8-2013

Common Raven Density and Greater Sage-Grouse Nesting Success in Southern Wyoming: Potential Conservation and Management Implications

Jonathan B. Dinkins
Utah State University

Recommended Citation

Dinkins, Jonathan B., "Common Raven Density and Greater Sage-Grouse Nesting Success in Southern Wyoming: Potential Conservation and Management Implications" (2013). *All Graduate Theses and Dissertations*. 1700.
https://digitalcommons.usu.edu/etd/1700

COMMON RAVEN DENSITY AND GREATER SAGE-GROUSE NESTING SUCCESS IN SOUTHERN WYOMING: POTENTIAL CONSERVATION AND MANAGEMENT IMPLICATIONS

by

Jonathan B. Dinkins

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

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

Approved:

Michael R. Conover Co-Major Professor	Shandra Nicole Frey Co-Major Professor
David N. Koons Committee Member	Terry A. Messmer Committee Member
Wayne A. Wurtsbaugh Committee Member	Mark R. McLellan Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2013

ABSTRACT

Common Raven Density and Greater Sage-Grouse Nesting Success in Southwest Wyoming: Potential Conservation and Management Implications

by

Jonathan B. Dinkins, Doctor of Philosophy

Utah State University, 2013

Major Professors: Dr. Michael R. Conover and Dr. Shandra Nicole Frey
Department: Wildland Resources

My research was focused on greater sage-grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) nest-site selection, nest success, and hen survival in relation to avian predators. The trade-off between using habitat and avoiding predators is a common decision for prey species including sage-grouse. In Chapter 2, I compared avian predator densities at sage-grouse nest and brood locations to random locations. Sage-grouse were located where densities of small, medium, and large avian predators were 65–68% less than random locations.

The effects of anthropogenic and landscape features on habitat use of sage-grouse hens have not been evaluated relative to avian predator densities. In Chapter 3, I compared anthropogenic and landscape features and avian predator densities among sage-grouse locations (nest, early-brood, late-brood) and random locations. I found sage-grouse hens chose locations with lower avian predator densities compared to random locations, and selected locations farther away from anthropogenic and landscape features.

Depredation of sage-grouse nests can be an influential factor limiting their productivity. Predator removal has been simultaneously proposed and criticized as a potential mitigation measure for low reproductive rates of sage-grouse. In Chapter 4, I hypothesized that sage-grouse nest success would be greater in areas where Wildlife Services lowered common raven (*Corvus corax*: hereafter “raven”) density. I found that Wildlife Services decreased raven density by 61% during 2008–2011 but I did not detect a direct improvement to sage-grouse nest success. However, sage-grouse nest success was 22% when ravens were detected within 550 m of a sage-grouse nest and 41% when no raven was detected within 550 m. In Chapter 5, I assessed interactive effects of corvid densities relative to anthropogenic and landscape features on sage-grouse nest success. I found that sage-grouse nest success was positively correlated with rugged habitat.

Survival of breeding-age birds is the most important demographic parameter driving sage-grouse abundance. In Chapter 6, I evaluated the effect of raptor densities, proximity to anthropogenic and landscape features, and hen behavior on survival of sage-grouse hens. I found that sage-grouse hen survival was negatively correlated with golden eagle (*Aquila chrysaetos*) density, proximity to anthropogenic and landscape features, and hen parental investment (nesting and brood-rearing).

(311 pages)

PUBLIC ABSTRACT

Common Raven Density and Greater Sage-Grouse Nesting Success in Southwest Wyoming: Potential Conservation and Management Implications

by

Jonathan B. Dinkins, Doctor of Philosophy

Utah State University, 2013

Declines in the distribution and abundance of greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") in western North America over the past century have been severe. The goal of my research was to increase the understanding of factors influencing where sage-grouse hens placed their nests, how common ravens (*Corvus corax*: hereafter "raven") impacted sage-grouse nest success, and whether high raptor densities negatively impacted hen survival of sage-grouse. I compared raven and raptor densities at sage-grouse nest and brood locations to available habitat. I also assessed how sage-grouse positioned their nests and broods relative to proximity to man-made structures, forested and riparian habitat, and rough topography. While evaluating the effect of ravens on nest success of sage-grouse, I hypothesized that nest success of sage-grouse would be greater in areas where Wildlife Services lowered the density of ravens. Finally, I evaluated the effect of raptor densities, proximity to man-made structures and forested and riparian habitat, rough topography, and hen behavior on survival of sage-grouse hens.

Several studies on birds have shown that avoidance of predators and dangerous habitat can have dramatic effects on habitat use by prey species. Sage-grouse hens chose locations with lower raven and raptor densities, selected locations farther away from man-made structures and forested habitat, and used locations that were flatter. Depredation of sage-grouse nests can be an influential factor limiting their populations. I found that Wildlife Services decreased raven density, but I did not detect a direct improvement to sage-grouse nest success. However, sage-grouse nest success was 22% when ravens were seen near a sage-grouse nest and 41% when no raven was seen near a sage-grouse nest. Survival of adult female sage-grouse has been demonstrated to be the most important aspect of a sage-grouse's life-cycle with respect to population growth. I found that sage-grouse hen survival was negatively related with golden eagle (*Aquila chrysaetos*) density when topography was flatter, proximity to man-made structures and forested habitat, and a hen's nesting and brood-rearing status (i.e., whether the hen was incubating eggs for caring for chicks).

ACKNOWLEDGMENTS

Research funding was provided by the Anadarko Petroleum Corporation, Jack H. Berryman Institute, Lincoln County Predator Management Board, Predatory Animal District of Sweetwater County, School of Energy Resources at the University of Wyoming, South Central Wyoming Local Sage-Grouse Work Group, Southwest Wyoming Local Sage-Grouse Working Group, Uinta County Predator Management Board, Utah Agricultural Experiment Station, Wyoming Animal Damage Management Board, Wyoming Game and Fish Department, and Wyoming Land Conservation Initiative. I especially want to thank Dr. Michael Conover and Dr. Shandra Nicole Frey, my co-advisors, for providing encouragement, direction, feedback, and the opportunity to learn throughout my graduate work. I thank my committee members, Dr. David Koons, Dr. Terry Messmer, and Dr. Wayne Wurtsbaugh, for their insight and support. I particularly want to thank Dr. Jeff Beck, honorary committee member, and Chris Kirol from the University of Wyoming for deciding to collaborate with me on several research projects. I greatly appreciate the logistical support provided by Frank Blomquist, Tom Christiansen, Tom Clayson, Justin Caudill, Matt Holloran, Neil Hymas, Ron Lockwood, Erik Norelius, Dan Oles, Lara Oles, Jeff Short, Norris Tratnik, Andy Warren, Jim Wasseen, Mark Zornes, and many others. This project could not have been completed without many field technicians including George Bowman, Jessica Boyd, Valerie Burd, Suzie Etschmaier, Mike Evans, Cooper Farr, Benjamin Funk, Emily Haug, Hillary Jones, Jessica Julien, Kraig Kelson, Rebecca Laymon, Scott Mabray, Paul Miles, Claire Polfus, Chris Potter, Zach Primeau, Rachel Pyles, Jennylyn Redner, Steve Rowbottom, Nathan

Schmitz, Kurt Smith, Nicholas Schwertner, Robert Watson, Drew White, and Micah Yarbrough. Craig Acres, Jeff Hansen, Vern Howey, Rod Merrell, and Luke Spanbauer of Wildlife Services deserve special thanks for implementing raven control, providing data, and giving feedback on the project. I thank Ted Jensen for flying for radio-collared birds in the winter. Thank you to fellow graduate students Dylan Brown, Dr. Jennifer Borgo, Dr. Michael Guttery, Michael Haney, Rebecca Ruzicka, and Tony Roberts, and volunteers Jordan Linell and Darren Johnson. I also give special thanks to the cooperation of the many landowners throughout southwest and south-central Wyoming for allowing access to private lands including John Espy, Ed Feeley (Uinta Development Company), Niels Hansen, Joe Hickey, Mike Hickey, Charley Jaure, Truman Julian, Carl Larsen, Pat O'Toole, Kathryn Sanger, Bill Taliaferro, and Ray Weber. I especially want to thank my family (Courtney, AnnaBeth, and Bridger) for encouraging me through this journey. Without their understanding, love, support, and hugs, I would not have completed this degree. My wife, Courtney, took care of our kids and me in every way imaginable; I would not have anything without her. My daughter and son were always happy to greet me with hugs after long weeks in the field. My wife's parents, Debbie and Mike Pariera, encouraged me through my graduate education. I finally want to thank my parents, Jerry and Terry Dinkins, for their help throughout my life.

Jonathan B. Dinkins

CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Greater sage-grouse (*Centrocercus urophasianus*: hereafter “sage-grouse”) distribution and abundance in western North America has declined over the last century (Connelly et al. 2004, Schroeder et al. 2004, Connelly et al. 2011). In 2000, sage-grouse inhabited approximately 56% of their range compared to pre-European settlement (Schroeder et al. 2004), and abundance has declined an average of 2% annually from 1965–2003 (Connelly et al. 2004). This decline led the U.S. Fish and Wildlife Service (2010) to conclude that sage-grouse are warranted for protection under the Endangered Species Act of 1973, but the listing was precluded because other species were at greater threat of extinction. Many factors have been attributed to this decline including reduction of quality sagebrush habitat (human development, drought, and wildfire) and factors affecting survival (i.e., predation, West Nile virus, and hunting; Braun 1998, Connelly et al. 2004, Schroeder et al. 2004, Connelly et al. 2011).

Sage-grouse are highly associated with sagebrush (*Artemisia* spp.) ecosystems, because they rely on sagebrush for food during most of the year, nesting, shelter, and escape cover (Connelly et al. 2004, Schroeder et al. 2004, Connelly et al. 2011). Loss, degradation, and fragmentation of sagebrush habitats have been detrimental to sage-grouse populations. Several studies have suggested that quantity and condition of breeding habitat is the most important factor that dictates the productivity of sage-grouse, because given adequate habitat, sage-grouse would be buffered from other threats

(Connelly et al. 1994, Braun 1998, Schroeder and Baydack 2001, Connelly et al. 2011). However, there are increasing levels of human development in sage-grouse habitat (Connelly et al. 2004, Leu et al. 2008, Doherty et al. 2010, Kirol 2012). One of the consequences of habitat modification and fragmentation associated with human development in native grouse habitats may be increased predation rates (Schroeder and Baydack 2001).

A diverse array of generalist predators have increased in distribution and abundance in sagebrush steppe habitats throughout the western United States by capitalizing on fragmented habitats and human provided resources. For example, densities of common ravens (*Corvus corax*; hereafter “ravens”) have increased in Wyoming and throughout the historic range of sage-grouse during the last century, (Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Sauer et al. 2011). Densities of generalist predators are not limited by the density of a particular species of prey (Schroeder and Baydack 2001, Evans 2004, Manzer and Hannon 2005, Coates 2007), and breeding success and survival of ground-nesting birds has been shown to be suppressed by generalist predators, such as ravens (Evans 2004, Manzer and Hannon 2005, Baxter et al. 2007, Bui et al. 2010, Coates and Delehanty 2010).

Trade-offs between using habitat and avoiding predators are common decisions for prey species. Prey species including sage-grouse may minimize risk of predation by avoiding predators, which can be achieved by using habitat with lower abundance of predators and selecting habitat with lower risk of predation (Lima 1998, Verdolin 2006, Cresswell 2008; see also Chapter 2). Thus, sage-grouse may not select optimal nesting or brood-rearing habitat when the risk of predation is high.

Sage-grouse select nest and brood sites at various scales. At the landscape scale, sage-grouse may avoid areas where there are high densities of avian predators—specifically, American kestrels (*Falco sparverius*; hereafter “kestrels”), *Buteo* hawks, black-billed magpies (*Pica hudsonia*; hereafter “magpies”), golden eagles (*Aquila chrysaetos*), northern harriers (*Circus cyaneus*; hereafter “harriers”), and ravens (Manzer and Hannon 2005, Mezquida et al. 2006, Dinkins et al. 2012). At the microhabitat scale (habitat directly surrounding a sage-grouse location—typically measured <25 m from a sage-grouse nest or brood), sage-grouse predominately choose nest sites in vegetation cover (Connelly et al. 2004). Several studies have reported that sage-grouse select nest sites based on a preference for different microhabitat characteristics, such as sagebrush density (Wallestad and Pyrah 1974, Connelly et al. 2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005, Kirol et al. 2012), and grass cover (Kaczor 2008, Kirol et al. 2012). Variability in reported microhabitat characteristic preferences of sage-grouse, with reference to nest and brood site selection, may indicate local differences in available microhabitat. Differences in available microhabitat among studies suggest that cover, in general, is important regardless of the type of vegetation cover that is available (e.g. sagebrush density, shrub height, or grass height). Alternatively, sage-grouse living in areas with different predator compositions may prefer different types of vegetation cover (Connelly et al. 2004, Coates and Delehanty 2010). Thus, the microhabitat characteristics upon which sage-grouse base their selection of nest-sites and the success of those nests may be a result of available vegetation and predator composition. For example, Coates and Delehanty (2010) found that microhabitat at sage-grouse nest-sites had a variable impact on nest depredation depending on whether a raven or a badger (*Taxidea taxus*) depredated the nest (greater cover protected from ravens, but exposed sage-grouse to greater badger depredation and vice versa).

Although reduction of quality sagebrush habitat is the driving factor that reduced populations of sage-grouse, nest success and hen survival are widely thought to be potential limiting factors for bird populations including sage-grouse (Connelly et al. 2004). Johnson and Braun (1999) and Taylor et al. (2012) found that adult hen survival was the most influential demographic parameter on sage-grouse population growth. Chick survival then nest success were the next most important factors affecting population growth for sage-grouse following adult hen survival. These conclusions may be related to the fact that sage-grouse are relatively long-lived ground-nesting birds with low productivity (Connelly et al. 2000b, Holloran et al. 2005, Connelly et al. 2011). Thus, many aspects of recruiting new individuals into a population are connected to sage-grouse hens (i.e., nest success and chick survival).

Local predator densities can affect habitat selection, nest success, survival, and parental behavior of ground-nesting birds such as prairie grouse species (Schroeder and Baydack 2001, Manzer and Hannon 2005, Coates and Delehanty 2010), farmland birds (Evans 2004), ducks (Sargeant et al. 1995), shorebirds (Smith et al. 2007), and passerines (Norrdahl and Korpimäki 1998, Roos and Pärt 2004, Thomson et al. 2006, Chalfoun and Martin 2009).

Unlike other population limiting factors (e.g., habitat condition, weather, and drought), reduction of predator numbers may be more feasible for wildlife management agencies to reduce predation rates (Cote and Sutherland 1997). For example, raven depredation of sage-grouse nests has been implicated as a potential factor limiting sage-grouse productivity in fragmented habitats (Batterson and Morse 1948, Willis et al. 1993, Gregg et al. 1994, Schroeder and Baydack 2001, Coates et al. 2008, Bui et al. 2010, Coates and Delehanty 2010). Predator removal has been simultaneously proposed and criticized as a potential mitigation measure for low reproductive rates of sage-grouse, specifically nest success. However, there are no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult), and sage-grouse have relatively high nest and adult survival rates compared to other gallinaceous birds (Connelly et al. 2011). No predator management study has provided evidence that lethal removal of predators would benefit sage-grouse on a large scale (Hagen 2011). Thus, Hagen (2011) suggested that predation was not limiting sage-grouse populations, and predator removal may only serve to provide a short-term release of predation rates in fragmented habitats and areas with human-subsidized predator populations.

Survival of breeding-age birds in relation to predator communities has been a focus of sage-grouse research and conservation. Survival and nest success related to predator communities were not likely to have been a problem during pre-European settlement because sage-grouse co-evolved with the predator communities present in sagebrush ecosystems (Schroeder et al. 1999, Schroeder et al. 2001). However, areas of habitat fragmentation and areas with human-subsidized predator populations have drastically increased in the recent past (Leu et al. 2008). For example, red fox (*Vulpes vulpes*), common raccoon (*Procyon lotor*), and raven have increased in abundance in sage-grouse habitat, especially near human activities (Connelly et al. 2000b, Baxter et al. 2007, Hagen 2011, Sauer et al. 2011). In addition, raptors and corvids use anthropogenic structures as perches and nesting structure (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010).

Sage-grouse hen survival has been related to habitat variables, such as topographic ruggedness and grass, forb, and sagebrush cover, by several studies and reviews (Connelly et al. 1994, Holloran 1999, Schroeder and Baydack 2001, Zablan et al. 2003, Moynahan et al. 2006, Kirol 2012). However, Dahlgren (2009) reported high sage-grouse hen survival rates (0.78 in a high survival year to 0.42 in a low survival year) with relatively lower quality habitat on Parker Mountain, Utah. Dahlgren (2006) described large contiguous sagebrush habitat and minimal vertical structure from human development at Parker Mountain, which may contribute to higher hen survival rates due to a lack of potential roost and nest sites for avian predators. Sage-grouse hens have been known to have high annual survival (48–78% in Wyoming; Holloran 2005, Connelly et al. 2011) with the breeding season having the lowest seasonal survival rate for sage-grouse hens (Connelly et al. 2000a).

RESEARCH OBJECTIVES

Although sage-grouse biology has been well studied, there has been little research regarding the effects of avian predator abundance on habitat selection of adult sage-grouse hens, nest success, and survival. My research provides information relative to the potential influences of avian predators on sage-grouse habitat selection, nest success, and survival of sage-grouse hens in relation to anthropogenic (oil and gas infrastructure, roads, power lines) and landscape (forested and riparian habitat and topographic ruggedness) features, and microhabitat.

In Chapter 2, I compared avian predator densities at sage-grouse nests and brood locations to available habitat. This comparison allowed me to assess the ability of sage-grouse to use locations with fewer avian predators during nesting and early brood rearing. In accordance with the predator-avoidance hypothesis, I hypothesized that at the landscape scale, sage-grouse would avoid nesting or raising broods in areas with high densities of avian predators, specifically kestrels, magpies, golden eagles, hawks (*Buteo* spp.), harriers, and ravens. Further, I hypothesized that adult survival would take precedence over nest or brood survival, and that sage-grouse habitat use would be shaped primarily by avoidance of avian predators that were a threat to adult hen survival, and secondarily by avoidance of avian predators that were a threat only to nests and broods. The effects of anthropogenic and landscape features on habitat selection of sage-grouse hens have not been evaluated in the context of avian predator abundance. In Chapter 3, I compared anthropogenic and landscape features and densities of avian predators among sage-grouse locations (nest, early-brood, late-brood) and available habitat.

Subsidized raven populations of increasing size have been anecdotally documented in southwest and south-central Wyoming associated with human activities such as livestock and natural gas development (R. J. Merrell, United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services [WS], personal communication), and raven abundance has increased in Wyoming during the past decade, 2001–2010 (Sauer et al. 2011). Raven control (lethal removal) efforts of varying intensity have been carried out by WS in Carbon, Lincoln, Sweetwater, and Uinta counties in Wyoming, 2007–2011 for the protection of livestock, which provided a unique opportunity to study the potential effects of raven removal on sage-grouse nest success. In Chapter 4, I hypothesized that sage-grouse nest success would be greater in areas where WS lowered the abundance of common ravens (*Corvus corax*: hereafter “raven”). To test this hypothesis, I assessed the change in density of ravens and sage-grouse nest success in areas associated with WS raven removal efforts and areas farther away during 2008–2011. As secondary objectives, I evaluated differences between yearling and adult sage-grouse nest success, and the effect of ravens on nest success at the sage-grouse nest level in relation to microhabitat. In Chapter 5, I tested the hypothesis that the negative effects of corvids would be amplified in areas closer to potential perches and areas with subsidized food resources (anthropogenic and landscape features).

Although avian predators have been reported to prey on sage-grouse, densities of avian predators have not been correlated with sage-grouse survival rates. For example, golden eagles have been implicated as the major sage-grouse predators (Willis et al. 1993, Connelly et al. 2000, Danvir 2002, Dahlgren 2006, Mezquida et al. 2006), and high golden eagle abundance has been suggested to decrease sage-grouse survival (Danvir 2002). However, no sage-grouse study has directly related site-specific densities of avian predators, including golden eagles, to sage-grouse hen survival. In Chapter 6, I evaluated the effect of raptor densities, proximity to anthropogenic and landscape features, and hen behavior on survival of sage-grouse hens.

The chapters of my dissertation are written as stand-alone manuscripts with Chapters 2 and 3 in the format of the Auk and Chapters 1 and 4–7 in the format of the Journal of Wildlife Management.

LITERATURE CITED

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission Fauna Service, Portland, USA.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the North American Wildlife and Natural Resources Conference 72:258–269.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, USA.

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.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Chalfoun, A. D., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497−503.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

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.

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.

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., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, California, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of

Fish and Wildlife Agencies. Unpublished Report, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, Idaho, USA.

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

Cote, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11:395–405.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

Dahlgren, D. K. 2006. Greater sage-grouse ecology and response to experimental management of mountain big sagebrush on Parker Mountain, Utah. Thesis, Utah State University, Logan, USA.

Dahlgren, D. K. 2009. Greater sage-grouse ecology, chick survival, and population dynamics, Parker Mountain, Utah. Dissertation, Utah State University, Logan, USA.

