat for important seasonal life stages (i.e. nesting), as well as the direct and indirect impacts actions taken to improve a population's growth (i.e. predator removal) will have on behavior, habitat selection and ultimately, long-term persistence.

LITERATURE CITED

ALDRIDGE, C.L., AND M.C. BOYCE. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17:508-526.

- ALDRIDGE, C.L., AND M.C. BOYCE. 2008. Accounting for fitness: combining survival and selection when assessing wildlife –habitat relationships. *Israel Journal of Ecology and Evolution* 54:389-419.
- ALDRIDGE, C.L., S.E. NIELSEN, H.L. BEYER, M.S. BOYCE, J.W. CONNELLY, S.T. KNICK, AND M.A. SCHROEDER. 2008. Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions* 14:983-994.
- ALDRIDGE, C.L., D.J. SAHER, T.M. CHILDERS, K.E. STAHLNECKER, AND Z.H. BOWEN. 2011. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. *Journal of Wildlife Management* 76:391-406.
- 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, AND B. BOLKER. 2011. Lme4:linear mixed-effects models using S4 classes. Version 0.999375-42. Available <<http://cran.r-project.org/web/packages/lme4/index.html>>
- BECK, J.L., AND D.L. MITCHELL. 2000. Influences of livestock grazing on sage grouse habitat. *Wildlife Society Bulletin* 28:993-1002.
- BERGER, K.M., E.M. GESE, AND J. BERGER. 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* 89:818-828.
- BEYER, H. [ONLINE]. 2012. Geospatial Modelling Environment (software version 0.7.2.0).<<http://spatialecology.com/gme>> (5 January 2013).

- BLICKLEY, J.L., D. BLACKWOOD, AND G.L. PATRICELLI. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. *Conservation Biology* 26:461-471.
- BOLKER, B.M., M.E. BROOKS, C.J. CLARK, S.W. GEANGE, J.R. POULSEN, M.H.H. STEVENS, AND J.S.S. WHITE. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127-135.
- BOYCE, M.S., AND L.L. MCDONALD. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution* 14:268-272.
- BRAUN, C.E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association of State Fish and Wildlife Agencies* 78:139-156.
- BRAUN, C.E., O.O. OEDEKOVEN, AND C.L. ALDRIDGE. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. *Transactions of the North American Wildlife and Natural Resources Conference* 67: 334-349.
- BRUCE, J.R., W.D. ROBINSON, S.L. PETERSON, AND R.F. MILLER. 2011. Greater sage-grouse movements and habitat use during winter in central Oregon. *Western North American Naturalist* 71:418-424.
- BURNETT, A.C. 2012. Modeling habitat use of a fringe greater sage-grouse population at multiple spatial scales. Thesis, Utah State University, Logan, UT.

- BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York.
- COATES, P.S., AND D.J. DELEHANTY. 2004. The effects of raven removal on sage grouse nest success, p. 17-20. *In* Proceedings of the 21st Vertebrate Pest Conference, University of California, Davis, CA.
- CONNELLY, J.W., AND C.E. BRAUN. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- CONNELLY, J.W., M.A. SCHROEDER, A.R. SANDS, AND C.E. BRAUN. 2000. Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967-985.
- 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, Cheyenne, WY.
- CRAWFORD, J.A., R.A. OLSON, N.E. WEST, J.C. MOSLEY, M.A. SCHROEDER, T.D. WHITSON, R.F. MILLER, M.A. GREGG, AND C.S. BOYD. 2004. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2-19.
- 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.

- DRUT, M.S., J.A. CRAWFORD, AND M.A. GREGG. 1994. Brood habitat use by sage grouse in Oregon. *Western North American Naturalist* 54:170-176.
- DZIALAK, M.R., C.V. OLSON, S.M. HARJU, S.L. WEBB, J. P. MUDD, J.B. WINSTEAD, AND L.D. HAYDEN-WING. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. *PLoS ONE* 6:e26273. doi: 10.1371/journal.pone.0026273.
- DZIALAK, M.R., C.V. OLSON, S.M. HARJU, S.L. WEBB, AND J.B. WINSTEAD. 2012. Temporal and hierarchical spatial components of animal occurrence: conserving seasonal habitat for greater sage-grouse. *Ecosphere* 3(4):1-17.
- 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.
- ELLIS-FELEGE, S.N., M.J. CONROY, W.E. PALMER, AND J.P. CARROLL. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. *Journal of Applied Ecology* 49:661-669.
- ENG, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. *Journal of Wildlife Management* 19:267-272.
- FEDY, B.C., AND C.L. ALDRIDGE. 2011. The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. *Journal of Wildlife Management* 75:1022-1033.
- FISCHER, R.A., AND K.P. REESE. 1996. Influence of vegetal moisture content and nest fate on timing of female sage grouse migration. *The Condor* 98:868-872.