Danvir, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and

Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, 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 74:1544–1553.

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

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.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson.

2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis, South Dakota State University, Brookings, USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

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

Lammers, W. M., and M. W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.

Manzer, D. L., 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 implication of coyote control on sage-grouse populations. Condor 108:747–759.

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

Norrdahl, K., and E. Korpimäki. 1998. Fear in farmlands: how much does predator avoidance affect bird community structure? Journal of Avian Biology 29:79–85.

Prather, P. R., and T. A. Messmer. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

Roos, S., and T. Pärt. 2004. Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). Journal of Animal Ecology 73:117–127.

Sargeant, A. B., M. A. Sovada, and T. L. Shaffer. 1995. Seasonal predator removal relative to hatch rate of duck nests in Waterfowl Production Areas. Wildlife Society Bulletin 23:507–513.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M.

McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage grouse in North America. Condor 106:363–376.

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*). Birds of North America. Philadelphia, Pennsylvania, USA.

Slater, S. J., and J. P. Smith. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

Smith, P. A., H. G. Gilchrist, and J. N. M. Smith. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. Condor 109:15–31

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.

Thomson, R. L., J. T. Forsman, F. Sardà -Palomera, and M. Mönkkönen. 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. Ecography 29:507–514.

U. S. Fish and Wildlife Service. 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 75:13909–14014.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144–154.

CHAPTER 2

GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) SELECT NEST-SITES AND BROOD-SITES AWAY FROM AVIAN PREDATORS[*]

ABSTRACT.–Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) distribution and abundance in western North America has declined over the last century. Depredation of sage-grouse nests and predation of chicks can be two of the most influential factors limiting their productivity. Prey species utilize anti-predation behaviors, such as predator avoidance, to reduce the risk of predation. Birds in general balance the dual necessity of selecting cover to hide from visual and olfactory predators to enhance prospects of survival and reproductive success, which may also be achieved by selecting habitat with relatively fewer predators. I compared avian predator densities at sage-grouse nests and brood locations to random locations within available sage-grouse habitat in Wyoming. This comparison allowed me to assess the ability of sage-grouse to avoid avian predators during nesting and early brood-rearing. During 2008–2010, I conducted 10-min point-count surveys at 218 sage-grouse nests, 249 sage-grouse brood locations from 83 sage-grouse broods, and 496 random locations. I found that random locations had higher densities of avian predators compared to sage-grouse nest and brood locations. Sage-grouse nested in areas where there were lower densities of Common Ravens (*Corvus corax*), Black-billed Magpies (*Pica hudsonia*), Golden Eagles (*Aquila chrysaetos*), and *Buteo* hawks compared to random locations. Additionally, sage-grouse selected brood-rearing locations that had lower densities of the same avian

---

[*] Jonathan B. Dinkins, Michael R. Conover, Christopher P. Kirol, and Jeffrey L. Beck

predators as during nesting, plus American Kestrels (*Falco sparverius*) compared to random. By selecting nest and brood-rearing locations with lower avian predator densities, sage-grouse may reduce the risk of nest depredation and predation on eggs, chicks, and hens.

INTRODUCTION

FOOD AND RISK of predation are two factors widely thought to have important influences on the choice of breeding habitat by birds and other animals, and actual habitat choice has often been described as a trade-off between access to resources and risk of predation (Verdolin 2006). Thus, avian species may not select optimal nesting or brood-rearing habitat for foraging when the risk of predation is high. Prey species utilize anti-predation behaviors, such as predator avoidance (predator-avoidance hypothesis), to reduce the risk of predation (Cresswell 2008, and references therein). Local predator densities can affect the productivity, parental behavior, and nest-site selection of ground-nesting birds such as prairie grouse species (Schroeder and Baydack 2001, Manzer and Hannon 2005, Coates and Delehanty 2010), farmland birds (Evans 2004), ducks (Sargeant et al. 1995), shorebirds (Smith et al. 2007), and passerines (Norrdahl and Korpimäki 1998, Roos and Pärt 2004, Thomson et al. 2006, Chalfoun and Martin 2009).

Declines in Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) abundance in western North America over the last century have been severe (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004), and recently led the U.S. Fish and Wildlife Service (2010) to conclude that sage-grouse are warranted for protection under the Endangered Species Act of 1973. Many factors have contributed to this decline including habitat loss, habitat fragmentation, habitat degradation, and predation (Braun 1998, Schroeder et al. 2004). Despite the U.S. Fish and Wildlife Service's assessment, listing was precluded in favor of other species under more severe threat of extinction.

Direct effects of nest predation on nesting productivity of birds is widely recognized, and even in high quality sage-grouse habitat, most sage-grouse nests are lost to predators (Gregg et al. 1994, Connelly et al. 2004, Coates et al. 2008). For example, Common Raven (*Corvus corax*; hereafter "raven") depredation of sage-grouse nests has been documented as a common occurrence in northeastern Nevada on the basis of infrared video cameras set up at nest sites (Coates et al. 2008). High mortality rates on chicks have also been attributed to predators, especially during early brood-rearing (Aldridge 2005, Gregg and Crawford 2009, Guttery 2011).

In addition to direct predator effects, perceived predation risk may have dramatic effects on nest success and chick survival (Cresswell 2008, Martin and Briskie 2009), and prey's perception of predation risk may have negative effects that are strong enough to effect population growth rates (Creel and Christianson 2008, Cresswell 2008, Zanette et al. 2011). For example, Zanette et al. (2011) manipulated perceived predation risk while excluding predators from Song Sparrow (*Melospiza melodia*) nests. In the absence of direct predation, Zanette et al. (2011) found a 40% reduction in offspring production as a result of reduction in the number of eggs laid, proportion of eggs hatched, and proportion of nestlings fledged.

In response to predation risk to adults and their nests, sage-grouse and other birds hide nests from predators by placing them primarily in areas with greater visual obstruction (Connelly et al. 1994, Braun 1998, Connelly et al. 2004, Kirol et al. 2012); hens and broods hide from avian predators through a combination of habitat selection and cryptic behavior (Gregg and Crawford 2009, Guttery 2011). Several studies have reported that sage-grouse select nest-sites based on greater sagebrush density (Wallestad and Pyrah 1974, Connelly et al. 2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005), and grass cover (Kaczor 2008, Kirol et al. 2012). Kirol et al. (2012) and Aldridge and Brigham (2002) found that sage-grouse brood hens selected locations with greater percentages of sagebrush and grass cover compared to random locations. Variability in reported nest and brood site habitat use among studies may indicate local differences in habitat and/or predator community composition. However, consistent placement of nests and broods in sites with greater visual cover, regardless of differences in the structure of local habitats, suggests that vertical (e.g., grass and shrub height) and horizontal (e.g., grass and shrub canopy cover) cover influence nest-site and brood-site selection.

Current evidence (Conover et al. 2010) suggests that sage-grouse use nest locations that hide their nests from visual but not olfactory predators. Conover et al. (2010) found that sage-grouse placed nests in areas that had greater vertical and horizontal concealment, taller shrubs, but also fewer updrafts, lower turbulence, and slower wind speeds than random locations. Updrafts, high turbulence, and high wind speeds are weather conditions that make it difficult for mammalian predators to use olfaction to locate nests (Conover 2007). These results are consistent with results of other sage-grouse research that showed sage-grouse preferred to nest in areas with greater visual cover. Further, locations that have good visual cover often have fewer updrafts, less atmospheric turbulence, and lower wind speeds. Thus, sage-grouse, and birds in general, often balance the dual necessity of selecting cover to hide from visual and olfactory predators to improve chances of surviving to breed successfully. Selection of nest-sites that conceal sage-grouse from visual predators but not olfactory predators suggests that the former are a greater threat to sage-grouse nests. On the other hand, it may be that sage-grouse cannot use olfactory cues to influence nest choice decisions, and visual predators may be a greater threat because their numbers have increased in association with anthropogenic development.

Sage-grouse select nest-sites based on habitat characteristics at local (habitat directly around a nest) and landscape scales (Doherty et al. 2010). In accordance with the predator-avoidance hypothesis, I hypothesized that at the landscape-scale, sage-grouse would avoid nesting or raising broods in areas of high densities of avian predators, specifically, American Kestrels (*Falco sparverius*; hereafter “kestrel”), Black-billed Magpies (*Pica hudsonia*; hereafter “magpies”), Golden Eagles (*Aquila chrysaetos*), hawks (*Buteo* spp.), Northern Harriers (*Circus cyaneus*; hereafter “harrier”), and ravens. Further, I hypothesized that adult survival would take precedence to nest or brood survival, and that sage-grouse habitat use would be shaped primarily by avoidance of avian predators that were a threat to adult hen survival, and secondarily to avian predators that were a threat only to nests and broods. I tested these hypotheses by comparing avian predator densities at sage-grouse (1) nest and (2) brood locations, and (3) random locations within nesting and brood-rearing habitat.

METHODS

Study Areas.—My study was conducted in southwest and south-central Wyoming at 12 study sites that were either 16 km (*n* = 8) or 24 km (*n* = 4) in diameter (Fig. 2-1). Sage-grouse are lekking species, and Holloran and Anderson (2005) found that 384 of 415 (92.5%) sage-grouse nests were within 8.5 km of leks in central and southwest Wyoming. Thus, the study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured. I used larger 24-km study sites in south-central Wyoming because sage-grouse were captured at several leks spread over a larger area. Five study sites were located in Lincoln County (16-km diameter each), two in Sweetwater County (one 16-km and one 24-km diameter), two in Uinta County (both 16-km diameter), and three in Carbon County (24-km diameter each). Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming with a variety of land uses and topographic features. Elevation ranged from 1,950 m to 2,530 m among study sites. Most of my sites were owned and administered by the Bureau of Land Management (BLM) with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in my study sites. All study sites had anthropogenic development consisting mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in six (50%) of my study sites; well density within study sites averaged 0.12 ± 0.22 (SD) wells km^{-2} (range = 0.0–0.64 wells km^{-2}).

Sagebrush (*Artemisia* spp.) dominated the landscape at all study sites; Wyoming Big Sagebrush (*A. tridentata wyomingensis*) and Mountain Big Sagebrush (*A. t. vaseyana*) were the most common. Black Sagebrush (*A. nova*) and Dwarf Sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in my study sites included: Antelope Bitterbrush (*Purshia tridentata*), Common Snowberry (*Symphoricarpos albus*), Chokecherry (*Prunus virginiana*), Alderleaf Mountain Mahogany (*Cercocarpus montanus*), Rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Greasewood (Sarcobatus vermiculatus), Saskatoon Serviceberry (*Amelanchier alnifolia*), and Spiny Hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and Quaking Aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides.

Sage-grouse Capture and Monitoring.—I monitored sage-grouse hens during nesting and early brood-rearing from 2008 through 2010. Hens were captured, radio-collared, and released in April of each year. Capture occurred at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, Minnesota).

I located hens on a weekly basis with Communications Specialists

(Communications Specialists, R-1000, Orange, California) receivers and 3-way Yagi antennas (Communications Specialists, Orange, California). Potential nests were identified by binoculars at a distance of ~15 m by circling a radio-marked hen until she was sighted under a shrub. Nests were verified by triangulating the hen under the same shrub from >50 m away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until it either hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left its nest. A successful nest was defined as having evidence that at least one egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation and no eggs hatched).

I located the broods of radio-marked hens weekly with binoculars from a distance of ~15 m. Brood hens were identified by either visually detecting chicks or observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, or clucking). I classified a sage-grouse hen as a brood hen if there was at least 1 chick with her. Monitoring of broods continued for as long as possible, which was usually until the chicks were at least 3-weeks old, the hen lost her brood, the hen died, or the hen could no longer be located.

Avian Predator Monitoring.—Between May and August of each year (sage-grouse nesting and brood-rearing season), I conducted point-count surveys at sage-grouse nests, sage-grouse brood locations, and random locations (hereafter; nest, brood, and random locations) within each study site to compare avian predator densities. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap version 9.2 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest GAP landcover data from 2008. Random locations were at least 1,000 m apart, but in practice, random points in all years averaged over 2,000 m apart (Table 2-1). I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year (total *n* = 504). A new set of random locations was generated each year to avoid spatial autocorrelation; thus, random locations between years were independent.

I used standard distance sampling techniques (Buckland et al. 1993, Ralph et al. 1995, Thomas et al. 2010) to count and record distance to all corvids and raptors observed during point-counts. I recorded distance from the observer when standing at the center point to where predators were first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with avian predators being attracted to or flushed away from an observer. In the uncommon event that an avian predator was displaced from the center of a point-count location as an observer approached (6% of detected birds), I recorded distance from that avian predator to the center of the point-count location while the observer approached as suggested by Ralph et al. (1995). A 1,500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, California) was used in conjunction with a GPS unit to estimate distances directly or to validate visually estimated distances.

I conducted 10-min point-count surveys during daylight hours on a weekly basis at each study site. I visited each point-count location 1 to 8 times with most locations visited ≥ 3 times. I did not survey during inclement weather (i.e., in rain or with wind speeds ≥25 km/h; Ralph et al. 1995). Avian predators that could not be identified to species were not included in analyses—2% of detections within truncated distances. Nest and brood point-counts were performed after nests and broods were initially located; thus, nest point-counts were conducted in May and June and brood point-counts were conducted from mid-May to early-August. I performed random point-counts throughout the nesting and early brood-rearing season (May to early-August).

I intermixed the sampling of nest, brood, and random point-counts within each study site, and each week I changed the time of day and the observer that conducted individual point-counts within a study site. The observers conducting point-counts within a particular study site changed each year, but all observers were trained and tested in corvid and raptor identification before conducting point-counts.

To avoid disturbing an incubating hen, nest point-counts were conducted 100 m to 200 m away from a sage-grouse nest but within a line-of-sight of that nest. I also performed brood point-counts 100 m to 200 m away from a brood hen—estimated by triangulation—immediately before verifying that a radio-marked brood hen was still with chicks. This was intended to record avian predator densities before the observer disturbed any avian predators and to avoid flushing a brood hen when a predator was nearby. If the hen did not have chicks, the brood point-count was discarded.

Data Analyses.—I used conventional distance sampling in DISTANCE 6.0

release 2 (Thomas et al. 2010) to estimate Ferruginous Hawk (*Buteo regalis*), Golden Eagle, harrier, kestrel, magpie, raven, Red-tailed Hawk (*Buteo jamaicensis*), and Swainson's Hawk (*Buteo swainsoni*) densities for nest, brood, and random locations across all years and all study sites. Ferruginous Hawks (*n* = 34), Red-tailed Hawks (*n* = 218), and Swainson's Hawks (*n* = 46) were combined into a single group (*Buteo* hawks) for analyses because all *Buteo* hawks likely had a similar effect on sage-grouse nest-site selection and most observed *Buteo* hawks were Red-tailed Hawks. For DISTANCE analyses, Golden Eagle, harrier, magpie, and raven detection distances were right truncated 5%; *Buteo* hawk detection distances were right truncated 7.5%; and kestrel detection distances were not right truncated (Table 2-2). I chose truncation distances by determining the smallest truncation that allowed for adequate fit of DISTANCE models.

I fit half-normal and hazard-rate key detection functions with cosine, simple polynomial, and hermite polynomial adjustments. I compared the fit of all possible detection functions with detection varying among point-count types to detection held constant among point-count types. I selected the appropriate key detection function and detection function adjustment for each avian predator species separately using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). For all avian predator species, DISTANCE models with detection held constant were at least 4 AIC_c lower than models with detection varying by point-count type. This was not surprising because all point-counts were in sagebrush-dominated habitat.

I used DISTANCE to estimate observer effective detection radius (EDR), which was defined as the distance that the number of detected birds beyond EDR was equal to the undetected birds within EDR (Buckland et al. 2001). For example, an EDR of 500 m for hawks would indicate that the number of detected hawks beyond 500 m was equal to the number of undetected hawks less than 500 m from an observer. I also fit DISTANCE models with detection allowed to vary among observers to assess differences in detection among observers, but the latter models did not fit the data well. For this reason, and because EDR did not differ among observers (95% confidence intervals [CI] around EDRs of all observers overlapped for all avian predator species), I did not incorporate observer differences in detection into my DISTANCE analyses.

I adjusted density estimates for survey effort (difference in the number of visits per point-count location) and scaled my density estimates by the maximum number of visits per point-count location. Survey effort was accounted for in DISTANCE by dividing the total number of detected avian predators at each point-count location by that point-count's proportion of actual visits to the maximum number of visits (e.g., the total number of Golden Eagles detected at point-count x = 3, visits to point-count x = 5, total visits possible = 8; thus, for DISTANCE analyses point-count x was given a golden eagle count of 3 / 0.625 = 4.8, which was then scaled appropriately in DISTANCE by dividing by 8; Thomas et al. 2010).

I used 95% CIs to compare raven, magpie, Golden Eagle, *Buteo* hawk, harrier, and kestrel densities separately at nest, brood, and random locations. Confidence intervals were generated empirically using density estimates and standard errors from DISTANCE with avian predator counts pooled over all study sites and years.

In addition to DISTANCE analyses, I modeled differences in avian predator densities between locations used by sage-grouse (nest and brood locations) and random locations with an information theoretic approach (Anderson 2008). Modeling was done with binomial generalized linear mixed models (GLMM) with restricted maximum likelihood (REML) estimation of degrees of freedom; locations used by sage-grouse were coded 1 and random locations 0. I fit GLMMs with function lmer in package lme4 (R 2.10.1; The R Foundation for Statistical Computing 2009). I calculated avian predator densities from the raw count data within the DISTANCE estimated EDR for each avian predator species. I thus compared avian predator densities using species-specific EDRs because I did not find differences in detection among brood, nest, and random point-count types. The raw densities were standardized by the number of visits to each point-count location. I log transformed raw avian predator densities to reduce the affects of influential observations. I used log transformed raw avian predator species densities to create additive variables (Table 2-3). This allowed me to compare 6 models between locations used by sage-grouse and random locations in which avian predator species were treated either (1) individually, (2) as a single group that ignored size and behavior, (3) as small or large predators, (4) as small, medium, or large predators, (5) by distinguishing between low-flying predators (L), omnivores (O), or soaring (S) species, or (6) by separating species as a threat primarily to adult hen (A), incubating hen (N), or brood-rearing hen (B) (Table 2-3). I compared models with associated variables with AIC_c and Akaike weights (w_i). Multicollinearity was not a problem because no avian predator species were correlated ($r \leq 0.17$) and variance inflation factors (VIF) for avian predator species were VIF ≤ 1.18. Mixed models were used to incorporate study site as a random factor, which accounted for study site differences including fragmentation, anthropogenic structures, landscape features, and vegetation.

DISTANCE estimates are known to be robust to spatial autocorrelation (Thomas et al. 2010). Nonetheless, spatial autocorrelation violates the independence assumption for GLMM, and therefore I used spline correlograms of Pearson residuals with 95% point-wise bootstrap CIs to assess spatial autocorrelation. GLMM residuals were spatially autocorrelated ≤ 2,500 m (Fig. 2-2). I used spatial eigenvector mapping (SEVM) as specified by Dormann et al. (2007) to account for spatial autocorrelation in model residuals (Fig. 2-2). I created an inverse weighted distance matrix to generate eigenvectors, where point-count locations > 8 km apart were not considered to be correlated. This distance related directly to the radius of my 16-km diameter study sites; however, 8 km was also larger than the home range size of breeding Golden Eagles (1.9–92.0 km^2; DeLong 2004) and breeding ravens (0.3–45.8 km^2; Boarman and Heinrich 1999), which had the largest home ranges of the avian predators in this study. Furthermore, I treated all point-count locations, regardless of type or year, within 8 km as correlated with the degree of correlation related to the distance among point-count locations. I found the smallest number of eigenvectors required to remove spatial autocorrelation (Moran's similarity index: $P \geq 0.1$) for each GLMM by using function ME in package spdep (R 2.10.1; The R Foundation for Statistical Computing 2009); I then refit each GLMM with eigenvectors included as fixed effects to account for residual spatial autocorrelation.

RESULTS

I conducted 3,006 point-count surveys over the three years at 963 point-count locations. This comprised 218 sage-grouse nest locations, 249 sage-grouse brood locations (with 83 separate broods), and 496 random locations (Table 2-1). On the whole, sage-grouse selected nest and brood locations with lower densities of avian predators than random locations (Fig. 2-3). I visited each brood between 1 to 9 weeks posthatch (mean = 3.04 ± 2.13 SD). In all years, distance to nearest neighboring location was shortest for broods. Distance between nearest nest and random locations were 2 to 3 times greater than brood locations and similar to each other (Table 2-1). Golden Eagles and ravens were the most commonly detected avian predators, *Buteo* hawks and magpies had an intermediate number of detections, and harriers and kestrels had the lowest number of detections (Table 2-2). EDR estimates ranged from 294 m for magpies to 1,006 m for Golden Eagles, and differed by avian predator species (Table 2-2). This verified the necessity of selecting detection functions for each avian predator species separately. All avian predator species or species groups had more than the 60–80 detections that Buckland et al. (1993) suggested was necessary for reliable density estimates (Table 2-2).

Comparison of 95% CIs showed that *Buteo* hawk, Golden Eagle, magpie, and raven estimated densities were significantly lower at sage-grouse nest and brood locations than random locations (Fig. 2-3). Kestrel densities were significantly lower at sage-grouse brood locations but similar at sage-grouse nest locations compared to random locations (Fig. 2-3). Harrier densities were similar at sage-grouse nest, brood, and random locations (Fig. 2-3); however, random and brood location CIs were only slightly overlapping.

The spline correlogram of Pearson residuals from the top AIC_c ranked GLMM showed that SEVM with 34 eigenvectors accounted for spatial autocorrelation (Fig. 2-2). The top AIC_c ranked GLMM model with SEVM was that which recognized and distinguished among small, medium, and large species (Table 2-4); coefficients for all three size classes were negative and did not overlap zero (Table 2-5). Negative coefficients indicated lower small, medium, and large avian predator densities at locations used by sage-grouse compared to random locations. Sage-grouse nest and brood locations had lower densities of all three size classes of avian predators (Table 2-5).

DISCUSSION

I found that sage-grouse selected habitat with lower densities of avian predators at nests and brood locations as predicted by the predator-avoidance hypothesis. By selecting habitat with lower densities of avian predators, sage-grouse lower their exposure to avian predation, and risk of reproductive failure. My three-size class model had $w_i = 0.91$ (Table 2-4), suggesting that sage-grouse avoided avian predators at nest and brood locations on the basis of the size of avian predators rather than individual species identity, equivalence of all species, foraging behavior of predators, or presumed threat to sage-grouse reproductive stage.

Although I estimated avian predator densities across all years, I did not expect the pattern of sage-grouse avoidance of avian predators to differ among years. The inclusion of SEVM in my GLMM analyses dealt with spatial autocorrelation and bias associated with nest-site fidelity between years, weekly movements of broods, and similarities in habitat within and among study sites. DISTANCE estimates are known to be robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My sampling was designed to attempt to count the greatest proportion of avian predators within a study site each week as suggested by Thomas et al. (2010) and Ralph et al. (1995). Conducting all point-counts within a study site in one day reduced the possibility of double-counting individual avian predators during that week's visit. Counting the same individual during different weeks, regardless of the particular point-count location, was properly scaled by accounting for survey effort. Replication of point-counts by sampling multiple weeks was done to increase the proportion of avian predators detected as suggested by Thomas et al. (2010).

I found raven abundances at sage-grouse nest and brood locations were lower than at random locations in available sagebrush habitat. In western Wyoming, Bui et al. (2010) claimed that raven density around sage-grouse nesting and brood-rearing areas (1.0 ± 0.2 [SE] ravens/km^2) was marginally higher than raven densities in available sagebrush habitat (0.7 ± 0.2 [SE] ravens/km^2); however, these results were not significantly different. The discrepancy between my results and Bui et al. (2010) may be a function of greater anthropogenic development and human activity in their study areas or raven behavioral adaptations related to available resources. Regardless, I agree with Bui et al. (2010) that as avian predators, especially ravens, increase in abundance in sage-grouse habitat, quality nesting and brood-rearing habitat will become more limited. This is consistent with predation risk trade-offs and non-lethal predator effects, such as avoidance of risky habitats or habitats occupied by predators (Evans 2004, Verdolin 2006, Cresswell 2008).

To my knowledge, my study is the first to document raven densities potentially impacting sage-grouse nest-site selection. However, my finding is not surprising because raven densities impact the nest success of prairie grouse species (Gregg et al. 1994, Manzer and Hannon 2005, Coates and Delehanty 2010). In southern Alberta, sharp-tailed grouse (*Tympanuchus phasianellus*) had 8-times greater nest success in landscapes with less than three corvids/km^2 as opposed to landscapes with greater than or equal to three corvids/km^2 (Manzer and Hannon 2005). Sage-grouse nest success in northeastern Nevada was related to the number of ravens per 10-km transect with the odds of a nest failure increasing 7.4% with every additional raven (Coates and Delehanty 2010). Around Jackson and Pinedale, Wyoming, Bui et al. (2010) found that higher occupancy rates of ravens was correlated with failed sage-grouse nests.

Magpies depredate sage-grouse nests (Holloran and Anderson 2003), and they are capable of consuming animals as large as sage-grouse chicks (Trost 1999). Magpies are known to be associated with riparian areas but also forage in sagebrush habitats (Trost 1999). Thus, sage-grouse avoidance of magpies during nesting may be related to sage-grouse avoidance of riparian areas within or adjacent to sagebrush habitat; however, sage-grouse are known to utilize riparian areas for foraging chicks (Connelly et al. 2004, Crawford et al. 2004). My results indicate sage-grouse select habitat for brood rearing with lower abundances of magpies, even while balancing the need to utilize habitats, such as riparian habitats, that provide forage to meet the energetic requirements of chicks. Sage-grouse hens typically move broods to riparian areas after early-brood rearing (Crawford et al. 2004, Gregg and Crawford 2009), which may correspond with chicks being more mobile and less susceptible to predation by magpies.

Golden Eagles are the primary predator of adult sage-grouse (Schroeder et al. 1999, Schroeder and Baydack 2001, Mezquida et al. 2006). In southwestern Wyoming, MacLaren et al. (1988) found that birds contributed to approximately 9% of the diet of nesting Golden Eagles, and sage-grouse was their primary avian prey. In Utah, 55% of radio-marked sage-grouse were killed by raptors, which Danvir (2002) attributed mainly to Golden Eagles. Hence, I was not surprised that sage-grouse pay particular attention to them in locating where to nest and raise their brood. Ferruginous Hawks, Red-tailed Hawks, and Swainson's Hawks take some adult sage-grouse but probably not substantial numbers of them (MacLaren 1988); harriers have been witnessed hunting sage-grouse adults and chicks (Schroeder et al. 1999, Schroeder and Baydack 2001, Fletcher et al. 2003). My GLMM analysis indicated that sage-grouse were avoiding all *Buteo* hawks, harriers, and ravens as a group based on their body size rather than differentiating among them.

My GLMM results showed that sage-grouse were able to avoid small, medium, and large avian predators. This suggests that sage-grouse are not subject to predator facilitation by avian predators. Predator facilitation predicts that anti-predation behaviors that protect prey species from one type of predator may expose them to predation from other types of predators (Kotler et al. 1992, Korpimäki et al. 1996). For example, the risk of predation by Eurasian Eagle Owls (*Bubo bubo*) resulted in gerbils (*Gerbillus allenbyi* and *G. pyramidum*) selecting habitat that increased their exposure to predation by Greater Sand Vipers (*Cerastes cerastes*; Kotler et al. 1992). By hiding from and avoiding avian predators, sage-grouse may reduce their risk of predation from avian predators of multiple sizes, while potentially exposing themselves to olfactory (mammalian) predation. However, the possible effects of predator facilitation between visual predators and olfactory predators are beyond the scope of this study and warrant further research.

Sage-grouse preferentially select for greater visual concealment cover for nesting to hide themselves and their nests from visual predators (Conover et al. 2010), and the probability of raven depredation of a sage-grouse nest has been found to be greater at nests with relatively less canopy cover (Coates and Delehanty 2010). This selection for hiding from and avoiding visual predators through indirect (i.e., habitat features and anthropogenic structures) and possibly direct means entails selection at multiple scales. At the local-scale, sage-grouse appear to be selecting for sites where they are visually concealed from avian predators (Connelly et al. 2004, Doherty et al. 2010, Kirol et al. 2012). At landscape-scales, sage-grouse may be selecting for areas where avian predators are less abundant. Sage-grouse selection of habitat at multiple scales achieves the same thing—reduced risk from avian predators.

Predator avoidance behavior is a common consequence of predation risk (Cresswell 2008). Sage-grouse avoidance of predators has been addressed in the context of using cover to hide from predators; however, nesting and brood-rearing sage-grouse may also directly avoid avian predators. Previous research has not looked at the possibility of sage-grouse directly avoiding predators, but studies on other avian species have demonstrated direct avoidance of avian predators. For example, large numbers of Western Sandpipers (*Calidris mauri*) avoided migration stopover areas with Peregrine Falcons (*Falco peregrinus*) present (Ydenberg et al. 2002), sandpipers also shortened duration at migratory stopover locations possibly to avoid migrating Peregrine Falcons (Ydenberg et al. 2004), Tengmalm's Owls (*Aegolius funereus*) nested away from Ural Owl (*Strix uralensis*) nests (Hakkarainen and Korpimäki 1996), Black Kite (*Milvus migrans*) nests were located away from nesting Eurasian Eagle Owls (Sergio et al. 2003), Skylarks (*Alauda arvensi*) and Yellowhammers (*Emberiza citrinella*) avoided nesting close to European Kestrel (*Falco tinnunculus*) nests (Norrdahl and Korpimäki 1998), Red-backed Shrikes (*Lanius collurio*) avoided nesting near magpie and Hooded Crow (*Corvus corone cornix*) breeding territories (Roos and Pärt 2004), and nesting Pied Flycatchers (*Ficedula hypoleuca*) avoided Eurasian Sparrowhawk (*Accipiter nisus*) nests (Thomson et al. 2006).

Increases in avian predator densities are likely to result in higher depredation rates on sage-grouse nests and reduced chick survival (Evans 2004, Cresswell 2008). Sage-grouse hens likely avoid avian predators for their own survival in addition to reducing depredation rates on their nests and chicks. Thus, the presence of greater abundances of avian predators, specifically corvids and raptors, may induce changes in sage-grouse behavior associated to habitat usage. Sage-grouse have been found to reduce time off of their nests when they inhabit areas near high abundances of ravens (Coates and

Delehanty 2008); thus, in addition to using indirect mechanisms, sage-grouse may be using avian predator abundance directly to evaluate predation risk while nesting. Habitat that has high quality cover and forage may become functionally unavailable to sage-grouse when avian predator densities are at high levels. In Cresswell's (2008) review of non-lethal effects of predator-avoidance, he illustrated that several studies on birds indicate that presence of a predator had dramatic impacts on prey species use of habitat. These effects were found to be as great or greater than the effects of direct predation. Regardless of the mechanisms behind sage-grouse hen selection of habitat with fewer avian predators, My results illustrate that sage-grouse were capable of avoiding areas with relatively higher densities of small, medium, and large avian predators or more specifically ravens, magpies, Golden Eagles, *Buteo* hawks, and kestrels compared to available sagebrush habitat.

LITERATURE CITED

ANDERSON, D. R. 2008. Model based inferences in the life sciences. Springer Science, New York.

ALDRIDGE, C. L. 2005. Identifying habitats for persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton.

ALDRIDGE, C. L., AND R. M. BRIGHAM. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433–444.

BOARMAN, W. I., AND B. HEINRICH. 1999. Common Raven (*Corvus corax*). *In* The Birds of North America, no. 476 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

BRAUN, C. E. 1998. Sage grouse declines in western North America: What are the problems? Proceedings of the Western Association of Fish and Wildlife Agencies 78:139−156.

BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P., AND LAAKE, J. L. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, New York.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Introduction to Distance Sampling. Oxford University Press, New York.

BUI, T. D., J. M. MARZLUFF, AND B. BEDROSIAN. 2010. Common Raven activity in relation to land use in western Wyoming: Implications for Greater Sage-Grouse reproductive success. Condor 112:65−78.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information–theoretic approach, 2nd ed. Springer-Verlag, New York.

CHALFOUN, A. D., AND T. E. MARTIN. 2009. Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497−503.

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.

COATES, P. S., AND D. J. DELEHANTY. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

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.

CONNELLY, J. W., S. T. KNICK, M. A. SCHROEDER, AND S. J. STIVER. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Unpublished Report, Cheyenne, Wyoming.

CONNELLY, J. W., K. P. REESE, AND M. A. SCHROEDER. 2003. Monitoring of Greater Sage-Grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80. University of Idaho, Moscow.

CONNELLY, J. W., K. P. REESE, W. L. WAKKINEN, M. D. ROBERTSON, AND R. A. FISCHER. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise.

CONOVER, M. R. 2007. Predator−Prey Dynamics: The Use of Olfaction. Taylor and Francis, Boca Raton, Florida.

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. Condor 112:331−336.

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.

CREEL, S., AND D. CHRISTIANSON. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194−201.

CRESSWELL, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

DANVIR, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff.

DELONG, J. P. 2004. Effects of management practices on grassland birds: Golden Eagle. Northern Prairie Wildlife Research Center, Jamestown. [Online.] Available at http://www.npwrc.usgs.gov/resource/literatr/grasbird/goea/goea.htm

DOHERTY, K. E., D. E. NAUGLE, AND B. L. WALKER. 2010. Greater Sage-Grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

DORMANN, C, F., J. M. MCPHERSON, M. B. ARAÚJO, R. BIVAND, J. BOLLIGER, G. CARL, R. G. DAVIES, A. HIRZEL, W. JETZ, W. D. KISSLING, I. KÜHN, R. OHLEMÜLLER, P. R. PERES-NETO, B. REINEKING, B. SCHRÖDER, F. M. SCHURR, AND R. WILSON. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. Ecography 30:609 –628.

EVANS, K. L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

FLETCHER, Q. E., C. W. DOCKRILL, D. J. SAHER, AND C. L. ALDRIDGE. 2003. Northern Harrier (*Circus cyaneaus*) attacks on Greater Sage-Grouse (*Centrocercus urophasianus*) in southern Alberta. Canadian Field-Naturalist 117:479–480.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

GREGG, M. A., AND J. A. CRAWFORD. 2009. Survival of Greater Sage-Grouse chicks and broods in the northern Great Basin. Journal of Wildlife Management 73:904–913.

GREGG, M. A., 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.

GUTTERY, M. R. 2011. Ecology and management of a high elevation southern range Greater Sage-Grouse population: Vegetation manipulation, early chick survival, and hunter motivations. Ph.D. dissertation, Utah State University, Logan.

HAKKARAINEN, H., AND E. KORPIMÄKI. 1996. Competitive and predatory interactions among raptors: An observational and experimental study. Ecology 77:1134–1142.

HOLLORAN, M. J., AND S. H. ANDERSON. 2003. Direct identification of northern sage-grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.

HOLLORAN, M. J., AND S. H. ANDERSON. 2005. Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

HOLLORAN, M. J., B. J. HEATH, A. G. LYON, S. J. SLATER, J. L. KUIPERS, AND S. H.

ANDERSON. 2005. Greater Sage-Grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

JOHNSGARD, P. A. 2002. Grassland Grouse and Their Conservation. Smithsonian Institution Press, Washington, D. C.

KACZOR, N. W. 2008. Nesting and brood-rearing success and resource selection of Greater Sage-Grouse in northwestern South Dakota. M.S. thesis, South Dakota State University, Brookings.

KIROL, C. P., J. L. BECK, J. B. DINKINS, AND M. R. CONOVER. 2012. Greater Sage-Grouse nesting and brood-rearing microhabitat selection in xeric big sagebrush. Condor 114:75–89.

KORPIMÄKI, E., V. KOIVUNEN, AND H. HAKKARAINEN. 1996. Microhabitat use and behavior of voles under weasel and raptor predation risk: Predator facilitation? Behavioral Ecology 7:30–34.

KOTLER, B. P., L. BLAUSTEIN, AND J. S. BROWN. 1992. Predator facilitation: The combined effects of snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici. 29:199–206.

MACLAREN, P. A., S. H. ANDERSON, AND D. E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Great Basin Naturalist 48:548–553.

MANZER, D. L., 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.

MARTIN, T. E., AND J. V. BRISKIE. 2009. Predation on dependent offspring: A review of the consequences for mean expression and phenotypic plasticity in avian life history traits. The Year in Evolutionary Biology 1168:201–217.

MEZQUIDA, E. T., S. J. SLATER, AND C. W. BENKMAN. 2006. Sage-grouse and indirect interactions: Potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

NORRDAHL, K., AND E. KORPIMÄKI. 1998. Fear in farmlands: How much does predator avoidance affect bird community structure? Journal of Avian Biology 29:79–85.

RALPH, C. J., S. DROEGE, AND J. R. SAUER. 1995. Managing and monitoring birds using point counts: standards and applications. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149, Berkeley.

ROOS, S., AND T. PÄRT. 2004. Nest predators affect spatial dynamics of breeding Red-backed Shrikes (*Lanius collurio*). Journal of Animal Ecology 73:117–127.

SARGEANT, A. B., M. A. SOVADA, AND T. L. SHAFFER. 1995. Seasonal predator removal relative to hatch rate of duck nests in Waterfowl Production Areas. Wildlife Society Bulletin 23:507–513.

SCHROEDER, M. A., C. L. ALDRIDGE, A. D. APA, J. R. BOHNE, C. E. BRAUN, S. D. BUNNELL, J. W. CONNELLY, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, G. D. KOBRIGER, S. M. MCADAM, C. W. MCCARTHY, J. J. MCCARTHY, D. L. MITCHELL, E. V. RICKERSON, AND S. J. STIVER. 2004. Distribution of sage grouse in North America. Condor 106:363–376.

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*). *In* Birds of North America, no. 425 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

SERGIO, F., L. MARCHESI, AND P. PEDRINI. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. Journal of Animal Ecology 72: 232–245.

SMITH, P. A., H. G. GILCHRIST, AND J. N. M. SMITH. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. Condor 109:15–31.

THOMAS, L., S. T. BUCKLAND, E. A. REXSTAD, J. L. LAAKE, S. STRINDBERG, S. L. HEDLEY, J. R. B. BISHOP, R. A. MARQUES, AND K. P. BURNHAM. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

THOMSON, R. L., J. T. FORSMAN, F. SARDÀ -PALOMERA, AND M. MÖNKKÖNEN. 2006. Fear factor: Prey habitat selection and its consequences in a predation risk landscape. Ecography 29: 507–514.

TROST, C. H. 1999. Black-billed Magpie (*Pica hudsonia*). *In* The Birds of North America, no. 398 (A. Poole, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

U. S. FISH AND WILDLIFE SERVICE. 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

75:13909–14014.

VERDOLIN, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

WAKKINEN, W. L., K. P. REESE, J. W. CONNELLY, AND R. A. FISCHER. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

YDENBERG, R. C., R. W. BUTLER, D. B. LANK, C. G. GUGLIELMO, M. LEMON, AND N. WOLF. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. Journal of Avian Biology 33:47–55.

YDENBERG, R. C., R. W. BUTLER, D. B. LANK, B. D. SMITH, AND J. IRELAND. 2004. Western Sandpipers have altered migration tactics as Peregrine Falcon populations have recovered. Proceedings of the Royal Society of London Series B 271:1263–1269.

ZANETTE, L. Y., A. F. WHITE, M. C. ALLEN, M. CLINCHY. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334:1398–1401.

TABLE 2-1. Summary of minimum, maximum, and mean distance (m) to nearest neighbor by location type (brood, nest, or random) reported by year. Data were collected in southwestern and south-central Wyoming, USA during 2008–2010.

Year	Location Type	*n*	Min	Mean	Max	SD
2008	Brood	92	15.3	790.7	4272.1	917.6
	Nest	54	240.6	2302.0	11811.8	2356.3
	Random	160	1000.0	2011.9	7215.6	1305.1
2009	Brood	103	2.8	831.5	5718.8	1120.3
	Nest	78	102.5	2099.0	8911.5	2091.8
	Random	174	1000.0	2122.1	7073.1	1093.9
2010	Brood	54	61.8	1128.4	9675.9	1707.8
	Nest	86	106.5	2042.6	10011.4	2279.2
	Random	162	1030.8	2493.0	6135.5	1016.0

TABLE 2-2. Truncated distance (m), number of separate detections of avian predators, and number of avian predators seen from 963 point-count locations. Data were collected in southwestern and south-central, Wyoming, USA during 2008–2010. Program DISTANCE was used to estimate effective detection radii (EDR; m) and standard error (SE).

Avian predator species	Truncated distance	Number of detections	Avian predators counted	EDR	SE
Common Raven	1800	546	853	606.8	22.3
Black-billed Magpie	850	138	157	294.2	19.1
Golden Eagle	2500	376	434	1006.3	42.7
Buteo hawk	1650	242	298	439.1	26.0
Northern Harrier	1100	100	107	318.4	26.3
American Kestrel	1500	118	129	397.1	36.1

TABLE 2-3. Model categories and variables considered in generalized linear mixed modeling with spatial eigenvector mapping to account for spatial autocorrelation. Models were developed to compare avian predator densities at locations used by sage-grouse (nest and brood locations) versus random. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.

Model categories	Variables
Individual species[a]	GOEA = Golden Eagle
	BUT = *Buteo* hawks
	CORA = Common Raven
	NOHA = Northern Harrier
	BBMA = Black-billed Magpie
	AMKE = American Kestrel
Single group	GOEA+BUT+CORA+NOHA+BBMA+AMKE
Small and large	Small = BBMA+AMKE
	Large = GOEA+BUT+CORA+NOHA
Small, medium and large	Small = BBMA+AMKE
	Medium = BUT+CORA+NOHA
	Large = GOEA
Behavior	Soaring = GOEA+BUT
	Low flight = NOHA+AMKE

	Omnivore = CORA+BBMA
Stage	Adults = GOEA+BUT+NOHA
	Brooding hen = AMKE
	Nesting hen = CORA+BBMA

[a] Variables in this model were used to compile the variables in all other model categorizations

TABLE 2-4. Generalized linear mixed models comparing avian predator densities between locations used by sage-grouse (nest and brood sites) and random locations. Avian predator models with associated variables were compared with Akaike's information criterion (adjusted for small sample sizes; AIC$_c$) and Akaike weights (w_i). All compared models include parameters generated with spatial eigenvector mapping (SEVM) to correct for spatial autocorrelation. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.