- FORMAN, R.T.T., AND L.E. ALEXANDER. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207-231.
- GARSHELIS, D.L. 2000. Delusions in habitat evaluation: measuring use, selection and importance, p. 111-164. *In* L. Boitani and T.K. Fuller [EDS], *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, NY.
- GIESEN, K.M., T.J. SCHOENBERG, AND C.E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- GREENWOOD, R.J., A.B. SARGENT, D.H. JOHNSON, L.M. COWARDIN, AND T.L. SHAFFER. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. *Wildlife Monographs* 128:1-57.
- GESSLER, P.E., I.D. MOOR, N.J. MCKENZIE, AND P.J. RYAN. 1995. Soil-landscape modeling and spatial prediction of soil attributes. *International Journal of Geographical Information Science* 9:421-432.
- HAGEN, C.A. 2011. Predation of greater sage-grouse: facts, process, and effects. *Studies in Avian Biology* 38:95-100.
- HAGEN, C.A., J.W. CONNELLY, AND M.A. SCHROEDER. 2007. A meta-analysis of greater sage-grouse (*Centrocercus urophasianus*) nesting and brood-rearing habitats. *Wildlife Biology* 13:42-50.
- HANSER, S.E. [ONLINE]. 2006. Proportion of sagebrush land cover (18-km scale) in the western US. USGS- Snake River Field Station, Boise, ID. <<http://sagemap.wr.usgs.gov>> (5 May 2013).

- HANSER, S.E. [ONLINE]. 2007. Oil and gas wells in the western United States. USGS-Snake River Field Station, Boise, ID.<<http://sagemap.wr.usgs.gov>> (5 May 2013).
- HEBBLEWHITE, M., AND E.H. MERRILL. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152:337-387.
- HEBBLEWHITE, M., AND E. MERRILL. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45:834-844.
- HEEZEN, K.L., AND J.R. TESTER. 1967. Evaluation of ratio-tracking by triangulation with special reference to deer movements. *Journal of Wildlife Management* 31:124-141.
- HESS, J. E., AND J. L. BECK. 2012*a*. Burning and mowing Wyoming big sagebrush: do treated sites meet minimum guidelines for greater sage-grouse breeding habitats? *Wildlife Society Bulletin* 36(1):85-93.
- HESS, J.E., AND J.L. BECK. 2012*b*. Disturbance factors influencing greater sage-grouse lek abandonment in north-central Wyoming. *Journal of Wildlife Management* 76:1625-1634.
- HOLLORAN, M.J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, WY.
- HOLLORAN, M.J. AND S.H. ANDERSON. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. *The Condor* 107(4):742-752.

- HOMER, C.G., T.C. EDWARDS, R.D. RAMSEY, AND K.P. PRICE. 1993. Use of remote sensing methods in modeling sage grouse winter habitat. *Journal of Wildlife Management* 57(1):78-84.
- HOSMER, D.W., AND S. LEMESHOW. 2000. *Applied logistic regression*. Second edition. John Wiley and Sons, New York, NY.
- KNICK, S.T., D.S. DOBKIN, J.T. ROTENBERRY, M.A. SCHROEDER, W.M. VANDER HAEGEN, AND C. VAN RIPER, III. 2003. Teetering on the edge of too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.
- JOHNSON, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- JOHNSON, D.H., M.J. HOLLORAN, J.W. CONNELLY, S.E. HANSER, C.L. AMUNDSON, AND S.T. KNICK. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007, p 407 – 450. *In* S.T. Knick and J.W. Connelly [EDS.], *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. *Studies in Avian Biology* 38. University of California Press, Berkeley, CA.
- LYON, A.G., AND S.H. ANDERSON. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486-491.
- MANLY, B.F.J., 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*. Second edition. Kluwer Academic, Norwell, MA.

- MANZER, L.D., AND S.J. HANNON. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. *Journal of Wildlife Management* 69(1):110-123.
- MEZQUIDA, E.T., S.J. SLATER, AND C.W. BENKMAN. 2006. Sage-grouse and indirect interactions: potential implications of coyote control on sage-grouse populations. *The Condor* 108:747-759.
- MOSS, R., I. STORCH, AND M. MULLER. 2010. Trends in grouse research. *Wildlife Biology* 16:1-11.
- MUSIL, D.D., J.W. CONNELLY, AND K.P. REESE. 1993. Movements, survival, and reproduction of sage grouse translocated in central Idaho. *The Journal of Wildlife Management* 57:85-91.
- NASA LAND PROCESSES DISTRIBUTED ACTIVE ARCHIVE CENTER (LP DAAC), MODIS TERRA: MOD13Q1. [ONLINE]. USGS-2006 National Land Cover Database land cover map. USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, SD. <https://lpdaac.usgs.gov/data_access> (1 June 2013).
- NELL, P.J., K.P. REESE, AND J.W. CONNELLY. 2000. Long-term effects of fire on sage grouse habitat. *Journal of Range Management* 53:586-591.
- NEILSEN, C.K., AND A. WOOLF. 2001. Spatial organization of bobcats (*Lynx rufus*) in southern Illinois. *The American Midland Naturalist* 146:43-52.
- NIELSON, R.P., J.M. LENIHAN, D. BACHET, AND R.J. DRAPEK. 2005. Climate change implications for sagebrush ecosystems, p. 145-159. *In* Transactions of the

70th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington, DC.

PATTERSON, R.L. 1952. The sage grouse in Wyoming. Sage Books, Denver, CO.

POWELL, R.A. 2000. Animal home ranges and territories and home range estimators, p. 65-110. *In* L. Boitani and T.K. Fuller [EDS.], Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, NY.

PITMAN, J.C., C.A. HAGEN, R.J. ROBEL, T.M. LOUGHIN, AND R.D. APPLGATE. 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. *Journal of Wildlife Management* 69:1259-1269.