Models	k	AIC$_c$	ΔAIC$_c$	w_i
Small, medium and large[a]	39	675.01	0.00	0.91
Small and large[a]	36	679.71	4.69	0.09
GOEA+CORA+BBMA	37	690.39	15.38	0.00
GOEA+BUT+CORA+NOHA+BBMA+AMKE[a]	39	691.65	16.64	0.00
GOEA+BUT+CORA+NOHA+BBMA	38	692.25	17.24	0.00
ALL[a]	34	695.57	20.56	0.00
Medium and large	36	698.17	23.15	0.00
Small	35	698.67	23.66	0.00
GOEA+BUT+CORA+BBMA+AMKE	38	699.46	24.45	0.00
Adult +Brood hen+Nesting hen[a]	36	704.95	29.94	0.00
Intercept-only model = 1,259.13				

[a] Denotes models with all species of avian predators incorporated into the model.

TABLE 2-5. Parameter estimates with *P* values and 95% confidence intervals (CI) from top AIC$_c$ selected generalized linear mixed model (GLMM) with spatial eigenvector mapping (SEVM). The top model compared log transformed avian predator densities between locations used by sage-grouse and random locations based on three size classes (small = magpie + kestrel, medium = raven + *Buteo* hawk + harrier, and large = Golden Eagle). SEVM was used to correct for spatial autocorrelation. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.

					95% CI	
Variable[a]	Estimate	SE	*Z*	*P*	Lower	Upper
Small	-0.19	0.05	-3.653	<0.0001	-0.30	0.09
Medium	-0.23	0.04	-5.906	<0.0001	-0.31	0.15
Large	-0.31	0.08	-3.975	<0.0001	-0.47	0.16

[a] Model included 34 SEVM variables

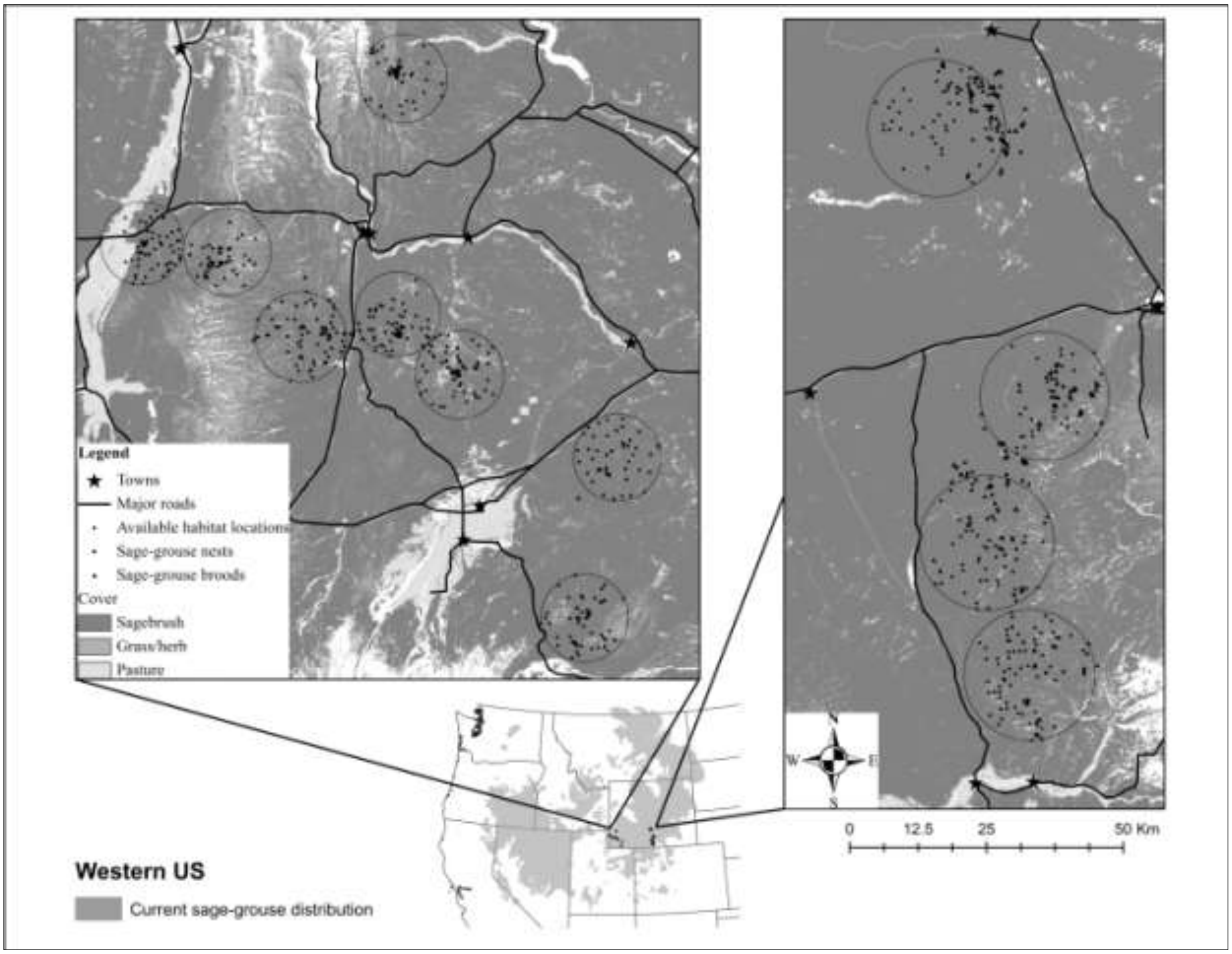


FIG. 2-1. Location map of southern Wyoming depicting eight 16-km diameter and four 24-km diameter study sites, 2008–2010, southwestern and south-central, Wyoming, USA. Magnified sections correspond on left to southwest and on right to south-central Wyoming.

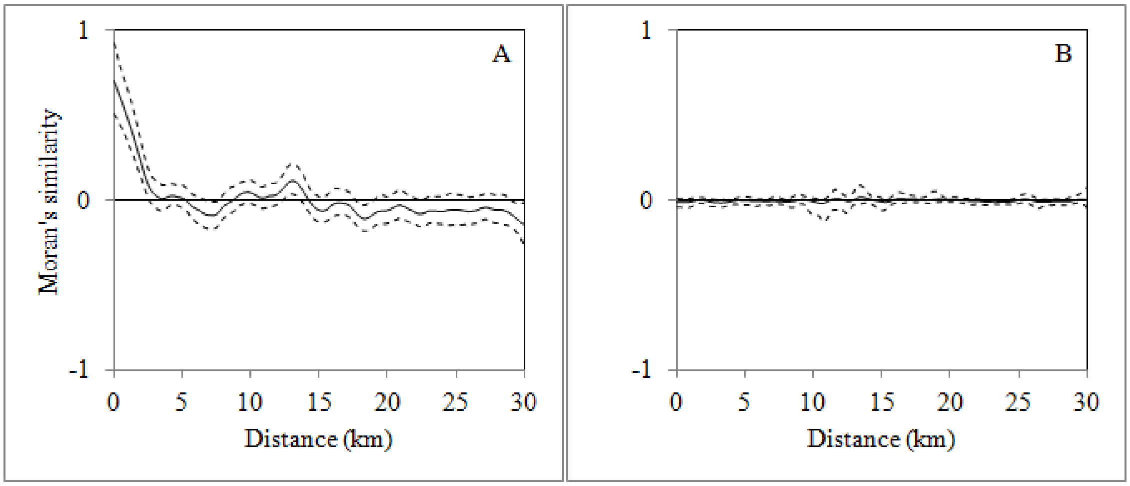


FIG. 2-2. Spline correlograms of Pearson residuals from the best ΔAIC_c ranked generalized linear mixed model with 95% point-wise bootstrapped confidence intervals (A) without spatial eigenvector mapping (SEVM) and (B) with SEVM. Spatial autocorrelation between model residuals was assessed with Moran's similarity index from 0 to 30 (km).

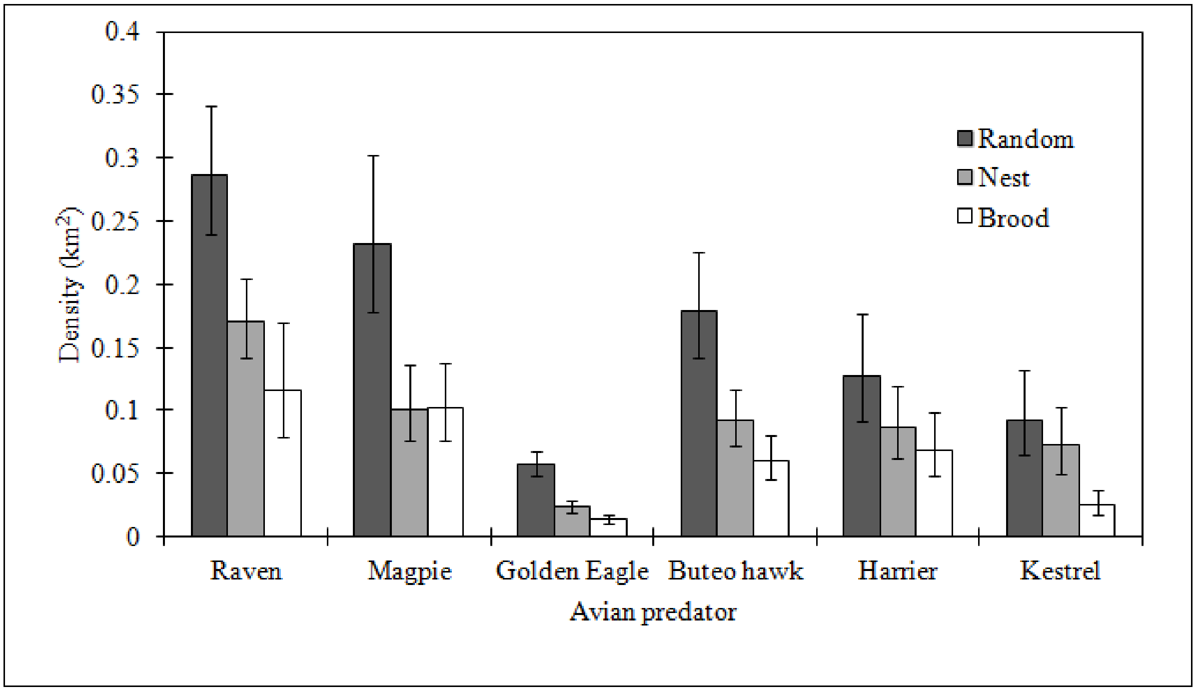


FIG. 2-3. Comparison of raven, magpie, Golden Eagle, *Buteo* hawk, harrier, and kestrel densities (per km^2) among sage-grouse nests, sage-grouse brood locations, and random locations. Data from 3,006 point-count surveys during 2008-2010 at 963 total point-count locations—218 sage-grouse nest locations, 249 sage-grouse brood locations (with 83 separate broods), and 496 random locations—in southwestern and south-central, Wyoming, USA. Densities were generated using radial point-count surveys and DISTANCE at sage-grouse nests, sage-grouse brood locations, and random locations. Error bars are 95% confidence intervals.

CHAPTER 3

GREATER SAGE-GROUSE NEST-SITE AND BROOD-SITE SELECTION IN RELATION TO AVIAN PREDATORS AND ANTHROPOGENIC AND LANDSCAPE FEATURES

ABSTRACT.—Trade-offs between using habitat and avoiding predators are common decisions for prey species such as ground-nesting birds. Prey species including Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") minimize risk of predation by avoiding predators through direct (avoid predators that are seen) and indirect (avoid riskier habitat) mechanisms. Effects of anthropogenic and landscape features on habitat selection of sage-grouse hens have not been evaluated in the context of local predator communities. From 2008–2011, I conducted 10-min point count surveys at 792 sage-grouse locations (340 nests, 331 early-brood [chicks <4 weeks of age], and 121 late-brood [chicks 4–8 weeks of age]) and 660 random locations. Brood locations were compiled from 124 separate sage-grouse broods. Using multinomial logistic regression, I compared anthropogenic and landscape features and densities of small (American Kestrel [*Falco sparverius*] and Black-billed Magpie [*Pica hudsonia*]), medium (*Buteo* spp., Common Raven [*Corvus corax*], and Northern Harrier [*Circus cyaneus*]), and large (Golden Eagle [*Aquila chrysaetos*]) avian predators among nest, early-brood, late-brood, and random locations within available sage-grouse habitat. Anthropogenic features included proximity to oil and gas structures, communication towers, power lines, roads, and rural houses; and landscape features included proximity to forested and riparian

habitats and topographic ruggedness. These comparisons allowed me to assess the relative importance of direct and indirect mechanisms of avian predator avoidance and habitat partitioning of sage-grouse hens at different reproductive stages. I found sage-grouse hens used both direct and indirect mechanisms to lower their exposure to predation and nest depredation, but avian predator densities independently described habitat selection of sage-grouse better than anthropogenic and landscape features combined. For direct avoidance, sage-grouse chose locations with lower densities of small, medium, and large avian predators compared to random locations. For indirect avoidance, sage-grouse selected locations farther away from oil and gas structures and major roads at all reproductive stages, power lines at brood locations, and riparian habitat at nest locations compared to random locations. Sage-grouse used locations closer to riparian habitat during late brood-rearing, which indicates use of areas with relatively more food to meet energy requirements of growing chicks. My analysis also suggested sage-grouse chose flatter locations at nest locations compared to random locations. My results suggest that the magnitude of direct avoidance of avian predators and the selection of proximity to anthropogenic and landscape features by sage-grouse hens were dependent on a sage-grouse's reproductive stage. Avoidance of avian predators and anthropogenic and landscape features allowed female sage-grouse to lower their risk of predation and nest depredation, while using habitat to meet energetic requirements of hens and chicks.

INTRODUCTION

PREDATOR-AVOIDANCE BEHAVIORS can have dramatic effects on the selection of habitat by birds and other terrestrial animals and can be achieved indirectly by reducing use of risky habitats (habitats correlated with higher risk of predation) or directly by avoiding predators that are seen (Lima 1998, Verdolin 2006, Cresswell 2008; see Chapter 2). Both indirect and direct mechanisms of predator avoidance are connected to an animal's perceived risk of predation (Cresswell 2008, Martin and Briskie 2009). Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse"), a species of conservation concern (Braun 1998, Schroeder et al. 2004, Connelly et al. 2011), have recently been shown to select habitat with lower densities of avian predators (see Chapter 2). In Chapter 2, findings are presented showing that sage-grouse avoided avian predators at nest and brood locations based on the size of avian predator species rather than individual species identity. However, there were no comparisons of potential mechanisms of avoidance, such as indirect versus direct avoidance.

Anthropogenic features can be used as perches or nest structure by avian predators or can be areas that provide food subsides. American Kestrels (*Falco sparverius*; hereafter "kestrel"), Common Ravens (*Corvus corax*; hereafter "raven"), Golden Eagles (*Aquila chrysaetos*), Ferruginous Hawks (*Buteo regalis*), Red-tailed Hawks (*Buteo jamaicensis*), and Swainson's Hawks (*Buteo swainsoni*) have been found to use power lines for nesting and perching and areas around power lines for foraging (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010). Roads provide food resources in the form of animals killed by vehicles that attract predators. Mammalian (Bradley and Fagre 1988, Frey and Conover 2006) and avian (Boarman 1993, Boarman et al. 1995) predators also use areas near roads, because predators have increased search ability and foraging efficiency in these areas. Several studies have demonstrated sage-grouse avoid habitat with man-made features, such as oil and gas infrastructure (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Carpenter et al. 2010, Holloran et al. 2010), power-lines (Hanser et al. 2011), and roads (Holloran 2005, Aldridge and Boyce 2007). Thus, birds including sage-grouse may avoid man-made features to avoid the avian predators they attract.

In addition to avoidance of tall man-made structures (structures >2 m tall) and roads, prey species including sage-grouse may avoid avian predators by avoiding landscape features that represent riskier habitat such as riparian areas, conifer forests, and rough terrain. In northeastern Wyoming, Doherty et al. (2010) found that sage-grouse selected nesting habitat with lower terrain roughness and percent cover of conifer, grassland, and riparian habitat; they also found that sage-grouse selected areas with greater density of sagebrush (*Artemisia* spp.) at the patch-scale (100 m to 350 m) compared to random locations within sagebrush. Greater density of sagebrush at relatively larger scales may reduce the foraging efficiency (i.e., predator’s search ability) of visual predators by increasing the number of locations available for a sage-grouse to be located, which has the potential to increase sage-grouse demographic parameters such as survival and nest success. For example, Brewer’s Sparrows’ (*Spizella breweri*) nesting in areas with greater shrub cover and greater density of vacant potential nest-sites had better nest success (Chalfoun and Martin 2009).

Previous research has not compared the relative importance of indirect versus direct predator avoidance in prey species' use of habitat. Sage-grouse may avoid avian predators indirectly by avoiding anthropogenic or landscape features that might attract avian predators or directly by observing them; however, it is more likely that sage-grouse use both indirect and direct means. Thus, I used sage-grouse as a model prey species to test the importance of both indirect and direct predator avoidance. From 2008–2011, I recorded avian predator densities and calculated distances from anthropogenic and landscape features to determine the importance of direct predator avoidance relative to indirect avoidance by sage-grouse hens. I hypothesized that sage-grouse primarily avoid nesting and raising their chicks in areas with high densities of avian predators and secondarily avoid anthropogenic and landscape features that posed greater risk of predation.

As a secondary objective, I evaluated habitat partitioning of sage-grouse females during different reproductive stages (nesting, early-brood-rearing [hereafter early-brood], and late-brood-rearing [hereafter late-brood]) in relation to avian predator densities and distance to anthropogenic and landscape features. Habitat partitioning is the differential use of habitat among groups of animals, and it commonly occurs between different reproductive stages (Bañuelos et al. 2008; e.g., the food resource and shelter requirements of hens on nests are different than brood-rearing hens). Predator avoidance may also be connected to prey species' decision making process regarding partitioning of habitat. Thus, I hypothesized that sage-grouse hens (1) primarily avoided avian predators that were a threat to adult hen survival during all reproductive stages, and secondarily avoided avian predators that were only a threat to nests and chicks; and (2) selected riparian habitat to meet the energetic requirement of adults and chicks after chicks were less vulnerable to predation.

METHODS

Study Areas.—My study was conducted in southwest and south-central Wyoming. I had 12 study sites, each 16 or 24 km in diameter (eight study sites of 16-km diameter and four study sites of 24-km diameter). Holloran and Anderson (2005) found that 92.5% of 415 observed nests were within 8.5 km of leks where they were captured in central and southwest Wyoming. Thus, the study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured. Study sites in south-central Wyoming were 24-km, because sage-grouse were captured at several nearby leks over a larger area. Five study sites were located in Lincoln County (16-km diameter each), two in Sweetwater County (one 16-km diameter and one 24-km diameter), two in Uinta County (both 16-km diameter), and three in Carbon County (24-km diameter each). Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming with a variety of land uses and topographic features. Elevation ranged from 1,950 m to 2,600 m among all study sites. Most of my study sites were federally owned and administered by the Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in my study sites. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in six (50%) of my study sites; mean well density among all study sites was 0.12 ± 0.22 SD wells km^{-2} (min–max = 0.0–0.64 wells km^{-2}).

The landscape at all study sites was dominated by sagebrush; Wyoming Big Sagebrush (*A. tridentata wyomingensis*) and Mountain Big Sagebrush (*A. t. vaseyana*) were the most common. Black Sagebrush (*A. nova*) and Dwarf Sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included Alderleaf Mountain Mahogany (*Cercocarpus montanus*), Antelope Bitterbrush (*Purshia tridentata*), Chokecherry (*Prunus virginiana*), Common Snowberry (*Symphoricarpos albus*), Greasewood (*Sarcobatus vermiculatus*), Rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon Serviceberry (*Amelanchier alnifolia*), and Spiny Hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and Quaking Aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included Arrowleaf Balsamroot (*Balsamorhiza sagittata*), Buckwheat (*Eriogonum* spp.), Common Yarrow (*Achillea millefolium*), Dandelion (*Taraxacum* spp.), Desert Parsley (*Cymopterus* spp.), Phlox (*Phlox* spp.), Lupine (*Lupinus* spp.), Sego Lily (*Calochortus nuttallii*), and Wild Onion (*Allium* spp.). Common grass species included: Bluegrasses (*Poa* spp.), Bluebunch Wheatgrass (*Pseudoroegneria* spicata), Green Needlegrass (*Nassella viridula*), Needle and Thread (*Hesperostipa comata*), Prairie Junegrass (*Koeleria macrantha*), and Western Wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in any of the study sites.

Sage-grouse Capture and Monitoring.—I monitored sage-grouse hens during nesting and brood-rearing from 2008-2011. Hens were captured, radio-collared, and released in April of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (RI-2D, Holohil Systems Ltd, Ontario, Canada; or A4060, Advanced Telemetry Systems Inc, Isanti, Minnesota).

I located hens on a weekly basis with Communications Specialists (R-1000, Communications Specialists, Orange, California) receivers and 3-way Yagi antennas (Communications Specialists, Orange, California). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until the nest hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least one egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation and no eggs hatched).

I located the broods of radio-marked hens weekly with binoculars from ~15 m. Brood hens were identified by either visually detecting chicks or observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, or clucking). I classified a sage-grouse hen as a brood hen if there was evidence of at least one chick with that hen. Monitoring of broods continued for as long as possible, which was usually until the chicks were at least 3 weeks old, the hen lost her brood, the hen died, or the hen could no longer be located (most broods were monitored 3–8 weeks post-hatch).

Avian Predator Monitoring.—Between May and August of each year (sage-grouse nesting and brood-rearing season), I conducted point count surveys at sage-grouse nests, sage-grouse brood locations, and random locations (hereafter; nest, brood, and random locations respectively) within each study site to compare avian predator densities. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap version 9.2 and 10.0 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest ReGAP landcover data from 2008 (Lennartz 2007). Random locations were designated to be ≥1,000 m apart, but after random selection average nearest neighbor distances among random point count locations was >2,000 m. I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. A new set of random locations was generated each year to avoid spatial autocorrelation; thus, random locations among years were independent.

To quantify avian predators, I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all avian predators observed during point counts and recording their distance from the observer (when standing at the center of the point count location). I recorded distance as the distance from the observer to where an avian predator was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with avian predators being attracted to or flushed away from an observer. When an avian predator was displaced from the center of a point count location as an observer approached (6% of all detected birds), I recorded distance from that avian predator to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). This was done when the approach of an observer resulted in an avian predator moving away from the center of the point count location. A 1500–m rangefinder (RE-1500 m, American Technologies Network Corp., San Francisco, California) in conjunction with a global positioning system (GPS) was used to estimate distances directly or to validate visually estimated distances.

To avoid disturbing an incubating hen, nest point counts were conducted 100–200 m away from a sage-grouse nest but within a line-of-sight of that sage-grouse nest. I also performed brood point counts 100–200 m away from a brood hen—estimated by triangulation—immediately before verifying that a radio-marked brood hen was still with chicks. This was intended to record avian predator densities before the observer disturbed any avian predators and to avoid flushing a brood hen when a predator was nearby. If the hen did not have chicks, the brood point count was discarded.

Observers were trained and tested in corvid and raptor identification before conducting point counts. Point counts were 10 min in length, and I conducted them during daylight hours on a weekly basis at each study site. I visited each point count location 1 to 8 times with most locations visited ≥3 occasions. I did not survey for avian predators in inclement weather (i.e., when raining or wind speeds greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed 2% of detections within truncated observation distances. Nest and brood point counts were performed after nests or broods were initially located; thus, nest point counts were conducted in May and June and brood point counts were conducted from mid-May to early-August. I performed random point counts throughout the nesting and early brood-rearing season (May to early-August).

I intermixed the sampling of nest, brood, and random point counts within each study site. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week (i.e., each individual point count location regardless of type—nest, brood, or random—would be conducted at a different time of day each week and by a different observer as best as possible). The observers conducting point counts within a particular study site changed each year. Thus, I minimized observer bias by changing the observer who collected data at each individual point count location.

All avian predator variables were calculated from the raw count data within effective detection radii (EDR) estimated with DISTANCE, version 6.0 release 2 (Thomas et al. 2010) as specified in Chapter 2. Thus, *Buteo* hawk, Golden Eagle, Northern Harrier (*Circus cyaneus*; hereafter “harrier”), kestrel, Black-billed Magpie (*Pica hudsonia*; hereafter “magpie”), and raven densities were individually calculated within 450 m, 1000 m, 350 m, 400 m, 300 m, and 600 m, respectively, of each point count location (see Chapter 2 for further details). The raw densities were standardized by the number of visits to each point count location. I used raw avian predator densities calculated by species to create small (magpie and kestrel), medium (*Buteo* hawk, harrier, and raven), and large (Golden Eagle) avian predator variables, which was shown in Chapter 2 to best describe sage-grouse avoidance of avian predators. I log transformed raw avian predator densities to reduce the effect of influential observations.

Anthropogenic and Landscape Feature Variables.—I used ArcMap 10.0 to calculate point count proximity (Euclidean distance) to anthropogenic features that could be used as perch or nest sites by avian predators or could provide food subsidies. Anthropogenic structures that were >2 m in height were considered available for perching or nesting by avian predators. I quantified the distance from point count locations to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings), major road, gravel road, communication tower, house, and power line for each point count location. Ongoing energy development was occurring in half of my study sites, which required me to assess the dates that energy-related structures and roads were added or removed from the landscape.

In distance calculations, I only included oil and gas structures and roads that existed when each point count was conducted. I obtained information on oil and gas structures, including date construction started on the structure and date when wells were plugged and abandoned (date structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; 2012). I verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture [USDA] 2010). Aerial imagery from NAIP is produced by the USDA on a 3-year rotation; thus, I used WOGCC data and on the ground GPS units to map energy development that occurred after August 2009.

I used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, and houses within a 5-km buffer around study sites; roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units. Major roads included paved, improved gravel roads, and railroads; whereas, all roads included major roads and all unimproved 4-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around study sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power line mapping.

Neither sage-grouse nor avian predators were likely to discriminate between many of different types of anthropogenic structures. Thus, I created 2 anthropogenic structure variables that represented the nearest (1) distance to either an oil and gas structure, communication tower, or house (WCH); and (2) distance to either an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from point count locations to individual types of anthropogenic structures.

Similar to anthropogenic features, some types of landscape features could be used as perches or nest structure by avian predators, or could be areas with higher productivity that attract predators. Thus, I used ArcMap 10.0 to calculate the distance from every point count location to forested (deciduous or conifer stands) and riparian habitats. Tree stands and riparian habitat were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007), and verified with NAIP imagery from 2009. Topography with greater surface roughness has the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that provide vantage points similar to perches. For every point count location, I used ArcMap 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion; TRI variables were developed using a moving window analysis at 0.27-km, 0.54-km, 1-km, and 3-km radii (0.23-km^2, 0.92-km^2, 3.14-km^2, and 28.26-km^2 scales, respectively). Riley et al. (1999) created TRI to describe the roughness of landscapes, and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map; the index is then averaged over a user-defined area.

Euclidean distance is not a good measure of habitat selection by wildlife, because the response of a species to anthropogenic or landscape features often decline as distance increases (Carpenter et al. 2010, Fedy and Martin 2011, Hanser et al. 2011). Thus, I calculated distance decay functions to allow for nonlinear avoidance of anthropogenic or landscape features, which were expressed as:

Decay function = exp^(Euclidean distance to feature (km)/-decay distance) 1)

I calculated all decay functions with 3 decay distances (0.25 km, 0.50 km, and 1 km). Decay functions scaled distance variables between 0 and 1 with greater values corresponding to point count locations closer to anthropogenic or landscape features.

Data Analyses.—To evaluate habitat selection of nesting and brood-rearing sage-grouse hens in reference to avoidance of avian predators and anthropogenic and landscape features, I fit multinomial logistic regression models with maximum likelihood using function multinom in package nnet version 7.3-4 in R (R 2.14.2; R Foundation for Statistical Computing 2009). Multinomial logistic regression models have been used to model habitat selection of wildlife species with >2 response categories. I categorized point count locations into 4 response categories (1) random, (2) sage-grouse nest, (3) early-brood (chicks <4 weeks of age), and (4) late-brood (chicks 4–8 weeks of age). Multinomial logistic regression uses 1 category as the reference for comparisons with all other categories. To compare sage-grouse habitat selection to available sagebrush habitat (random locations), I made comparisons of sage-grouse locations to random locations by coding random locations as the reference category. I then alternated nest and early-brood as the reference category to compare between sage-grouse locations. Modeling of sage-grouse habitat selection was conducted with an information theoretic approach (Anderson 2008). I compared models with Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002) with function aictab in package aiccmodavg version 1.25 in R. I employed sequential AIC_c modeling of covariate sets, which was suggested by Arnold (2010) as an appropriate approach for identifying and ranking the most parsimonious models. Non-informative covariates (85% confidence intervals [CIs] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top AIC_c selected models among covariate sets (Arnold 2010). I classified models within 2 AIC_c of the null model as being non-competitive (Burnham and Anderson 2002); thus, any model within 2 AIC_c of the null was omitted from further analyses.

Anthropogenic and landscape covariate sets were evaluated sequentially (Step 1) then compared with the best avian predator model from Chapter 2 (Step 2). Details on avian predator modeling procedures can be found in Chapter 2. I did not include WCH or ANTH with any anthropogenic structure variable that was used to create WCH or ANTH. The best variable describing the effect of anthropogenic structures on habitat selection by sage-grouse was determined through AIC_c selection within the anthropogenic feature covariate set. For all distance decay functions, I chose the best decay distance (0.25 km, 0.50 km, and 1 km) for each distance variable by comparing all 3 decay distances with AIC_c. I compared models with individual TRI variables measured at 0.27-km, 0.54-km, 1-km, and 3-km radii with AIC_c to choose the best spatial scale for the TRI variable to be used in the landscape feature covariate set; the TRI variable scale with the lowest AIC_c was used in all further modeling. As the final modeling step, I compared all top AIC_c selected models from every covariate set (models within 2 AIC_c of the top model within each covariate set) among each other and as additive models with combinations of the avian predator model and anthropogenic and landscape feature covariate set models. I based my inference on models within 2 AIC_c of the top selected model (Burnham and Anderson 2002). I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any model ($r > 0.65$) as determined with a Pearson’s correlation matrix. In this situation I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤ 5, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

Although I could not test for spatial autocorrelation in multinomial logistic regressions, avian predator densities derived from distance sampling techniques are robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My avian predator sampling was designed to count the greatest proportion of avian predators within a study site each week while not counting the same avian predator more than once per week as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a study site in one day reduced the possibility of double-counting individual avian predators during that week's visit. Counting the same individual avian predator during different weeks, regardless of the particular point count location, was properly scaled by accounting for survey effort. Replication of point counts by sampling multiple weeks was done to increase the proportion of avian predators detected as suggested by Thomas et al. (2010). When evaluating avian predator densities between sage-grouse and random locations, the findings from Chapter 2 accounted for spatial autocorrelation in generalized linear mixed models; however, accounting for spatial autocorrelation did not significantly change coefficient values of their avian predator models. Furthermore, multinomial logistic regression only requires that successive habitat selection choices be independent (Agresti 2007). I made the assumption that successive locations from the same sage-grouse were sufficiently far apart in time to be effectively independent. This was reasonable because sage-grouse locations were ~1 week apart in my study.

RESULTS

I conducted 4,441 point count surveys at 1,452 locations during 2008–2011 including 340 sage-grouse nest, 331 sage-grouse early-brood, 121 sage-grouse late-brood, and 660 random locations. Brood locations were compiled from 124 separate sage-grouse broods. I counted 196 *Buteo* hawks, 295 Golden Eagles, 77 harriers, 105 kestrels, 143 magpies, and 688 ravens within species-specific EDRs (see Chapter 2), which equated to 248 small, 961 medium, and 295 large avian predators. Brood, nest, and random locations were on average 841 m, 1,997 m, and 2,301 m apart, respectively. There was no evidence of multicollinearity between avian predator variables and anthropogenic or landscape feature variables, because avian predator variables did not co-vary with any other variable ($r^2 < 0.02$) and VIF ≤ 5.

During Step 1 of sequential modeling, I found sage-grouse selection of nest and brood locations was partially based on anthropogenic and landscape feature variables (Table 3-1). The top AIC_c selected anthropogenic feature model ($w_i = 0.99$) included proximity to oil and gas structures, power lines, rural houses, and major roads; and the top AIC_c selected landscape feature model ($w_i = 0.50$) included proximity to riparian habitat and TRI (Table 3-1). Proximity to oil and gas structures was best described as a distance decay function calculated with the 0.25-km distance decay ($\text{OGS}_{0.25}$). Power lines, rural houses, major roads, and riparian habitat were best described as distance decay functions calculated with the 1-km distance decay ($\text{POW}_{1.0}$, $\text{HOM}_{1.0}$, $\text{MRD}_{1.0}$, and $\text{RIP}_{1.0}$, respectively). Thus, the effect of proximity to oil and gas structures on sage-grouse selection of nesting and brood locations became negligible closer to sage-grouse locations compared to proximity to all other predictive anthropogenic and landscape features (i.e., the effect of distance from sage-grouse locations to oil and gas structures [0.25-km distance decay function] decayed faster than the effects of distance to power lines, rural houses, major roads, and riparian habitat [1-km distance decay functions]). I found TRI calculated at the 0.54-km radius ($TRI_{0.54}$) fit the data best.

During Step 2 of sequential modeling, my analyses indicated that sage-grouse hen selection of nest and brood locations was best described by avian predator densities in conjunction with proximity to anthropogenic and landscape features with $w_i = 1.00$ (Table 3-2). Even though the best model incorporated avian predator densities and anthropogenic and landscape feature variables, the avian predator density model (AIC_c = 88.57) independently described sage-grouse selection of nest and brood locations much better than the anthropogenic and landscape feature (AIC_c = 313.52) model (Table 3-2). This indicated that small, medium, and large avian predators had a relatively greater correlation with sage-grouse selection of nest and brood locations compared to anthropogenic and landscape features.

Greater densities of small, medium, and large avian predators were negatively correlated with sage-grouse nest, early-brood, and late-brood locations compared to random locations (Table 3-3). My analysis also indicated that early-brood and late-brood sage-grouse locations had lower avian predator densities compared to nesting sage-grouse (Table 3-4). During each reproductive stage, sage-grouse avoided small and medium avian predators at similar magnitudes, and also exhibited greater avoidance of large avian predators than small or medium avian predators (Tables 3-3 and 3-4).

Sage-grouse responded to anthropogenic features by avoiding them regardless of the sage-grouse's reproductive stage. I found nesting, early-brood, and late-brood sage-grouse were farther away from oil and gas structures and major roads compared to random locations (Table 3-3). Early-brood and late-brood sage-grouse were farther away from power lines compared to random locations (Table 3-3). In contrast to the avoidance of other anthropogenic structures, my analysis indicated that early-brood and late-brood sage-grouse were closer to houses compared to random locations and nest locations (Tables 3-3 and 3-4).

For landscape feature variables, I found sage-grouse differed in their response to proximity to riparian habitat and TRI depending on their reproductive stage. Compared to random locations, sage-grouse selected nest locations farther away from riparian habitat, early-brood sage-grouse neither selected for nor avoided habitat based on proximity to riparian habitat, and late-brood sage-grouse selected locations closer to riparian habitat (Table 3-3). However, both early-brood and late-brood locations were closer to riparian habitat compared to nest locations, and late-brood locations were closer to riparian habitat than early-brood locations (Table 3-4). Sage-grouse nest-sites were located in areas with flatter topography compared to random locations (Table 3); I did not find this effect at sage-grouse early-brood or late-brood locations. Sage-grouse at early-brood and late-brood locations selected relatively more rugged topography compared to nesting sage-grouse (Table 3-4).

DISCUSSION

Sage-grouse hens used direct and indirect mechanisms to lower their exposure to predation and nest depredation particularly from avian predators. In general, sage-grouse avoided risky habitat by directly avoiding areas with higher densities of small, medium, and large avian predators and indirectly by avoiding areas close to anthropogenic and landscape features. Similar to previous research, my analyses confirmed that sage-grouse select locations farther away from anthropogenic and landscape features that could be used as perches or provide subsidized food resources for predators, which included oil and gas structures (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Holloran et al. 2010, Kirol 2012) and major roads (Holloran 2005, Aldridge and Boyce 2007) at all reproductive stages, power lines (Hanser et al. 2011) at brood locations, and riparian habitat (Doherty et al. 2010, Dzialak et al. 2011) at nest locations. Sage-grouse also chose flatter locations at nest-sites similar to findings from Doherty et al. (2010), Dzialak et al. (2011), and Kirol (2012). Habitat partitioning during vulnerable reproductive stages by female sage-grouse relative to predation risk and food availability was a means for sage-grouse hens to lower their risk of predation and nest depredation, while using habitat to meet energetic requirements of hens and chicks (Connelly et al. 2004, Aldridge and Boyce 2007, Dzialak et al. 2011).

High densities of avian predators including *Buteo* hawks (MacLaren et al. 1988, Schroeder et al. 1999, Schroeder and Baydack 2001), Golden Eagles (MacLaren et al. 1988, Danvir 2002), harriers (Schroeder et al. 1999, Thirgood et al. 2000, Fletcher et al.

2003), kestrels (Schroeder et al. 1999), magpies (Holloran and Anderson 2003, Vander Haegen et al. 2002), and ravens (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010) have the potential to negatively affect nest success or adult and chick survival of grouse species, and one of the responses of prey species to the presence of these predators is avoidance (Lima 1998, Evans 2004, Cresswell 2008, Dinkins et al. 2012). Similar to Dinkins et al. (2012), my analysis indicated that sage-grouse avoidance of avian predators occurred during many reproductive stages—nesting, early-brood, and late-brood—but at different magnitudes. My results also suggest sage-grouse hens have the ability to distinguish between threats to their survival, nests, and offspring.

Large avian predators (Golden Eagles) were avoided by sage-grouse hens at greater magnitudes than smaller avian predators within each reproductive stage suggesting sage-grouse hens were predominantly concerned with their own survival (i.e., smaller parameter estimates for large avian predators compared to small and medium avian predators when comparing sage-grouse locations to random locations; Table 3-3). It was not surprising that sage-grouse hens protected themselves from their primary predator (Golden Eagle; Schroeder et al. 1999, Schroeder and Baydack 2001, Mezquida et al. 2006), because sage-grouse are a relatively long-lived bird (Connelly et al. 2011). Johnson and Braun (1999) and Taylor et al. (2012) found adult survival was the most influential demographic parameter on sage-grouse population growth, and they also illustrated that following adult survival, chick survival then nest success were the next most important factors affecting population growth for sage-grouse. My results also indicate that early-brood and late-brood locations had greater magnitudes of avian predator avoidance than nest locations, which can be explained by the greater mobility of broods compared to nests and the duration of time spent in a particular location. Thus, reducing risk of nest depredation and chick mortality by avoiding small and medium sized avian predators likely increased sage-grouse reproductive output.

In addition to avoidance of avian predators, sage-grouse selected habitat in response to anthropogenic and landscape features. As expected, I found that sage-grouse primarily used direct avoidance of avian predators and secondarily avoided riskier habitat. Direct and indirect avoidance of avian predators were not necessarily linked (correlated) from the perspective of a sage-grouse, because indirect cues (perches and areas with subsidized food for predators) were not correlated with any avian predator species ($r^2 < 0.02$). This indicated that anthropogenic and landscape features may not be the best indicators of potential predation risk, but represent areas of greater perceived risk of predation by sage-grouse. Prey species' ability to predict and avoid risky habitat increases survival and reproductive success, but the ability to directly avoid predators is more beneficial than indirect cues of predation risk (Thomson et al. 2006). Both mechanisms presumably achieve reduced predation rates; however, there may be other population limiting effects as a result of predator avoidance such as reduced foraging ability of prey species in areas of lower habitat quality (Lima 1998, Evans 2004, Cresswell 2008).

Habitat use is a trade-off among protection from exposure to the environment (weather), starvation, and predation (Verdolin 2006), which can be considered habitat partitioning. Similar to Dzialak et al. (2011), my results confirmed that sage-grouse have opposing responses to proximity to riparian habitat depending on reproductive stage. Sage-grouse were farther away from riparian habitat while nesting, but chose locations closer to riparian areas during late-brood. Nesting occurred away from riparian areas, because starvation was not a factor for nesting sage-grouse hens. However, chicks have increasing energetic demands as they grow, and sage-grouse hens typically move broods to riparian areas after early-brood-rearing (Crawford et al. 2004, Gregg and Crawford 2009). Riparian habitats provide forbs and invertebrates that meet the energetic demands of growing sage-grouse chicks (Connelly et al. 2004, Aldridge and Boyce 2007, Dzialak et al. 2011). Sage-grouse appear to minimize the negative effects of increased predation risk associated with riparian areas by directly avoiding avian predators and indirectly by avoiding riparian habitat during relatively more vulnerable reproductive stages (nest and early-brood). Sage-grouse early-brood and late-brood locations were closer to rural houses compared to random and nest locations, which may be explained by the distribution of rural houses in higher quality sagebrush habitat (more productive); however, this is speculative and deserves more research. Thus, sage-grouse selection of brood locations closer to rural houses was likely a response similar to their response to riparian habitat.