R DEVELOPMENT CORE TEAM. [ONLINE]. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.<<http://www.R-project.org>> (1 September 2011)

SEAMAN, D.E. 1993. Home range and male reproductive optimization in black bears. Dissertation, North Carolina State University, Raleigh, NC.

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.L. MCCARTHY, J.J. MCCARTHY, D.L. MITHCHELL, E.V. RICKERSON, AND S.J. STIVER. 2004. Distribution of sage-grouse in North America. *The Condor* 106(6):363-376.

SEDINGER, J.S., G.C. WHITE, S. ESPINOSA, E.T. PARTEE, AND C.E. BRAUN. 2009. Assessing compensatory versus additive harvest mortality: an example using greater sage-grouse. *Journal of Wildlife Management* 74:326-332.

- SMITH, J.T., L.D. FLAKE, K.F. HIGGINS, G.D. KOBRINGER, AND C.G. HOMER. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. *Western North America Naturalist* 65:310-320.
- STAHLECKER, D.W., AND T.G. SMITH. 1993. A comparison of home range estimates for a bald eagle wintering in New Mexico. *Journal of Raptor Research* 27:42-45.
- SVEUM, C.M., M.D. EDGE, AND J.A. CRAWFORD. 1998. Nesting habitat selection in south-central Washington. *Journal of Range management* 51:265-269.
- USFWS. 2010. Endangered and Threatened Wildlife and Plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 50 CFR Part 17 [FWS-RS-ES-2010-00189].
- WALKER, B.L., D.E. NAUGLE, AND K.E. DOHERTY. 2007. Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management* 71:2644-2654.
- WHITAKER, D.M., D.F. STAUFFER, G.W. NORMAN, P.K. DEVERS, J. EDWARDS, W.M. GIULIANO, C. HARPER, W. IGO, J. SOLE, H. SPIKER, AND B. TEFFT. 2007. Factors associated with variation in home-range size of Appalachian Ruffed Grouse (*Bonasa umbellus*). *The Auk* 124:1407-1424.
- WHITE, G.C., AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.
- WIEBE, K.L., AND K. MARTIN. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behavior* 56:1137-1144.

Table 3.1. Variables fit to logistic models (GLMM) to predict habitat selection for greater sage-grouse (2011 – 2013) at annual or seasonal (breeding (March – May), brood (June – late August), inter-seasonal (September – November)) time scales for Bighorn Basin, Wyoming, USA. Each annual logistic model was based on 6,309 used and 19,156 available points. Each seasonal logistic model was based on 5,713 used and 17, 139 available points.

Category	Covariate	Description
Habitat features		
Land cover	landCV	GAP vegetation classes (1-arc second National Land Cover Database [NLCD] at 30 m resolution)
Shrub/grassland		Dominated by low-growing woody vegetation with aerial stems including true shrubs mixed with upland grasses and forbes
Semi-desert		Characterized by xeric shrub, grass and other woody species (sagebrush steppe)
Forest		Characterized by tree cover with overlapping crown canopy (25-100% cover)
High montane		Characterized by sub-alpine/alpine vegetation, meadows, high elevation

		shrub and forest vegetation
Agriculture		Cultivated areas characterized by food/feed/fiber production (pasture/hay, row crops, small grains, fallow)
Disturbed/developed		Dominated by abiotic substrate, scattered sparse (< 25% cover) vegetation, nonvascular vegetation (lichens/bryophytes), barren or introduced/planted species, and disturbed or developed ($\geq 30\%$ constructed materials – asphalt, concrete, buildings)land
Open water		All areas of open water – $\geq 25\%$ cover of water (per pixel)
Sagebrush density	sage_dens	Proportion of sagebrush land cover in a 18-km search radius
Stream density	stream_dens	Linear density (km/km ²) of all streams within 900m radius window
Distance to nearest stream	dist_water	Euclidean distance (km) to stream or river (quadratic)
Terrain features		
Elevation	elev	Elevation (km) calculated from a digital elevation model (DEM; 1 arc-second National Elevation Dataset [NED] at 30-m resolution)
Slope	slope	Average change in vertical elevation per unit horizontal distance (i.e.

steepness), calculated as percent rise from 30-m DEM using spatial analyst

CTI	cti	Compound topographic index calculated from slope and flow accumulation
-----	-----	--

Anthropogenic features

Distance to nearest road	dist_rds	Euclidean distance (km) to any road
Distance to nearest well	dist_wells	Euclidean distance (km) to well structure
Distance to nearest coyote removal	dist_CLremoved	Euclidean distance (km) to coyote removal event
Well pad density	well_dens	Kernel density (km/km ²) of all well pad structures within 900m radius window

Predator features

Distance to nearest predation site	dist_CLpredation	Euclidean distance (km) to coyote nest or hen predation
Distance to nearest coyote detection	dist_CLpresence	Euclidean distance (km) to coyote sign (scat, track, photograph)

^a Measure of relative risk of predation based on the density of predation events (coyote caused nest and hen kills).

Table 3.2. Average sage-grouse home range size over annual, breeding (March – May), brood rearing (June – August), and inter-seasonal (late August – early November) periods across three sites with varying levels of predator management and anthropogenic features. Fixed kernel density estimates (KDE) were used to generate 95% probability contours. Core use areas represent 25% density kernel areas. Total home ranges are 99% density kernel areas. Inter-seasonal ranges include multiple seasonal time frames as birds transitioned through areas during spring and fall. Asterisks identify significant ($\alpha = 0.10$) differences between sites.