Predation risk trade-offs and non-lethal predator effects, such as avoidance of risky habitats and habitats occupied by greater density of avian predators (Evans 2004, Verdolin 2006, Cresswell 2008), are mechanisms that explain habitat partitioning of female sage-grouse. High densities of avian predators and close proximity to anthropogenic and landscape features—specifically oil and gas infrastructure, power lines, major roads, riparian habitat, and rugged topography—are likely to result in reduced adult survival and higher depredation rates on sage-grouse nests (Lima 1998, Evans 2004, Cresswell 2008). My results indicated that both direct (avian predators) and indirect (oil and gas structures, power lines, roads, rugged topography, and riparian habitat) mechanisms were used by sage-grouse to presumably avoid predation and nest depredation. Sage-grouse use of habitat was negatively connected to avian predator densities with quality sage-grouse habitat presumably having lower densities of small, medium, and large avian predators. The presence of greater abundances of avian predators may induce changes in sage-grouse behavior associated to habitat usage. Thus, human manipulation of habitat that structurally changes habitat and promotes greater density of avian predators may limit sage-grouse populations, because habitat that has high quality cover and forage may become functionally unavailable to sage-grouse when avian predator densities are at high levels and anthropogenic features are nearby.

LITERATURE CITED

AGRESTI, A. 2007. An Introduction to Categorical Data Analysis, 2nd ed. John Wiley and Sons, Hoboken, New Jersey.

ALDRIDGE, C. L. 2005. Identifying habitats for persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton, Canada.

ALDRIDGE, C. L., AND M. S. BOYCE. 2007. Linking occurrence and fitness to persistence:

Habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 17:508–526.

ANDERSON, D. R. 2008. Model Based Inference in the Life Sciences: A Primer on Evidence. Springer Science, New York.

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

BAÑUELOS, M., M. QUEVEDO, AND J. OBESO. 2008. Habitat partitioning in endangered Cantabrian Capercaillie (*Tetrao urogallus cantabricus*). Journal of Ornithology 149:245–252.

BOARMAN, W. I. 1993. When a native predator becomes a pest: A case study. Pages 191–206 *in* Conservation and Resource Management (S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz, Eds.). Pennsylvania Academy of Science, Easton, Pennsylvania.

BOARMAN, W. I., R. J. CAMP, M. HAGAN, AND W. DEAL. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside.

BRADLEY, L. C., AND D. B. FAGRE. 1988. Coyote and Bobcat responses to integrated ranch management practices in south Texas. Journal of Range Management 41:322−327.

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.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Introduction to Distance Sampling. Oxford University Press, New York.

BUI, T. D., J. M. MARZLUFF, AND B. BEDROSIAN. 2010. Common Raven activity in relation to land use in western Wyoming: Implications for Greater Sage-Grouse reproductive success. Condor 112:65−78.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach, 2nd ed. Springer-Verlag, New York.

CARPENTER, J., C. L. ALDRIDGE, AND M. S. BOYCE. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806−1814.

CHALFOUN, A. D., AND T. E. MARTIN. 2009. Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497−503.

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.

CONNELLY, J. W., C. A. HAGEN, AND M. A. SCHROEDER. 2011. Characteristics and dynamics of Greater Sage-Grouse populations. Pages 53–67 *in* Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and Its Habitats (S. T. Knick and J. W. Connelly, Eds.). Studies in Avian Biology, University of California Press, Berkeley.

CONNELLY, J. W., S. T. KNICK, M. A. SCHROEDER, AND S. J. STIVER. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Unpublished Report, Cheyenne, Wyoming.

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.

CRESSWELL, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

DANVIR, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, Utah.

DOHERTY, K. E. 2008. Sage-grouse and energy development integrating science with conservation planning to reduce impacts. Ph.D. dissertation, University of Montana, Missoula.

DOHERTY, K. E., D. E. NAUGLE, AND B. L. WALKER. 2010. Greater Sage-Grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

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 6:1–18.

EVANS, K. L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

FEDY, B., AND K. MARTIN. 2011. The influence of fine-scale habitat features on regional variation in population performance of alpine White-tailed Ptarmigan. Condor 113:306–315.

FLETCHER, Q. E., C. W. DOCKRILL, D. J. SAHER, AND C. L. ALDRIDGE. 2003. Northern Harrier (*Circus cyaneaus*) attacks on Greater Sage-Grouse (*Centrocercus urophasianus*) in southern Alberta. Canadian Field-Naturalist 117:479–480.

FREY, S. N., AND M. R. CONOVER. 2006. Habitat use by meso-predators in a corridor environment. Journal of Wildlife Management 70:1111–1118.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

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

HANSER, S. E., M. LEU, S. T. KNICK, AND C. L. ALDRIDGE. 2011. Sagebrush Ecosystem Conservation and Management: Ecoregional Assessment Tools and Models for the Wyoming Basins. Allen Press, Lawrence, Kansas.

HOLLORAN, M. J. 2005. Greater Sage-Grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Ph.D. dissertation, University of Wyoming, Laramie.

HOLLORAN, M. J., AND S. H. ANDERSON. 2003. Direct identification of northern sage-grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.

HOLLORAN, M. J., AND S. H. ANDERSON. 2005. Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

HOLLORAN, M. J., R. C. KAISER, AND W. A. HUBERT. 2010. Yearling Greater Sage-Grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

JOHNSON, K. H., AND C. E. BRAUN. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

KIROL, C. P. 2012. Quantifying habitat importance for Greater Sage-Grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. M. S. thesis, University of Wyoming, Laramie.

LAMMERS, W. M., AND M. W. COLLOPY. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

LENNARTZ, S. 2007. USGS Gap Analysis Program (GAP) species distribution model. Sanborn Map Corporation. Portland, Oregon.

LIMA, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.

MACLAREN, P. A., S. H. ANDERSON, AND D. E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Great Basin Naturalist 48:548–553.

MANZER, D. L., 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.

MARTIN, T. E., AND J. V. BRISKIE. 2009. Predation on dependent off-spring: A review of the consequences for mean expression and phenotypic plasticity in avian life history traits. Annals of the New York Academy of Sciences 1168:201–217.

MEZQUIDA, E. T., S. J. SLATER, AND C. W. BENKMAN. 2006. Sage-grouse and indirect interactions: Potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

PRATHER, P. R., AND T. A. MESSMER. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

RALPH, C. J., S. DROEGE, AND J. R. SAUER. 1995. Managing and monitoring birds using point counts: Standards and applications. United States Department of Agriculture, Forest Service General Technical Report PSW-GTR-149, Berkeley, California.

RILEY, S. J., S. D. DEGLORIA, AND R. ELLIOT. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

SCHROEDER, M. A., C. L. ALDRIDGE, A. D. APA, J. R. BOHNE, C. E. BRAUN, S. D. BUNNELL, J. W. CONNELLY, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, G. D. KOBRIGER, S. M. MCADAM, C. W. MCCARTHY, J. J. MCCARTHY, D. L. MITCHELL, E. V. RICKERSON, AND S. J. STIVER. 2004. Distribution of sage grouse in North America. Condor 106:363–376.

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*). *In* Birds of North America, no. 425 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

SLATER, S. J., AND J. P. SMITH. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

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.

THIRGOOD, S. J., S. M. REDPATH, P. ROTHERY, AND N. J. AEBISCHER. 2000. Raptor predation and population limitation in Red Grouse. Journal of Animal Ecology 69:504–516.

THOMAS, L., S. T. BUCKLAND, E. A. REXSTAD, J. L. LAAKE, S. STRINDBERG, S. L. HEDLEY, J. R. B. BISHOP, R. A. MARQUES, AND K. P. BURNHAM. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

THOMSON, R. L., J. T. FORSMAN, F. SARDÀ -PALOMERA, AND M. MÖNKKÖNEN. 2006. Fear factor: Prey habitat selection and its consequences in a predation risk landscape.

Ecography 29:507–514.

U.S. DEPARTMENT OF AGRICULTURE. 2010. 2009 NAIP survey: Summary report. Farm Service Agency, Aerial Photography Field Office, Salt Lake City, Utah.

VANDER HAEGEN, W. M., M. A. SCHROEDER, AND R. M. DEGRAAF. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. Condor 104:496–506.

VERDOLIN, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

WAKKINEN, W. L., K. P. REESE, J. W. CONNELLY, AND R. A. FISCHER. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

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.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

WYOMING OIL AND GAS CONSERVATION COMMISSION (WOGCC). 2012. WOGCC homepage. [Online.] Available at http://wogcc.state.wy.us.

TABLE 3-1. Multinomial logistic regression models comparing proximity to anthropogenic and landscape features among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations. Anthropogenic and landscape features covariate sets were compared separately with Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (w_i). The anthropogenic feature covariate set included distance decay functions to the nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$); power line (1.0-km decay function; $POW_{1.0}$); rural house (1.0-km decay function; $HOM_{1.0}$); major road (1.0-km decay function; $MRD_{1.0}$); gravel road (1.0-km decay function; $GRD_{1.0}$); closest oil and gas structure, communication tower, or house (0.25-km decay function; $WCH_{0.25}$); and closest oil and gas structure, communication tower, house, or power line (0.50-km decay function; $ANTH_{0.50}$). The landscape feature covariate set included distance decay functions to riparian (1.0-km decay function; $RIP_{1.0}$) and forested (0.25-km decay function; $TREE_{0.25}$) habitat and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$). Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

Models[a]	k	ΔAIC_c	w_i	Deviance
Anthropogenic covariate set				
$OGS_{0.25}$, $POW_{1.0}$, $HOM_{1.0}$, $MRD_{1.0}$ [a]	15	0.00	0.99	3539.60

OGS$_{0.25}$, POW$_{1.0}$, HOM$_{1.0}$	12	9.19	0.01	3554.92
OGS$_{0.25}$, POW$_{1.0}$, MRD$_{1.0}$	12	17.88	0.00	3563.60
OGS$_{0.25}$, POW$_{1.0}$	9	20.77	0.00	3572.58
OGS$_{0.25}$, MRD$_{1.0}$	9	26.80	0.00	3578.60
HOM$_{1.0}$, MRD$_{1.0}$	9	28.28	0.00	3580.10
WCH$_{0.25}$, POW$_{1.0}$, MRD$_{1.0}$	12	28.89	0.00	3574.62
WCH$_{0.25}$, POW$_{1.0}$	9	30.63	0.00	3582.44
POW$_{1.0}$, MRD$_{1.0}$	9	33.42	0.00	3585.24
POW$_{1.0}$	6	35.25	0.00	3593.12
ANTH$_{0.50}$, MRD$_{1.0}$	9	36.44	0.00	3588.26
OGS$_{0.25}$	6	38.26	0.00	3596.14
WCH$_{0.25}$, MRD$_{1.0}$	9	38.41	0.00	3590.22
ANTH$_{0.50}$	6	44.67	0.00	3602.54
MRD$_{1.0}$	6	44.72	0.00	3602.60
HOM$_{1.0}$	6	47.03	0.00	3604.90
WCH$_{0.25}$	6	48.28	0.00	3606.16
GRD$_{1.0}$	6	49.44	0.00	3607.32
Intercept only	3	55.20	0.00	3619.12
Landscape covariate set				
RIP$_{1.0}$, TRI$_{0.54}$ [b]	9	0.00	0.50	3569.22
TREE$_{0.25}$, RIP$_{1.0}$	9	1.26	0.27	3570.48

$TREE_{0.25}$, $RIP_{1.0}$, $TRI_{0.54}$	12	1.60	0.22	3564.74
$RIP_{1.0}$	6	8.52	0.01	3583.80
$TRI_{0.54}$	6	25.38	0.00	3600.66
$TREE_{0.25}$, $TRI_{0.54}$	9	27.68	0.00	3596.90
$TREE_{0.25}$	6	29.81	0.00	3605.10
Intercept only	3	37.79	0.00	3619.12

[a] AIC_c = 3569.94

[b] AIC_c = 3587.34

TABLE 3-2. Multinomial logistic regression models comparing avian predator densities and proximity to anthropogenic and landscape features among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations. Combinations of singular and additive models created from the top AIC$_c$ selected avian predator model and anthropogenic and landscape feature models were compared with Akaike's information criterion (adjusted for small sample sizes; AIC$_c$) and Akaike weights (w_i). The avian predator model (avian) included log transformed small, medium, and large avian predator densities. The anthropogenic feature model (anthropogenic) included distance decay functions to nearest oil and gas structure (0.25-km decay function; OGS$_{0.25}$), power line (1.0-km decay function; POW$_{1.0}$), rural house (1.0-km decay function; HOM$_{1.0}$), and major road (1.0-km decay function; MRD$_{1.0}$). The landscape feature model (landscape) included a distance decay function to the nearest riparian habitat (1.0-km decay function; RIP$_{1.0}$) and topographic ruggedness calculated at 0.54-km radius (TRI$_{0.54}$). Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

Models	k	ΔAIC$_c$	w_i	Deviance
Avian, anthropogenic, landscape [a]	30	0.00	1.00	3171.92
Avian, anthropogenic	24	36.56	0.00	3220.94
Avian, landscape	18	50.67	0.00	3247.42

Avian	12	88.57	0.00	3297.58
Anthropogenic, landscape	18	313.52	0.00	3510.26
Anthropogenic	12	351.18	0.00	3560.18
Landscape	9	354.13	0.00	3569.22
Intercept only	3	391.92	0.00	3619.12

[a] $AIC_c = 3125.62$

TABLE 3-3. Parameter estimates with 95% confidence intervals (CI) from top AIC_c selected multinomial logistic regression. The top model compared log transformed avian predator densities (small, medium, and large avian predators); distance decay functions to nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$), power line (1.0-km decay function; $POW_{1.0}$), rural house (1.0-km decay function; $HOM_{1.0}$), major road (1.0-km decay function; $MRD_{1.0}$), and riparian habitat (1.0-km decay function; $RIP_{1.0}$); and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$) among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random (reference level) locations. Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

				95% CI	
Group	Variable	Estimate	SE	Lower	Upper
Nest					
	Intercept	-2.63	0.58	-3.79	-1.48^{*}
	Small avian predator	-0.06	0.03	-0.12	-0.00^{*}
	Medium avian predator	-0.08	0.02	-0.13	-0.04^{**}
	Large avian predator	-0.17	0.04	-0.25	-0.08^{*}
	$OGS_{0.25}$	-1.63	0.80	-3.21	-0.05^{*}
	$POW_{1.0}$	-0.54	0.47	-1.47	0.39

	HOM$_{1.0}$	1.31	0.77	-0.21	2.82
	MRD$_{1.0}$	-2.64	0.87	-4.35	-0.94*
	RIP$_{1.0}$	-0.63	0.26	-1.14	-0.12*
	TRI$_{0.54}$	-0.02	0.01	-0.04	-0.01*
Early brood					
	Intercept	-13.03	1.30	-15.58	-10.47*
	Small avian predator	-0.33	0.06	-0.46	-0.21*
	Medium avian predator	-0.32	0.04	-0.40	-0.24*
	Large avian predator	-0.62	0.12	-0.85	-0.39*
	OGS$_{0.25}$	-3.11	1.12	-5.32	-0.89*
	POW$_{1.0}$	-1.65	0.59	-2.83	-0.49*
	HOM$_{1.0}$	3.21	0.79	1.64	4.78*
	MRD$_{1.0}$	-2.14	0.86	-3.83	-0.44*
	RIP$_{1.0}$	-0.01	0.27	-0.55	0.59
	TRI$_{0.54}$	-0.01	0.01	-0.03	0.01
Late brood					
	Intercept	-13.49	1.66	-16.76	-10.21*
	Small avian predator	-0.30	0.08	-0.46	-0.14*
	Medium avian predator	-0.32	0.06	-0.43	-0.21*
	Large avian predator	-0.49	0.14	-0.76	-0.22*
	OGS$_{0.25}$	-10.01	4.18	-18.23	-1.78*

$POW_{1.0}$	-1.77	0.86	-3.46	-0.07*
$HOM_{1.0}$	4.19	0.92	2.37	6.01*
$MRD_{1.0}$	-3.01	1.45	-5.87	-0.16*
$RIP_{1.0}$	1.43	0.37	0.70	2.16*
$TRI_{0.54}$	0.00	0.01	-0.01	0.02

*Denotes a 95% confidence interval that does not include zero.

TABLE 3-4. Parameter estimates with 95% confidence intervals (CI) from top AIC$_c$ selected multinomial logistic regression. The top model compared log transformed avian predator densities (small, medium, and large avian predators); distance decay functions to nearest oil and gas structure (0.25-km decay function; OGS$_{0.25}$), power line (1.0-km decay function; POW$_{1.0}$), rural house (1.0-km decay function; HOM$_{1.0}$), major road (1.0-km decay function; MRD$_{1.0}$), and riparian habitat (1.0-km decay function; RIP$_{1.0}$); and topographic ruggedness calculated at 0.54-km radius (TRI$_{0.54}$) among sage-grouse locations (nest, early-brood, and late-brood locations) by alternating the reference level. Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

				95% CI	
Group [a]	Variable	Estimate	SE	Lower	Upper
Early-brood vs. Nest					
	Intercept	-11.14	1.39	-13.88	-8.40*
	Small avian predator	-0.26	0.07	-0.39	-0.13*
	Medium avian predator	-0.20	0.03	-0.27	-0.14*
	Large avian predator	-0.45	0.12	-0.69	-0.22*
	OGS$_{0.25}$	-1.53	1.25	-3.97	0.92
	POW$_{1.0}$	-0.99	0.65	-2.27	0.28

	$HOM_{1.0}$	1.86	0.84	0.20	3.52*
	$MRD_{1.0}$	0.65	1.08	-1.47	2.77
	$RIP_{1.0}$	0.61	0.30	0.03	1.19*
	$TRI_{0.54}$	0.02	0.01	0.00	0.03*
Late-brood vs. Nest					
	Intercept	-11.40	1.76	-14.88	-7.93*
	Small avian predator	-0.22	0.09	-0.39	-0.05*
	Medium avian predator	-0.20	0.05	-0.29	-0.10*
	Large avian predator	-0.32	0.14	-0.60	-0.05*
	$OGS_{0.25}$	-8.52	4.20	-16.80	-0.24*
	$POW_{1.0}$	-1.09	0.90	-2.86	0.68
	$HOM_{1.0}$	2.85	0.96	0.95	4.75*
	$MRD_{1.0}$	-0.32	1.61	-3.49	2.84
	$RIP_{1.0}$	2.05	0.39	1.28	2.82*
	$TRI_{0.54}$	0.03	0.01	0.01	0.04*
Late-brood vs. Early-brood					
	Intercept	-0.26	2.08	-4.35	3.84
	Small avian predator	0.04	0.10	-0.16	0.24
	Medium avian predator	0.01	0.05	-0.10	0.11
	Large avian predator	0.13	0.18	-0.22	0.47
	$OGS_{0.25}$	-6.99	4.23	-15.32	1.33

$POW_{1.0}$	-0.10	0.92	-1.90	1.71
$HOM_{1.0}$	0.99	0.83	-0.64	2.62
$MRD_{1.0}$	-0.97	1.52	-3.97	2.02
$RIP_{1.0}$	1.44	0.38	0.70	2.18[*]
$TRI_{0.54}$	0.01	0.01	-0.01	0.03

[a] The second category was denoted as the reference level to display parameter estimates.

[*] Denotes a 95% confidence interval that does not include zero.

CHAPTER 4

EFFECTS OF COMMON RAVEN REMOVAL ON GREATER SAGE-GROUSE NESTING SUCCESS IN SOUTHERN WYOMING

ABSTRACT Predator removal has been simultaneously proposed and criticized as a potential mitigation measure for low reproductive rates of greater sage-grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”). Depredation of sage-grouse nests can be an influential factor limiting their productivity, and most failed sage-grouse nests are depredated by predators including common ravens (*Corvus corax*: hereafter “raven”). In Wyoming, lethal removal of ravens was conducted by USDA/APHIS/Wildlife Services (WS) for the protection of livestock. I hypothesized that sage-grouse nest success would be greater in areas where WS lowered the abundance of ravens. I assessed the change in density of ravens and nest success of sage-grouse in areas within 15 km of WS raven removal efforts and areas farther away. I also evaluated sage-grouse nest success in relation to: 1) differences between yearling and adult sage-grouse, and 2) the effect of ravens (nest site-level and study site-level) on nest success of sage-grouse in relation to microhabitat. During 2008–2011, I conducted 3,842 10-minute point count surveys at 341 sage-grouse nests and 660 random locations in southern Wyoming. Point counts were conducted to assess raven density. I found that raven densities at removal study sites decreased 61% between 2008 and 2011, whereas raven densities at non-removal study sites increased 42% between 2008 and 2011. A year × study site type (removal or non-removal) model did not fit the data well, which suggested that I did not detect a direct improvement to nest success of sage-grouse from reduction of ravens by WS; however, generalized linear modeling indicated that higher nest success of sage-grouse was correlated with study sites that had lower values of site-specific change in raven density (raven density relative to a particular study site [study site-level] with lower values of site-specific change in raven density found in removal study sites after removal had occurred). Nest success of sage-grouse was negatively impacted by occupancy of ravens within 550 m of a sage-grouse nest (nest site-level). Nest success of sage-grouse nests that were not occupied by ravens during the last nest check was estimated at 41% (95% confidence interval [CI] = 35% to 46%) using a 28-day incubation period with Program MARK; whereas, the success of nests occupied by ravens was estimated at only 22% (95% CI = 11% to 37%). My mixed results with respect to the potential benefit of raven removal by WS indicated that there was not a strong connection between raven removal and increased sage-grouse nest success; nevertheless, predator removal may have a place in sage-grouse management as an interim mitigation measure when sage-grouse populations are subjected to high densities of ravens. However, long-term solutions to reduce human-subsidized raven populations are necessary to address the growing raven and sage-grouse conflict.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*: hereafter “sage-grouse”) distribution and abundance in western North America has declined over the last century (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004). This decline has recently led the U.S. Fish and Wildlife Service (2010) to conclude that sage-grouse are warranted for protection under the Endangered Species Act of 1973, but the listing was precluded in favor of other species under severe threat of extinction. Many factors have been attributed to this decline including habitat loss, habitat fragmentation, habitat degradation, and predation (Braun 1998, Schroeder et al. 2004). Several studies have suggested that quantity and condition of breeding habitat is the most important factor that dictates the productivity of sage-grouse (Connelly et al. 1994, Braun 1998, Schroeder and Baydack 2001, Coates 2007, Hagen 2011). However, even in excellent sage-grouse habitat, most sage-grouse nests are lost to predators such as red fox (*Vulpes vulpes*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), black-billed magpies (*Pica hudsonia*: hereafter “magpie”), and common ravens (*Corvus corax*: hereafter “ravens”; Willis et al. 1993, Gregg et al. 1994, Heath et al. 1997, Holloran 1999, Connelly et al. 2004). Unlike other population limiting factors (e.g., habitat, weather, and drought), predation can realistically be reduced by wildlife management agencies (Cote and Sutherland 1997). However, there are no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult), and sage-grouse have relatively high nest and adult survival rates (Connelly et al. 2011). Thus, Hagen (2011) suggested that in general predation is not limiting sage-grouse populations, and predator removal may only serve to provide a short-term release of predation rates in fragmented habitats and areas with human-subsidized predator populations.