		Home Range Size (km ²)							
Site	MCP	Annual		Breeding		Brood		Inter-seasonal	
		KDE	KDE	KDE	KDE	KDE	KDE	KDE	KDE
Management ^a	(<i>n</i> = 12)	(<i>n</i> = 12)	(<i>n</i> = 6)	(<i>n</i> = 7)	(<i>n</i> = 10)				
		Core*	Total*	Core	Total	Core	Total	Core*	Total*
Control	18.66	0.70	4.24	0.30	3.73	0.52	2.56	0.33	1.98
Moderate	401.12	4.12	27.34	0.87	9.87	0.37	3.27	1.95	18.86
High	240.51	2.20	41.66	0.92	10.88	0.13	1.24	6.48	42.00

^a Predator management level based on treatment levels for simultaneous predator removal experiment. Control site had no predator removals. Moderate management site received seasonal predator management for ungulate production. High management site received year-round predator management for domestic livestock depredation and agriculture damage with additional lethal coyote removal near sage-grouse nests (14 March – 15 June 2012).

Table 3.3. Average seasonal range distances between breeding, brood-rearing, and inter-seasonal use areas for GPS marked sage-grouse hens ($n = 12$) in Bighorn Basin, Wyoming, USA.

Site Management ^a	Life Stage Movement Distance (km)						Total Movement Distance (km)				
	Breed – Brood		Breed – Seasonal		Brood – Seasonal		\bar{x}	SD	Min	Max	Inter-Seasonal ^b (% birds)
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD					
Control	12.20 ^c	-	4.40 ^c	-	5.90	1.15	7.10	3.54	4.40	12.20	66
Moderate	35.78	24.62	30.50	8.38	15.76	5.71	28.55	17.35	10.47	59.64	81
High	16.27	3.91	13.45	1.58	3.85	2.61	12.48	7.33	2.00	21.80	80

^a Predator management level based on treatment levels for simultaneous predator removal experiment. Control site had no predator removals. Moderate management site received seasonal predator management for ungulate production. High management site received year-round predator management for domestic livestock depredation and agriculture damage with additional lethal coyote removal near sage-grouse nests (14 March – 15 June 2012).

^b Proportion of all marked (VHF and GPS, $n = 57$) hens

^c From one individual

Table 3.4. Fit statistics for models incorporating anthropogenic, predator, habitat, terrain, and all variable (habitat+terrain+anthropogenic+predator) logistic mixed effect models explaining annual resource selection for sage-grouse in Bighorn Basin, Wyoming, USA 2011 – 2013. Each logistic model had random intercepts for individual bird ($n = 12$) and was based on 6,309 used and 19,156 available points. Models are ranked by the change in Akaike Information Criterion corrected for small sample size (ΔAIC_c) values. For each logistic model we report K (number of parameters in the model), LL (log-likelihood), and Akaike weights (w_i , the likelihood the model is the best of those evaluated).

Model	Model structure	K	LL	AIC_c	ΔAIC_c	w_i
full1	dist_CLpredation ^a + dist_CLpresence ^b + dist_CLremoved ^c + dist_rds ^d + dist_wells ^e + well_den ^f + cti ^g + elev ^h + slope ⁱ + dist_water ^j + dist_water ² + stream_dens ^k + sage_dens ^l + landCV ^m + site ⁿ	21	-8509.65	17061.36	0.00	1.00
full5	dist_CLpresence + dist_CLremoved + dist_rds + dist_wells + well_den + cti + elev + slope + dist_water + dist_water ² + stream_dens + sage_dens + landCV + site	20	-8528.14	17096.33	34.97	0.00
terrain1	cti + elev + slope + site	7	-9942.40	19898.80	2837.44	0.00

anthro4	dist_CLremoved + dist_rds + dist_wells + well_den + site	8	-13064.09	26144.19	9082.83	0.00
habitat2	dist_water + dist_water ² + sage_dens + stream_dens + landCV + site	14	-13278.70	26585.41	9524.05	0.00
pred3	dist_CLpredation + dist_CLpresence + site	6	-13472.50	26957.01	9895.65	0.00
null	random intercept (individual bird)	2	-14256.62	28517.25	11455.8	0.00

9

^a Euclidean distance (km) to coyote nest or hen predation	^h Elevation (km)
^b Euclidean distance (km) to coyote sign (scat, track, photograph)	ⁱ Percent rise
^c Euclidean distance (km) to coyote removal event	^j Euclidean distance (km) to stream or river
^d Euclidean distance (km) to any road	^k Linear density (km/km ²) of all streams
^e Euclidean distance (km) to well structure	^l Proportion of sagebrush land cover
^f Kernel density (km/km ²) of all well pad structures	^m GAP vegetation classes
^g Compound topographic index	ⁿ Control, moderate, high predator management

Table 3.5. Fit statistics for models incorporating anthropogenic, predator, habitat, terrain, and all variable (habitat+terrain+anthropogenic+predator) logistic mixed effect models explaining seasonal range resource selection for sage-grouse in Bighorn Basin, Wyoming, USA 2011 – 2013. Seasons were defined as breeding (March – May), brood (June – late August), inter-seasonal (September – November). Each logistic model had random intercepts for site ($n = 3$) and individual bird ($n = 12$), and was based on 5,713 used and 17, 139 available points. Models are ranked by the change in Akaike Information Criterion corrected for small sample size (ΔAIC_c) values. For each logistic model we report K (number of parameters in the model), LL (log-likelihood), and Akaike weights (w_i , the likelihood the model is the best of those evaluated).