In contrast, breeding success of other ground-nesting birds has been shown to be suppressed by generalist predators, such as ravens, magpies, red fox, coyotes, and badgers (Evans 2004). Generalist predators can reach high densities in landscapes with human-associated resources. Their densities are not limited by the density of a particular species of prey (Schroeder and Baydack 2001, Evans 2004, Manzer and Hannon 2005, Coates 2007). These factors enable a generalist predator to potentially suppress prey populations. Sage-grouse populations may also be impacted by increases in generalist predator populations, or decreases in the primary prey of generalist predators that cause these predators to switch prey (Schroeder and Baydack 2001, Connelly et al. 2004).

There are increasing levels of human development in sage-grouse habitat, which has brought a range of new stresses to sage-grouse from habitat fragmentation to predation (Connelly et al. 2004, Doherty et al. 2010, Kirol 2012). Human activities are impacting sage-grouse habitat resulting in increased fragmentation, and one of the consequences of fragmentation may be increased predation rates (Schroeder and Baydack 2001). During the last century, densities of ravens have increased in Wyoming and throughout the historic range of sage-grouse (Larsen and Dietrich 1970, Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Sauer et al. 2011). Ravens utilize human-provided food resources, such as road-kill, dead livestock, and garbage (Knight and Call 1980, Boarman 1993, Boarman et al. 1995), especially during winter. Raven depredation of sage-grouse nests has been implicated as a potential factor limiting sage-grouse productivity in fragmented habitats (Batterson and Morse 1948, Willis et al. 1993, Gregg et al. 1994, Schroeder and Baydack 2001, Coates and Delehanty 2010, Bui et al. 2010). Raven depredation on sage-grouse nests is a common occurrence in northeast Nevada based on infrared video cameras set up at nest sites (Coates et al. 2008), and sage-grouse nest success in northeast Nevada was related to the number of ravens per 10-km transect with nest failure rates increasing 7.4% with every additional raven/10 km (Coates and Delehanty 2010).

Leu et al. (2008) developed a corvid-presence risk model to predict the presence of ravens in sage-grouse habitat based on average daily raven movements from Boarman and Heinrich (1999). Factors used to model the increased risk of corvid-presence were populated areas, campgrounds, rest stops, agricultural land, and landfills (Leu et al. 2008). In the corvid-presence risk model, 58% of all sage-grouse habitat was classified as high or medium risk of corvid presence, whereas only 7% of sage-grouse habitat was classified as negligible risk of corvid presence (Leu et al. 2008). In addition, lambing and calving areas are known to provide short-term food rich areas that attract ravens from vast distances during the spring (Heinrich 1988, Marzluff and Heinrich 1991). Higher raven densities around livestock areas increase the likelihood that ravens will depredate sage-grouse nests around these areas.

Subsidized raven populations of increasing size have been anecdotally documented in southwest and south-central Wyoming associated with human activities (e.g., livestock and natural gas development; R. J. Merrell, United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services [WS], personal communication), and raven abundance has increased in Wyoming during the past decade, 2001–2010 (Sauer et al. 2011). Raven control (lethal removal; hereafter “raven removal”) efforts of varying intensity have been carried out by WS in Carbon, Lincoln, Sweetwater, and Uinta counties in Wyoming, 2007–2011 for the protection of livestock, which provided a unique opportunity to study the potential effects of raven removal on sage-grouse nest success. I hypothesized that sage-grouse nest success would be greater in areas where WS lowered the abundance of ravens. To test this hypothesis, I assessed the change in density of ravens and sage-grouse nest success in areas associated with WS raven removal efforts and areas farther away during 2008–2011. As secondary objectives, I evaluated differences between yearling and adult sage-grouse nest success, and the effect of ravens on nest success at the sage-grouse nest level in relation to microhabitat.

STUDY AREA

My study was conducted in southwest and south-central Wyoming. I had 12 study sites, each 16 or 24 km in diameter (eight study sites of 16-km diameter and four study sites of 24-km diameter; Fig. 4-1). To evaluate sage-grouse response to raven removal in a similar area, study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured based on results found by Holloran and Anderson (2005). Study sites in south-central Wyoming were 24 km, because sage-grouse were captured at several nearby leks over a larger area. Five out of 12 study sites were within 15 km of WS raven removal activities (Fig. 4-1). Study sites within 15 km of WS raven removal were considered ‘removal study sites’, those at a distance >15 km were considered ‘non-removal study sites’. Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming with a variety of land uses, topographic features, and raven management.

Removal and non-removal study sites had similar topographic features, weather, and vegetation. Elevation ranged from 1,950 m to 2,600 m among removal study sites and 1,925 m to 2,550 m among non-removal study sites. Most of the land within all of the study sites was federally owned and administered by the Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in two of the removal study sites and four of the non-removal study sites.

The landscape at all study sites was dominated by sagebrush (*Artemisia* spp.); Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and dwarf sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included arrowleaf balsamroot (*Balsamorhiza sagittata*), buckwheat (*Eriogonum* spp.), common yarrow (*Achillea millefolium*), dandelion (*Taraxacum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), lupine (*Lupinus* spp.), sego lily (*Calochortus nuttallii*), and wild onion (*Allium* spp.). Common grass species included: bluegrasses (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in any of the study sites.

METHODS

Sage-grouse Capture and Monitoring

From 2008 to 2011, I monitored sage-grouse hens during the nesting season (late-April to mid-July). Hens were captured, radio-collared, and released in April of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, MN, USA). I aged sage-grouse hens as yearlings or adults by examining outer primaries (Patterson 1952).

Between May 1 and July 15, I located hens weekly with VHF receivers (Communications Specialists, R-1000, Orange, CA, USA) and 3-way Yagi antennas (Communications Specialists, Orange, CA, USA). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. I used handheld global positioning system (GPS) units (eTrex, Garmin

Inc., Olathe, Kansas) to record hen locations. Location accuracy on the GPS ranged from 2 – 8 m.

Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until the nest hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least 1 egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation).

Raven Abundance Monitoring

Between May 1 and August 1 of each year, I conducted point count surveys at sage-grouse nests and random locations within each study site to compare raven densities. To avoid disturbing an incubating hen, nest point counts were conducted 100–200 m away from a sage-grouse nest but within a line-of-sight of that sage-grouse nest. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap 10.0 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest GAP landcover data from 2008. Random locations were designated to be >1000 m apart; however, random selection led to average nearest neighbor distances among random point count locations of >2000 m (Table 4-1). I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. I generated a new set of random locations each year to avoid spatial autocorrelation; thus, random locations among years were independent.

I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all ravens observed during point counts and recording each raven's distance from the observer (when standing at the center of the point count location). I recorded distance as the distance from the observer to where a raven was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with ravens being attracted to or flushed away from an observer. When a raven was displaced from the center of a point count location as an observer approached (6.4% of all detected ravens), I recorded distance from that raven to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). This was done when the approach of an observer resulted in a raven moving away from the center of the point count location. A 1500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, California) in conjunction with a GPS was used to estimate distances directly or to validate visually estimated distances.

Observers were trained and tested in corvid and raptor identification before conducting point counts. Point counts were 10 min in length, and I conducted them during daylight hours on a weekly basis at each study site. I visited each point count location 1 to 8 times with most locations visited ≥3 occasions. I did not survey for ravens in inclement weather (i.e., when raining or wind speeds greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed to 2% of detections within truncated observation distances. Nest point counts were performed after nests were initially located; thus, nest point counts were conducted in May to early-July. I performed random point counts May to 1 August each year.

I intermixed the sampling of nest and random point counts within each study site. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week (i.e., each individual point count location regardless of type—nest or random—was conducted at a different time of day each week and by a different observer as best as possible). The observers conducting point counts within a particular study site changed each year.

Raven Removal

WS began lethally removing ravens in Carbon, Lincoln, and Sweetwater counties in March 2007 and Uinta County in February 2008 (R. J. Merrell, personal communication). Removal of ravens was conducted in response to livestock depredation; thus, WS removal activities were implemented at raven foraging areas or roosts near areas used by livestock (0–15 km). WS removal activities were more focused on raven foraging areas (lambing and calving grounds and landfills; Table 4-2) from February 2009 to June 2011.

WS personnel performed concentrated raven removal using DRC-1339 (3-chloro-p-toluidine hydrochloride) by treating 1.3-cm meat cubes or dog food or shooting them with shotguns (R. J. Merrell, personal communication); however, direct removal was uncommon (Carbon, Lincoln, Sweetwater, and Uinta counties four year total n = 57 ravens). Typical WS raven removal methods entailed pre-baiting with non-treated bait for a few days to acclimate ravens to foraging on bait (meat cubes or dog food) before applying DRC-1339 to bait (R. J. Merrell, personal communication). The amount of DRC-1339 and bait applied at individual removal locations was proportional to the number of ravens WS personnel witnessed in that area. DRC-1339 concentration was applied as specified by the U.S. Environmental Protection Agency label (LD_{50} = 5.6 mg/kg; Larsen and Dietrich 1970). Each spatiotemporal specific application of DRC-1339 or direct removal was considered a ‘removal event’.

To assess the efficacy of WS raven removal, I constructed spatiotemporal variables to describe the number of proportional removal events around nest and random point count locations during 2008–2011. Time was incorporated by including all removal events that occurred within 3 or 6 months prior to a sage-grouse nest’s fate or prior to the last date a random point count was conducted. The distance to the nearest removal event within 3 or 6 months was calculated for each point count location with ArcMap 10.0. The total number of removal events within 7 km, 15 km, or 25 km of a point count location were calculated for 3 and 6 months with ArcMap 10.0. I also calculated the number of removal events at landfills and other locations separately within 3 and 6 months. Removal events at landfills were calculated within 25 km under the assumption that ravens may be drawn into landfills from farther away, while non-landfill removal events were calculated at 7 km, 15 km, and 25 km from a point count location for 3 and 6 months excluding removal events at landfills. I report means (SE) of all removal event variables for removal and non-removal study sites (Table 4-3). I adapted the 7-km (153.9

km^2), 15-km (706.5 km^2), and 25-km (1962.5 km^2) search radii around point count locations to correspond to reported raven average home-range (California 0.3–45.8 km^2 [Linz et al. 1992], Minnesota 27.3–195 km^2 [Bruggers 1988]), average daily movements (Mojave Desert 4.5 km [Boarman et al. 1995], Idaho 6.9 km [>95% of movements within 12.5 km; Engel and Young 1992]), and documented roaming distances (Minnesota average 1,252 km^2 [Bruggers 1988], Maine >1,800 km^2 [Heinrich 1988], and Michigan average radius 27 km [range 3–147 km; Boarman and Heinrich 1999]). The smallest home-ranges correspond to breeding pairs, and larger distances correspond to non-breeding individuals.

Vegetation Variables

I sampled vegetation at sage-grouse nests in late-May to early-July 1 to 2 weeks after sage-grouse nests hatched or failed. I recorded the max height and the average canopy cover of the nest shrub. I quantified vegetation within 5 m surrounding sage-grouse nests by orienting 2 vegetation transects—each 10 m in length—at the cardinal directions and intersecting at a sage-grouse nest. Vegetation transects were conducted to measure average total shrub cover—including antelope bitterbrush, greasewood, rabbitbrush, sagebrush, Saskatoon serviceberry, and snowberry—using the line-intercept method (Canfield 1941). Average percent cover of shrubs was calculated by dividing the total shrub intercepted line length (cm) by the total line length (2000 cm) and then multiplying by 100. Gaps <3 cm were not recorded (Wambolt et al. 2006), and no section of shrub cover was measured more than once. I averaged the height of shrubs that intersected the vegetation transect for average total shrub height; shrub heights excluded inflorescences. I calculated percent cover of grass, perennial grass, forbs, bare ground, and litter in six cover classes (1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%; Kirol et al. 2012) by averaging 9 20-cm × 50-cm quadrats placed along vegetation transects at 2 m, 4 m, 5 m, 6 m, and 8 m (Daubenmire 1959). Perennial grass height was measured by recording the maximum grown height (droop height) excluding flowering stalks within 1 m of the 9 quadrats. The lowest visible 5-cm section of a Robel pole—that was placed in the center of a sage-grouse nest—was recorded to provide an index of general line-of-sight obstruction (hereafter “visual obstruction”; Robel et al. 1970). I recorded Robel pole readings from 1 m off the ground and 5 m away at the 4 cardinal directions and averaged these values to report 1 visual obstruction measurement per site. I report means and standard errors (SE) for vegetation variables used in models for removal and non-removal study sites (Table 4-4).

Data Analyses

I implemented a spatiotemporal modeling strategy to evaluate general trends in 1) the effects of WS removal activities on raven abundance and 2) the effects of study site-level and sage-grouse nest-level raven abundance and microhabitat on sage-grouse nest success. A spatiotemporal strategy was implemented because many variables describing raven abundance and sage-grouse nest survival were exclusive to a given year or study site type (removal or non-removal). Modeling of raven abundance and sage-grouse nest survival were conducted with an information theoretic approach (Anderson 2008), and I compared models with Akaike's information criterion adjusted for sample size (AIC$_c$) and Akaike weights (w_i; Burnham and Anderson 2002). I classified models <2 AIC$_c$ compared to the null model as having moderate support, and models with <4 AIC$_c$ compared to the null as having a greater degree of support (Burnham and Anderson 2002, Arnold 2010). To allow for direct comparison of raven and microhabitat variables, I reported all *a priori* models with explanations of non-informative variables as suggested by Arnold (2010). I evaluated goodness-of-fit of top selected AIC$_c$ models by computing a ratio of Zheng's (2000) proportional reduction of deviance (RDR) for covariate models to spatiotemporally saturated models (maximum proportional reduction in deviance; Iles 2012), which has been considered appropriate for generalized linear models (Zheng 2000, Aubry et al. 2011, Iles 2012). Deviance reduction for each spatiotemporally saturated model and top covariate models of interest were calculated relative to null models (time and study site type invariant):

$$D_{\text{int}} = 1 - (\text{deviance}_{\text{interest}}/\text{deviance}_{\text{null}}) \quad (1)$$

$$D_{\text{sat}} = 1 - (\text{deviance}_{\text{saturated}}/\text{deviance}_{\text{null}})$$

$$\text{RDR} = D_{\text{int}} / D_{\text{saturated}} \quad (2)$$

thus, the ratio gives an assessment of a covariate model's relative ability to explain spatiotemporal processes effecting raven abundance and sage-grouse nest survival. The ratio is 1 for the spatiotemporally saturated model and 0 for the null model (Iles 2012). I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any model (r >0.65) as determined with a Pearson's correlation matrix. In this situation I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤ 5, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

Raven density analysis.– I used function ‘distsamp’ in package UNMARKED version 0.9-5 (Fiske and Chandler 2011) in R (R 2.14.2, www.r-project.org, accessed 15 Apr 2012) to model the effects of year, year trend, point count type (nest or random), and removal event variables on the abundance of ravens in removal and non-removal study sites. I assessed general annual raven abundance within removal and non-removal study sites by modeling year, year trend, and point count type. I compared year and year trend in additive models with point count type to assess which form of year best described raven density; thus, year and year trend were not combined in any single model.

For models describing WS removal events, I only included distance to the nearest removal event, number of removal events per area (total and landfill excluded), and landfill removal events that were calculated at the same temporal scale in all modeling. I did not include landfill removal event variables in models with total number of removal events. To assess WS removal effects, the top AIC_c selected WS removal event variable model was compared to a spatiotemporally saturated model with RDR. The saturated model included year, point count type, and year × point count type for removal and non-removal study sites modeled separately. The ‘distsamp’ function fits a multinomial-Poisson mixture model (Royle et al. 2004) that allows for analysis of standard distance sampling data (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010) at discrete distance intervals, while simultaneously modeling detection and abundance (Fiske and Chandler 2011).

For 'distsamp' analyses, raven detection distances were binned into 250-m intervals and right truncated at 1500 m. I chose distance intervals and truncation distances by determining the smallest interval and largest truncation that allowed for adequate fit of distance sampling models. I used 95% confidence intervals (CI) to compare parameter estimates from top AIC_c selected 'distsamp' models. I generated CIs empirically using parameter estimates and SE from 'distsamp'.

I fit half-normal, hazard-rate, uniform, and exponential key detection functions. I compared the fit of all possible key detection functions with detection held constant between point count types (random and nest) and allowing detection to vary between point count types. I selected the appropriate key detection function for removal and non-removal study sites separately using AIC_c. For removal and non-removal study sites, 'distsamp' models with hazard-rate key detection functions held constant were at least 10 AIC_c lower than models with all other key detection functions and detection varying by point count type. This was not surprising, because all point counts were in sagebrush-dominated habitat. I adjusted 'distsamp' parameter estimates for survey effort (difference in the number of visits per point count location) by incorporating the number of visits per point count location as an offset, which is similar to the procedure used in Program DISTANCE (Thomas et al. 2010).

I used 'distsamp' to estimate observer effective detection radius (EDR), which was defined as the distance from the observer that the number of detected ravens beyond EDR was equal to the undetected ravens within EDR (Thomas et al. 2002). ‘Distsamp’ does not allow fitting of observation specific covariates; thus, I was unable to compare models with detection varying among observers; however, I did not find differences in EDR among observers on data collected for the first 3 years of this study in Chapter 2. Thus, I did not incorporate differences in detection among observers into my ‘distsamp’ analyses.

Sage-grouse nest success analysis.– I analyzed daily survival rate (DSR) of sage-grouse nests by fitting generalized linear models of DSR using maximum likelihood in Program MARK (White and Burnham 1999). Model building was conducted in a two-step process to increase efficiency and avoid model dredging. For “Step 1,” I evaluated the effect of year, year trend, study site type, a nesting sage-grouse’s age (AGE), raven density at the study site-level, and raven density or occupancy at the sage-grouse nest-level on sage-grouse nest DSR. For “Step 2,” I used the top AIC_c selected model from Step 1 to evaluate raven abundance effects on sage-grouse nest DSR in comparison to microhabitat variables associated with the nest shrub and habitat directly surrounding the nest (5 m).

I calculated all raven variables from the raw count data within 550 m, which was the ‘distsamp’ estimated EDR. The raw densities were weighted by the number of visits to each point count location. Raven density at the study site-level was calculated at the study site-level by averaging the raven density at all random locations within each study site separately. I had noted through observation that relative changes in raven density within many study sites had positive or negative effects on nest success of sage-grouse. I attributed this phenomenon to the possibility of ravens being more or less effective predators on sage-grouse nests depending on the study site due to overall characteristics of a particular study site (combination of individual raven behavior, topographic roughness, large scale cover, anthropogenic development, etc.). The combination of multiple large scale differences in study sites were not accounted for with the microhabitat variables that I used, such as shrub cover within 5 m around a nest. In addition to landscape raven densities, I calculated site-specific change in raven density—from random point count locations—as the increase or decrease in landscape raven density (annual density) relative to the raven density in a particular study site at the beginning of the study (2008). Thus, site-specific change in raven density was 0 for all study sites in 2008. The site-specific change in raven density variable was intended to look at relative change in risk of depredation within each study site (i.e., does site specific increase or decrease of raven densities effect nest success of sage-grouse). Thus, site-specific change in raven density was not quantifying the effect of the exact density of ravens on nest success of sage-grouse among all study sites. Rather, it was assessing site-specific change in exposure to ravens, which more directly related to the potential effects of WS reducing raven populations within a study site (reducing risk of raven depredation with a study site). Sage-grouse nest-level raven abundance was calculated from nest point counts as 1) raven density (hereafter “nest-level raven density”) at the nest and 2) occupancy (0 or 1) of at least 1 raven during the last nest check when the sage-grouse hen was still on the nest (hereafter “raven occupancy”). In addition to additive models, I included interactions between year × study site type and year trend × study site type to directly assess the effect of WS removal activities at removal study sites on DSR of sage-grouse nests; year and year trend were not included in models with raven variables because raven variables were temporally explicit to year. I did not include both nest-level raven density and raven occupancy in any model, because nest-level raven density and raven occupancy were measured at the same spatiotemporal scale.