Model	Model structure	K	LL	AIC_c	ΔAIC_c	w_i
full1	dist_CLpredation ^a + dist_CLpresence ^b + dist_CLremoved ^c + dist_rds ^d + dist_wells ^e + well_den ^f + cti ^g + elev ^h + slope ⁱ + dist_water ^j + dist_water ² + stream_dens ^k + sage_dens ^l + landCV ^m + season ⁿ	23	-8638.61	17323.30	0.00	0.54
full5	dist_CLpresence+ dist_CLremoved + dist_rds + dist_wells + well_den + cti + elev + slope + dist_water + dist_water ² + stream_dens + sage_dens + landCV + season	22	-8639.76	17323.59	0.29	0.46

full 3	dist_CLpredation + dist_CLpresence + dist_CLremoved + well_den + cti + elev + slope + dist_water + dist_water ² + stream_dens + sage_dens + landCV + season	20	-8661.16	17362.38	39.09	0.00
terrain1	cti + elev + slope + season	6	-8890.85	17793.70	470.40	0.00
habitat2	dist_water + dist_water ² + sage_dens + stream_dens + landCV + season	14	-12147.78	24323.59	7000.29	0.00
anthro4	dist_CLremoved + dist_rds + dist_wells + well_den + season	9	-12403.38	24824.77	7501.47	0.00
pred3	dist_CLpredation + dist_CLpresence + season	7	-12428.86	24871.72	7548.43	0.00
null	random intercepts (individual bird and site)	3	-12434.35	24874.71	7551.41	0.00

^a Euclidean distance (km) to coyote nest or hen predation

^b Euclidean distance (km) to coyote sign (scat, track, photograph)

^c Euclidean distance (km) to coyote removal event

^d Euclidean distance (km) to any road

^e Euclidean distance (km) to well structure

^f Kernel density (km/km²) of all well pad structures

^g Compound topographic index

^h Elevation (km)

ⁱ Percent rise

^j Euclidean distance (km) to stream or river

^l Linear density (km/km²) of all streams

^m Proportion of sagebrush land cover

ⁿ GAP vegetation classes

^o Breed, brood, or seasonal

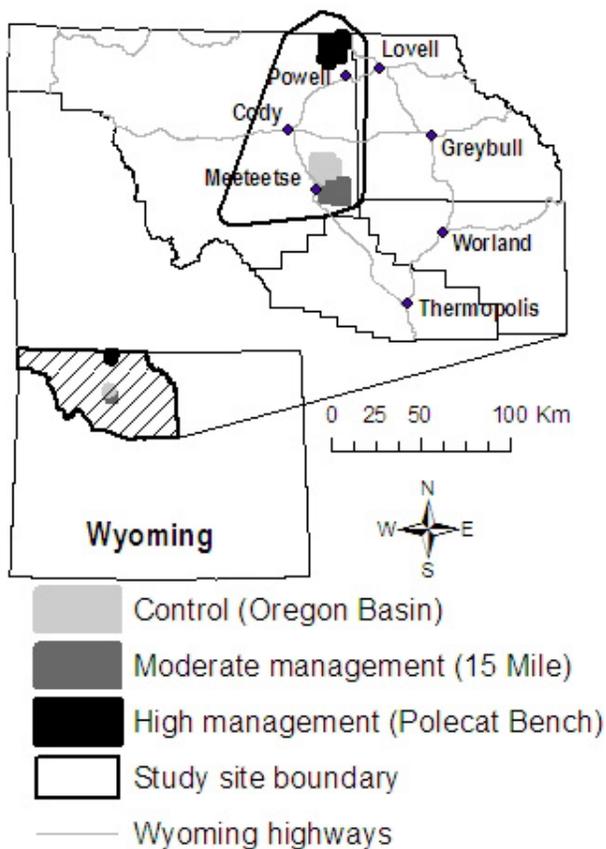


Figure 3.1. Location of our study of anthropogenic impacts on greater sage-grouse habitat selection and space use in Bighorn Basin, Wyoming, USA 2011 – 2013. We implemented resource selection modeling in conjunction with a predation study to evaluate the effects of anthropogenic features related to different levels of predator management at three sites with subsequent no (Oregon Basin), moderate (15 Mile), and high (Polecat Bench) predator management levels.

CHAPTER 4

CONCLUSION

The purpose of this thesis research was to evaluate predator removal and predation effects on sage-grouse survival, nest success, and space use. The objectives of my research were achieved by quantifying data on the types and impacts of predators on sage-grouse hen survival and nest success (Chapter 2), observing the response of important demographic variables to alterations in predator communities (Chapter 2), and examining sage grouse home range, inter-seasonal movement patterns, and habitat selection relative to predator management and anthropogenic features (Chapter 3).

My results suggest the application of coyote removal as a treatment to enhance sage-grouse growth in Bighorn Basin provides little benefit to nest success and only improves survival over the time period treatment is applied, relegating the overall effectiveness in protecting populations to a short-term basis in Bighorn Basin. My results also suggest that the short-term intensifications in management associated with the implementation of a predator removal scheme may disturb sage-grouse space use and habitat selection during critical life stages of breeding (lek attendance and nesting), brood rearing, and inter-seasonal movement (recruitment and overwinter survival). Although we were able to identify alterations in inter-seasonal movement behavior, home range size, and habitat selection as it relates to both short and long-term anthropogenic features, the scale and threshold at which these mechanisms act to inhibit sage-grouse populations is less clear. Whether the driving force behind changes in sage-grouse space use and habitat selection is from direct (i.e. survival, nest success, recruitment) or indirect (altered

predation patterns or predation risk) processes relative to specific management practices needs to be examined further.

My research provides information quantifying the effects of predator removal on sage-grouse in Bighorn Basin by taking an experimental approach to understand direct predator impacts on vital demographic parameters and behavioral responses. This study attempted to advance our knowledge of sage-grouse ecology by conducting a field experiment to understand, identify, and monitor changes in both sage-grouse and predator populations. The development and use of models that incorporate unique variables associated with management and anthropogenic features shows promise for identifying changes in behavior as they relate to both habitat resources and proposed management, propagating the best management possible for sage-grouse populations. By conducting this study via a simultaneous predator removal experiment with spatial analysis components, I could examine the question of whether management and human presence impacted sage-grouse vital rates and spatial ecology in Bighorn Basin. Thus, advancing our abilities to test management options, expand our perspective on an action's effectiveness, and reach conservation and management goals.

Identifying the role predation plays in a specific population's system is imperative to test and understand in order to provide the most effective management possible. This study attempted to tease apart complex predator-prey interactions relative to changes in predator community structure and behavior. While my study suggests predator removal does not benefit nest success, and provides only a short-term improvement in survival, the time frame and natural annual variation may have prevented long-term or time-lag effects (positive or negative) from emerging in the parameters measured. There is still the

potential that removal of key predators during specific life stages other than nesting, or over increased time periods could produce benefits to sage-grouse populations through other parameters like chick survival and recruitment. I had limited success in obtaining unbiased measures of predator density, abundance, or population size which would have furthered my ability to identify direct changes in predator community structure (i.e. how both coyote and other predator populations change in response to removal efforts), detect the presence of mesopredator release, or distinguish density-dependent cycles. It is also conceivable altered predator community structure and distribution will respond to anthropogenic influences at a yet unreached threshold, and understanding the way predator-prey relationships are determined by human land use will be imperative to the effective use of predator management as a conservation tool in sage-grouse management in Bighorn Basin or other systems. Continued efforts and time are needed to determine if management actions can produce measureable changes in the context of other environmental and habitat fluctuations inherent in natural systems. By taking an experimental approach to examining the effects of predation and predator removal, my study advances our current knowledge of sage-grouse ecology by identifying changes in demographic vital rates, habitat resources, and the effects of proposed management, allowing managers to make informed decisions and provide the best management strategy possible for sage-grouse populations.

APPENDICES

APPENDIX A

Table S1. Species visitation to scent station surveys conducted pre- (14 Mar – 14 Jun) and post-treatment (20 Jun – 10 Aug) at three sites in Bighorn Basin, Wyoming, USA in 2012. Treatment was lethal removal of coyotes to determine the effects on greater sage-grouse.

Site	Total visits	Coyote	Fox	Bobcat	Skunk	Raccoon	Badger	Dog	Cat	Weasel	Lagomorph
Heavy Treatment											
pre	52	4	1	0	1	0	0	2	0	0	10
post	108	2	1	0	0	1	1	0	1	0	6
Moderate Treatment											
	124	3	4	2	0	0	2	0	0	1	12

pre

post	77	3	0	1	0	0	0	0	1	0	6
------	----	---	---	---	---	---	---	---	---	---	---

Control (No Treatment)

pre	110	2	2	0	0	0	1	0	0	0	8
-----	-----	---	---	---	---	---	---	---	---	---	---

post	92	11	1	0	0	0	1	0	0	0	16
------	----	----	---	---	---	---	---	---	---	---	----

Table S2. Avian predator detections from point count surveys conducted pre (13 Mar – 14 Jun) and post (26 Jun – 11 Aug) coyote removal as part of predation study on greater sage-grouse at three sites in Bighorn Basin, Wyoming, USA in 2012.

Common name	Scientific name	# Detections		# Points
		Pre	Post	species detected
Raptors				
Golden eagle	<i>Aquila chrysaetos</i>	31	27	32
Bald eagle	<i>Haliaeetus leucocephalus</i>	1	0	1
Red-tailed hawk	<i>Buteo jamaicensis</i>	4	3	6
Northern harrier	<i>Circus cyaneus</i>	5	14	14
American kestrel	<i>Falco sparverius</i>	23	42	18
Prairie falcon	<i>Falco mexicanus</i>	1	0	1
Corvidae				
Common raven	<i>Corvus corax</i>	223	153	50
Pinyon jay	<i>Gymnorhinus cyanocephalus</i>	4	13	2
American crow	<i>Corvus brachyrhynchos</i>	1	0	1
Black-billed magpie	<i>Pica hudsonia</i>	34	35	18

Table S3. Sage-grouse nest shrub vegetal characteristics at three sites treated with coyote removal as part of predation study in Bighorn Basin, Wyoming, USA in 2012.

Site	# Nest Shrubs	Maximum width (cm)	Perpendicular width (cm)	Height (cm)	Vigor (%)	Branch density (1-5)
Control	2	106.20	82.40	55.70	57.50	3
Moderate treatment	3	105.30	80.40	51.20	59.50	3
High treatment	3	98.47	76.73	51.53	51.33	3
All	3	102.63	79.40	52.63	55.43	3

APPENDIX B

Table S1. Resource selection function parameter estimates incorporating anthropogenic, habitat, predator, and terrain variables for female sage-grouse over seasonal (breeding (March – May), brood (June – late August), inter-seasonal (September – November)) and annual ranges in Bighorn Basin, Wyoming, USA from 2011 – 2013. Each logistic model had random intercepts for individual bird ($n = 12$) and was based on 6,309 used and 19,156 available points. Each seasonal logistic model was based on 5,713 used and 17,139 available points. Bold identifies significant ($\alpha = 0.10$) variable responses. Asterisks identify similar significant response across scales and underlines identify differing significant response across scales.

Variables	Seasonal			Annual		
	β	SE	P	β	SE	P
Intercept	-2.7823	1.8109	0.1244	0.9185	1.7913	0.6081
Distance to coyote predation	0.0127	0.0083	0.1273	0.0386	0.0062	< 0.0005
<u>Distance to coyote presence</u>	-0.0234	0.0111	0.0344	0.0443	0.0081	< 0.0005
Distance to coyote removal	-0.0038	0.0134	0.7777	0.0061	0.0106	0.5644
Distance to road*	0.0922	0.0339	0.0066	0.3513	0.0475	< 0.0005
Distance to well	0.0381	0.0143	0.0077	0.0109	0.0141	0.4394
Well density*	-1.7464	0.4054	< 0.0005	-1.2560	0.3107	< 0.0005
Distance to water *	1.9370	0.1563	< 0.0005	2.6203	0.1668	< 0.0005

Distance to water ² *	-0.6077	0.0573	< 0.0005	-1.0144	0.0632	< 0.0005
Stream density*	1.6648	0.1701	< 0.0005	2.0352	0.1643	< 0.0005
Sage density*	1.8725	0.4389	< 0.0005	1.1850	0.3088	< 0.0005
Land Cover ^a						
Semi-Desert (Sagebrush)*	-0.81672	0.083	< 0.0005	-0.5181	0.0819	< 0.0005
Forest	-0.0388	0.1350	0.7740	-0.0793	0.1355	0.5584
High Montane	0.5388	2.9450	0.0032	-	-	-
<u>Agriculture</u>	-1.8124	0.2624	< 0.0005	0.7453	0.1194	< 0.0005
Disturbed/Developed	0.0422	0.1325	0.7502	-1.6188	0.2500	< 0.0005
CTI	-0.6671	1.7823	0.7082	-4.3423	2.9302	0.1384
Elevation	0.4562	0.3047	0.1343	-0.8123	0.2686	0.0025
Slope*	-16.4661	2.5618	< 0.0005	-9.1037	0.5799	< 0.0005
Season ^b						
Brood	0.0546	0.1267	0.6666	-	-	-
Seasonal	0.0455	0.0914	0.6188	-	-	-
Site ^c						
Moderate management	-	-	-	0.0291	0.0780	0.7091

High management	-	-	-	-0.4658	0.1030	< 0.0005
-----------------	---	---	---	----------------	---------------	--------------------

^a Shrub/grassland as base reference group.

^b Breeding season as base reference group.

^c Control site as base reference group.

Table S2. Resource selection function models included habitat, terrain, predator, and anthropogenic variables for female sage-grouse annual ranges at three sites with varying levels of predator management in Bighorn Basin, Wyoming, USA 2011 - 2013. Coefficient estimates were from the top performing general linearized mixed effect model with a random effect for individual bird ($n = 12$). The top logistic model predicted coefficients were based on 6,309 used and 19,156 available points. Bold identifies significant ($\alpha = 0.10$) variable responses. Asterisks identify similar significant response across sites and underlines identify differing significant response across sites.

Variables	Control			Moderate			High		
				Predator Management			Predator Management		
	β	SE	<i>P</i>	β	SE	<i>P</i>	β	SE	<i>P</i>
Intercept	-4.2777	32.2304	0.8944	-36.3118	70.9853	0.6090	-5.6926	3.0799	0.0646
Distance to coyote predation *	0.1301	0.0436	0.0029	0.2467	0.0315	< 0.0005	-0.0409	0.0269	0.1277

<u>Distance to coyote presence</u>	-0.1185	0.0424	0.0052	-0.1367	0.0443	0.0020	0.1947	0.0319	< 0.0005
<u>Distance to coyote removal</u>	-0.1696	0.0451	< 0.0005	0.2376	0.0328	< 0.0005	-0.3794	0.0400	< 0.0005
<u>Distance to road</u>	-2.0369	0.1330	< 0.0005	0.4132	0.1093	< 0.0005	1.2044	0.0914	< 0.0005
<u>Distance to well</u>	-0.3867	0.0650	< 0.0005	-0.3476	0.0444	< 0.0005	0.3789	0.0521	< 0.0005
Well density*	-0.4446	1.2444	0.7209	-1.7455	1.0128	0.0848	0.0449	0.4492	0.9204
Distance to water*	3.7324	0.6129	< 0.0005	6.4244	0.6507	< 0.0005	1.3942	0.2343	< 0.0005
Distance to water ² *	-2.8283	0.7583	< 0.0005	-3.3473	0.6351	< 0.0005	-0.8485	0.0816	< 0.0005
Stream density*	3.6722	0.3135	< 0.0005	3.3688	0.3995	< 0.0005	-0.0053	0.3462	0.9879
Sage density*	-22.5817	3.8390	< 0.0005	-7.7642	1.9223	< 0.0005	-1.8722	0.5004	< 0.0005
Land Cover ^a									

Semi-Desert (Sagebrush)*	-0.2876	0.1580	0.0687	-1.1715	0.1478	< 0.0005	-0.0850	0.1962	0.6647
<u>Forest</u>	0.3824	0.2009	0.0570	-1.5945	0.3352	< 0.0005	-0.3727	0.7925	0.6382
<u>Agriculture</u>	0.1424	0.4676	0.7607	-1.0762	0.3614	0.0029	0.9865	0.2349	< 0.0005
Disturbed/Developed*	-0.8138	0.5066	0.1082	-2.3523	0.3581	< 0.0005	-1.1601	0.5686	0.0413
CTI	13.1704	54.6006	0.8094	84.0111	121.0294	0.4876	-3.7265	3.6677	0.3096
<u>Elevation</u>	6.6886	0.9815	< 0.0005	-6.0034	0.7957	< 0.0005	5.0001	1.4295	< 0.0005
Slope*	-7.8057	0.8983	< 0.0005	-5.6598	0.9219	< 0.0005	-22.6513	2.3930	< 0.0005

^a Shrub/grassland as base reference group.

Table S3. Resource selection function models included habitat, terrain, predator, and anthropogenic variables for female sage-grouse across three seasons (breeding (March – May), brood (June – late August), seasonal (September – November)) in Bighorn Basin, Wyoming, USA 2011 - 2013. Coefficient estimates were from the top performing general linearized mixed effect model with a random effect for individual bird ($n = 12$) and site ($n = 3$). The top logistic model predicted coefficients were based on 5,713 used and 17, 139 available points. Bold identifies significant ($\alpha = 0.10$) variable responses. Asterisks identify similar significant response across seasons and underlines identify differing significant response across seasons.

Variables	Breeding			Brood			Seasonal		
	β	SE	P	β	SE	P	β	SE	P
Intercept	-13.5333	48.0048	0.7780	18.7093	85.8673	0.8275	-4.3171	2.4847	0.0823
<u>Distance to coyote predation</u>	-0.1951	0.0448	< 0.0005	-0.2083	0.0432	< 0.0005	0.1791	0.0243	< 0.0005
Distance to coyote presence	-0.7145	0.0634	< 0.0005	0.0084	0.0718	0.9066	-0.0221	0.0360	0.5393

<u>Distance to coyote removal</u>	0.2296	0.0310	< 0.0005	0.1138	0.0506	0.0246	-0.1199	0.0448	0.0075
<u>Distance to road</u>	0.0109	0.1028	0.9150	0.5461	0.0574	< 0.0005	-0.5768	0.1807	0.0014
<u>Distance to well</u>	0.7229	0.0495	< 0.0005	-0.2175	0.0570	< 0.0005	0.1402	0.0659	0.0334
Well density	-3.1978	0.7802	< 0.0005	-1.2122	4.2537	0.7757	1.0735	0.7386	0.1461
Distance to water*	1.7979	0.2913	< 0.0005	1.1430	0.3241	< 0.0005	0.7795	0.5505	0.1567
Distance to water ^{2*}	-0.4599	0.0916	< 0.0005	-0.6125	0.1504	< 0.0005	-0.7608	0.3200	0.0174
Stream density	-0.2349	0.3318	0.4790	2.0708	0.3413	< 0.0005	0.3382	0.4650	0.4670
<u>Sage density</u>	11.0730	1.5207	< 0.0005	-24.7216	3.8690	< 0.0005	1.3519	0.9697	0.1633
Land Cover ^a									
<u>Semi-Desert (Sagebrush)</u>	0.4166	0.2457	0.0900	-1.3592	0.1231	< 0.0005	-0.3858	0.1820	0.0340

Forest	0.4089	0.4633	0.3770	-0.0461	0.1912	0.8096	0.5261	0.3138	0.0936
High Montane	-	-	-	2.1289	7.8650	< 0.0005	-	-	-
Agriculture*	-0.7284	0.4536	0.1080	-1.4234	0.4386	0.0012	-1.8500	0.6364	0.0037
Disturbed/Developed	1.7851	1.1593	0.1240	-0.4505	0.1801	0.0124	0.4446	0.3048	0.1446
CTI	-21.9146	49.7941	0.6600	5.1570	89.1655	0.9539	-1.9571	2.1544	0.3637
<u>Elevation</u>	15.1207	1.0725	< 0.0005	-5.7106	0.6905	< 0.0005	2.3408	0.8494	0.0059
Slope*	-23.0935	5.5301	< 0.0005	4.1452	3.7697	0.2715	-65.3819	8.3099	< 0.0005

^a Shrub/grassland as base reference group.