I compared the top AIC$_c$ selected sage-grouse nest DSR models from Steps 1 and 2 to a spatiotemporally saturated model with RDR. The saturated model for sage-grouse nest DSR included year; study site type; max nest shrub, average total shrub, and average perennial grass height; average nest shrub, total shrub, grass, forb, bare ground, and litter cover; and visual obstruction. Grass and perennial grass cover were highly correlated ($r > 0.65$), and grass cover fit the data better than perennial grass cover; thus, I included grass cover in modeling instead of perennial grass cover.

Spatial autocorrelation.– Distance sampling estimates are known to be robust to spatial autocorrelation (Thomas et al. 2010); however, spatial autocorrelation violates the independence assumption for generalized linear models. Thus, I created an inverse weighted distance matrix to assess spatial autocorrelation among sage-grouse nests, where nest locations >12 km apart were not considered to be correlated. This distance was used to directly relate to the radius of my 24-km diameter study sites; however, 12 km was also larger than the home range size of breeding ravens (0.3–45.8 km^{-2}; Boarman and Heinrich 1999). Furthermore, I treated all sage-grouse nests, regardless of year, as correlated within 12 km with the degree of correlation related to the distance among nests. I used function ‘moran.test’ in package SPDEP version 0.5-46 in R to calculate Moran’s I for Pearson residuals of top AIC$_c$ selected generalized linear models of sage-grouse nest success.

RESULTS

Raven Density

I conducted 3,842 point count surveys (1,621 at removal study sites and 2,221 at non-removal study sites) during 2008–2011 at 1,001 total point count locations with 341 sage-grouse nest locations and 660 random locations (Table 4-1). I counted 1179 ravens (687 at removal study sites and 492 at non-removal study sites), and ‘distsamp’ estimated EDR was 552 m. The number of detected ravens was greater than 60–80 detections, which Buckland et al. (1993) suggested was necessary for reliable density estimates.

I found that raven densities at removal study sites decreased over time, whereas raven densities at non-removal study sites increased over time (Tables 4-5 and 4-6; Fig. 4-2). For removal and non-removal study sites, raven densities at sage-grouse nests were lower than raven densities at random locations (Table 4-6). The average nearest removal event was 14.5 km (0.4 SE) and 39.3 km (1.0 SE) for removal study sites and non-removal study sites, respectively (Table 4-3).

For models describing general annual raven abundance, top AIC$_c$ ranked ‘distsamp’ models included year and point count type for both removal and non-removal study sites (w_i = 0.65 and w_i = 0.45, respectively; Table 4-5). In removal study sites, I found that 2009 raven densities were only moderately lower than 2009 (95% CI overlapped 0; Table 4-6, Fig. 4-2); whereas, raven densities in 2010 and 2011 were lower than 2008 (Table 4-6, Fig. 4-2). The top removal study site model also included year × point count type (Table 4-5). The interaction between year and point count type indicated that raven density at sage-grouse nests was lower in all years but the difference in raven density at sage-grouse nests and random locations was not as large in 2011. Thus, the density of ravens at sage-grouse nests was similar for 2008 and 2011 and lower in 2009 and 2010 (Table 4-6).

For models describing removal events, I found that removal events calculated at 6 months fit better than removal events at 3 months. Decreases in raven density at removal study sites were best described by the parameter estimates of the number of landfill removal events (-0.073; 95% CI = -0.092 to -0.054), the number of non-landfill removal events within 15 km (-0.134; 95% CI = -0.188 to -0.080), and the distance to the nearest removal event (-0.002; 95% CI = -0.013 to 0.010; Table 4-7, Fig. 4-3). Increases in raven density at non-removal study sites were best described by the parameter estimate of the number of non-landfill removal events within 25 km (0.060; 95% CI = 0.031 to 0.089; Table 4-7, Fig. 4-4). Raven density at removal study sites was not affected by the distance to the nearest removal event, but the distance to the nearest removal event contributed to describing the data. There were 156 out of 593 point counts (26%) within non-removal study sites that had a number of non-landfill removal events within 25 km >0, whereas removal study sites had 358 out of 407 point counts (88%) >0. The top selected AIC$_c$ model for removal study sites (w_i = 1.00) had RDR = 0.908, whereas, the top selected AIC$_c$ model for non-removal study sites (w_i = 0.44) had RDR = 0.491. Thus, removal event variables accounted for most of the reduction in deviance in removal study sites and approximately half of the deviance in non-removal study sites.

Sage-grouse Nest Success

In the four years of study (2008–2011), I found 121 sage-grouse nests in removal study sites with 52%, 35%, 50%, and 57% apparent nest success, respectively, and 220 sage-grouse nests in non-removal study sites with 54%, 57%, 45%, and 43% apparent nest success, respectively (Fig. 4-5). I did not find any differences in DSR of sage-grouse nests among year, year trend, study site type (removal or non-removal), and landscape raven density from Program MARK models; all models with year, year trend, study site type, and raven density at the study site-level had AIC_c values greater than the null model (Table 4-8). However, I found that sage-grouse nest DSR was negatively impacted by site-specific change in raven density (study site-level) and raven occupancy (nest site-level), and microhabitat variables did not greatly improve the fit of DSR models (Tables 4-8 and 4-9). Average DSR for sage-grouse nests that were not occupied by a raven was 0.969 (± 0.003 SE), which yielded an estimated 41% (95% CI = 35% to 46%) nest survival using a 28-day incubation period. This estimate was lower than the apparent nest success of all but one year by study site combination, and highlighted the necessity to account for nests that were depredated or abandoned before I found them by using the nest survival model in Program MARK. Average DSR for sage-grouse nests that were occupied by a raven was 0.948 (± 0.010 SE), which yielded an estimated 22% (95% CI = 11% to 37%) nest survival using a 28-day incubation period. Spatial autocorrelation was not a problem for the top AIC_c selected sage-grouse nest DSR models (Moran's *I*: $P > 0.4$).

Step 1 of sage-grouse nest DSR modeling illustrated that raven occupancy fit the data better than nest-level raven density, and nest level (raven occupancy) and site-level (site-specific change in raven density) variables explained the sage-grouse nest success data better than models with year, year trend, study site type, year × study site type, year trend × study site type, or AGE (Table 4-8). Models with raven occupancy and site-specific change in raven density accounted for 45% and 33% of the cumulative w_i, respectively; whereas, models with year, year trend, study site type, or AGE accounted for lower w_i (13%, 9%, 12%, and 4%, respectively; Table 4-8). Thus, the sage-grouse nest DSR model with raven occupancy + site-specific change in raven density was used in step 2 to compare with microhabitat variables. In step 2, all models that explained the data better than the null model included raven occupancy and site-specific change in raven density, and no microhabitat only model was better than the null (Table 4-9). The best model from Step 2 included raven occupancy, site-specific change in raven density, and average perennial grass height (Table 4-9). The parameter estimates of raven occupancy (-0.52; 95% CI = -0.96 to -0.07) and site-specific change in raven density (-1.27; 95% CI = -2.71 to 0.17) were negatively associated with sage-grouse nest DSR (Fig. 4-6), and the parameter estimate of average perennial grass height was positively associated with sage-grouse nest DSR (0.01; 95% CI = -0.01 to 0.03; Fig. 4-6). Site-specific change in raven density and average perennial grass height were imprecise predictors (95% CI overlapped zero); however, parameter estimates for site-specific change in raven density (95% CI was slightly overlapping 0) had greater explanatory power than average perennial grass height (95% CI was drastically overlapping 0). The top AIC_c model from Step 2 and the raven occupancy + site-specific change in raven density both had $w_i = 0.12$ (Table 4-9). The best Step 1 model had RDR = 0.54 versus RDR = 0.72 for the best Step 2 model; thus, average perennial grass height decreased the deviance but did not add much to w_i or prediction of DSR.

DISCUSSION

Sage-grouse nest success was negatively impacted by the presence of ravens near sage-grouse nests (local scale) and greater values of site-specific change in raven density (landscape scale); although, site-specific change in raven density was a slightly imprecise predictor. My sage-grouse nest success results suggest that sage-grouse nesting in areas with subsidized raven populations may have suppressed nest success, which may contribute to lower sage-grouse population growth rates. I did not find an overall difference in sage-grouse nest DSR between removal and non-removal study sites, which may indicate that all study sites had a similar sage-grouse nest DSR capacity. However, study site differences in raven abundance were accounted for by calculating the change in raven abundance relative to abundance within a study site at the start of the study. Alternatively, there may have been variability in sage-grouse nest DSR among study sites related to factors other than ravens and microhabitat, such as weather. The best sage-grouse nest DSR model had an RDR = 0.72, which indicated that a large proportion of spatiotemporal variability in sage-grouse nest success was not accounted for in my models. The negative effect of ravens on the nest success of grouse has been well documented (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010). For example sharp-tailed grouse (*Tympanuchus phasianellus*) in southern Alberta had 8-times greater nest success in landscapes with <3 corvids/km^2 as opposed to landscapes with ≥3 corvids/km^2 (Manzer and Hannon 2005). Around Jackson and Pinedale, Wyoming, Bui et al. (2010) found that higher occupancy rates of ravens were correlated with failed sage-grouse nests.

Although I could not test for spatial autocorrelation in ‘distsamp’ analyses, densities derived from distance sampling are robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My raven sampling was designed to count the greatest proportion of ravens within a study site each week as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a study site in one day reduced the possibility of double-counting individual ravens during that week’s visit. Counting the same individual raven during different weeks, regardless of the particular point count location, was properly scaled by accounting for survey effort. Replication of point counts by sampling multiple weeks was done to increase the proportion of ravens detected as suggested by Thomas et al. (2010). Spatial autocorrelation was not found to be a problem with nest success models.

Microhabitat variables did not substantially differ between successful and unsuccessful sage-grouse nests, which indicated that all sage-grouse selected nest-sites with relatively equal concealment cover (relative to the habitat that was available) and microhabitat was not a limiting factor. Simultaneous comparison of raven and microhabitat vegetation variables accounted for differences among study sites in relation to sage-grouse nest-site selection. Thus, differences in nest success may be attributed to local and landscape scale raven abundance, local scale composition of other predators, weather, and habitat fragmentation (anthropogenic features).

Local predator densities can impact parental behavior, nest-site selection, and productivity of several prairie grouse species (Gregg et al. 1994, Schroeder and Baydack 2001, Manzer and Hannon 2005, Coates 2007). The presence of predators may induce changes in sage-grouse behavior associated with habitat usage. For instance, sage-grouse reduced time off of their nests when nesting in areas with high abundances of ravens (Coates and Delehanty 2008). Sage-grouse select nest sites at various scales. At the microhabitat scale, sage-grouse predominately choose nest sites in vegetation cover (Connelly et al. 2004). Several studies have reported that sage-grouse select nest sites based on a preference for different microhabitat characteristics, such as: sagebrush density (Wallestad and Pyrah 1974, Connelly et al. 2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005, Kirol et al. 2012), and grass cover (Kaczor 2008, Kirol et al. 2012). Variability in reported microhabitat characteristic preferences of sage-grouse, with reference to nest-site selection, may indicate local differences in available microhabitat. Differences in available microhabitat among studies suggest that cover, in general, is important regardless of the type of vegetation cover that is available (e.g. sagebrush density, shrub height, or grass height). Alternatively, sage-grouse living in areas with different predator compositions, such as avian or mammalian predators, may prefer different types of vegetation cover (Connelly et al. 2004, Coates and Delehanty 2010). Thus, the microhabitat characteristics upon which sage-grouse base their selection of nest-sites and the success of those nests may be a result of available vegetation and predator composition. For example, Coates and Delehanty (2010) found that microhabitat at sage-grouse nest-sites was correlated to nest failure depending on whether a raven or a badger depredated the nest (greater cover protected from ravens, but exposed sage-grouse to greater badger depredation and vice versa—predator facilitation). At the landscape scale, sage-grouse may avoid areas where there are high densities of ravens (Manzer and Hannon 2005, Mezquida et al. 2006; see Chapter 2).

I found that sage-grouse nested in areas with lower densities of ravens in both removal and non-removal study sites compared to random locations as predicted by the predator-avoidance hypothesis. Only 11% of sage-grouse nests had a raven detected during the last nest check with the hen on the nest. In Chapter 2, I found that in general sage-grouse nests had lower densities of avian predators, including ravens, compared to random locations in sagebrush habitat. This pattern of avoidance of avian predators was present when looking at average avian predator densities across years and study sites. My results from ‘distsamp’ for general annual raven abundance indicate that sage-grouse selected nest-sites with fewer ravens compared to the habitat available to them—within a removal or non-removal study site. By selecting habitat with lower raven densities, sage-grouse lower their exposure to avian predation, and risk of reproductive failure. In western Wyoming, Bui et al. (2010) claimed that raven density around sage-grouse nesting and brood-rearing areas (1.0 ± 0.2 [SE] ravens/km^2) was marginally higher than raven densities in available sagebrush habitat (0.7 ± 0.2 [SE] ravens/km^2). The discrepancy between my results and Bui et al. (2010) may be a function of greater anthropogenic development and human activity in their study areas, or raven behavioral adaptations related to available resources (i.e., availability of nesting structure within sage-grouse nesting habitat and sage-grouse eggs).

Sage-grouse may avoid ravens indirectly by avoiding habitats with features that attract ravens (e.g., roads, livestock, rough topography, and tall structures) or directly by watching them; it is more likely that sage-grouse use both indirect and direct means. Arguments against only indirect avoidance include the fact that over half of my study sites had few anthropogenic structures (8 out of 12 study sites had <0.04 km^{-2} of well infrastructure or communication towers). Yet, I found that sage-grouse avoided ravens in all of my study sites. Perhaps in addition to avoiding risky habitats (e.g., near anthropogenic features), sage-grouse also avoid nesting in areas where they see ravens. Clearly more research needs to be done before conclusions can be drawn about the mechanisms behind sage-grouse avoidance of ravens.

My spatiotemporal modeling strategy allowed me to evaluate the general effect of WS removal efforts on raven abundance and raven abundance on sage-grouse nesting success. By using Iles's (2012) ratio of deviance reduction, I was able to assess the relative explanatory power of covariates compared to spatial and temporal processes—fully saturated spatiotemporal models. Raven management conducted by WS during this study was not implemented as a regimented experiment—it was carried out where ravens were causing problems for livestock operations; thus, some spatial locations of removal events changed among years, and DRC-1339 and the number of baits with toxicant were applied proportional to the number of ravens in an area. Thus, utilizing a modeling strategy that acknowledged and incorporated spatiotemporal processes into the evaluation of the data allowed for interpretation of the relative effect of WS raven management compared to annual and spatial variation. Proportional raven removal conducted by WS did not allow me to investigate variability in the concentration of DRC-1339, amount of DRC-1339 laced bait placed in an area, or the type of bait (e.g., meat or dog food). Even without rigorous implementation of WS raven management, my assessment of raven density and sage-grouse nest DSR was beneficial to assessing management as it can be provided from a practical logistics point-of-view.

Raven densities were reduced by WS up to 15 km from locations where WS was controlling ravens for the benefit of livestock (removal study sites; RDR = 0.908). The number of removal events conducted by WS within 15–25 km of non-removal study sites predicted higher raven densities; however, this only partially (RDR = 0.49) accounted for the change in the annual abundance of ravens. There was more anthropogenic development associated with natural gas extraction in non-removal study sites compared to removal study sites; thus, increases in raven density may have also been connected to human activity in non-removal study sites. Removal events were performed near areas with high densities of ravens (areas of raven conflict with livestock). Thus, my results indicate that higher densities of ravens in non-removal study sites were correlated with the point counts within non-removal study sites that were closer to areas with inherently higher densities of ravens (a potential spill-over effect).

Coates (2007) studied the effect of raven removal on sage-grouse nest success at four study areas in Nevada—1 study area with raven removal and 3 study areas without raven removal. Ravens were removed with DRC-1339 treated egg baits (Coates 2007, Coates et al. 2007). With every 1 km increase in distance away from raven removal routes, Coates (2007) found that sage-grouse nests were 2.1% more likely to fail, and ravens were 13% more likely to be the culprit. This information provided a good indication that reduction of raven abundance by WS may provide a benefit for sage-grouse nesting in areas with subsidized raven populations. My study verified that WS raven management can reduce the abundance of ravens at a relatively large scale (15-km radius or 706.5 km^2, Fig. 4-2), and higher sage-grouse nest success was correlated with lower densities of ravens on the landscape (Fig. 4-6). Even though my year × study site type model did not fit the data well, site-specific change in raven density (density of ravens on the landscape) was lowest in study sites that had the greatest WS removal effort within a given year and those were the areas with the highest sage-grouse nest success.

Raven removal by WS during my study most likely removed transient ravens that traveled vast distances from roost to foraging sites. In removal study sites, average distance to the nearest removal event was 14.5 (0.4 SE) km with no removal event conducted <1.1 km from a point count location, which indicates that most breeding ravens (coastal California median home range radius = 0.62 km and Mojave Desert California average home range radius = 0.57 km [Boarman and Heinrich 1999]) were not likely to have encountered removal events. Breeding pairs of ravens actively forage close to their nests, which entails relying on natural food sources (including sage-grouse eggs) more than food subsidies associated with human activities (road-kill, dead livestock, and landfills). Bui et al. (2010) hypothesized that higher densities of ravens near sage-grouse nesting areas were associated with breeding pairs of ravens, and occupancy of breeding pairs was negatively correlated with sage-grouse nest success. Increased anthropogenic structures in natural gas fields potentially allowed for greater overlap of breeding ravens and sage-grouse nesting areas (Bui et al. 2010). Coates (2007) results indicated that sage-grouse nests closer to removal routes had higher nest success, which may have been associated with a reduction in the number of raven breeding pairs. My results indicate that local scale and landscape scale raven abundance had negative consequences for sage-grouse nest success, which was likely correlated with breeding and non-breeding ravens. Kristan and Boarman (2003) found that breeding and non-breeding ravens were associated with increased predation of desert tortoises (*Gopherus agassizii*). Thus, both breeding and transient ravens may contribute to sage-grouse nest failure with greater abundances of transient ravens associated with incidental sage-grouse nest depredations.

Increased raven densities, regardless of breeding status, are likely to result in higher depredation rates on sage-grouse nests (Evans 2004, Bui et al. 2010, Coates and Delehanty 2010). As sagebrush habitat is developed, raven occupancy and density will increase in areas adjacent to and overlapping quality sage-grouse habitat. Increases in the human footprint have occurred and are likely to continue throughout most of the range of sage-grouse (Leu et al. 2008). In addition, high-quality sagebrush habitat may become functionally unavailable to sage-grouse when raven densities are high (see Chapter 2). In removal study sites, I found that the density of ravens at sage-grouse nests was similar in 2008 and 2011; however, the density of ravens on the landscape was much less in 2011 (Table 4-6). This suggests that sage-grouse may have been utilizing a greater proportion of sagebrush habitat in 2011. Thus, habitat availability in removal study sites may not have been as limited in 2011 as opposed to 2008. Holloran and Anderson (2005) suggested that large intact sagebrush habitat with low sage-grouse nest densities was necessary to retain a viable sage-grouse population. In some areas, reductions in raven density at a landscape level may increase the amount of functional habitat for sage-grouse. Several studies on predator-avoidance in birds indicate that the presence of a predator has dramatic impacts on prey species use of habitat (Cresswell 2008). These non-lethal effects were found to be as great or greater than the effects of direct predation. Thus, quality nesting habitat for sage-grouse has become more limited from the loss of functional habitat, which has also resulted in more direct depredation of nests.

MANAGEMENT IMPLICATIONS

The management of ravens may be a potential mitigating strategy for areas of low sage-grouse nest success. Coates (2007), Bui et al. (2010), and Hagen (2011) suggested that predator removal may provide a short-term release in predation rates within fragmented habitats and areas with subsidized predator populations. However, Hagen (2011) indicated that predator removal will not mitigate sage-grouse population declines throughout the range of sage-grouse. I agree that the positive effects of raven removal for sage-grouse nest success are likely short-lived gains. I monitored WS raven management as it applied to livestock depredation; thus, targeted raven management to benefit sage-grouse may produce better results. However, identification of areas where sage-grouse may benefit from raven removal and implementation of a raven removal program targeted at benefitting sage-grouse will not be an easy task. Management of both breeding and transient ravens will be necessary, which will present many challenges. Predator removal may have a place in sage-grouse management when sage-grouse populations are subjected to high densities of ravens as an interim mitigation measure. However, low reproductive rates may persist in many areas due to compensatory predation by other predators (Coates 2007, Bui et al. 2010). Long-term solutions to reduce human-subsidized raven populations are necessary to address the growing raven and sage-grouse conflict. Reducing raven abundance may be possible through non-lethal means, such as reducing availability of supplemental food (road-kill, dead livestock, and garbage) and nesting and perching structures (oil and gas structures, power lines, telephone poles, communication towers, etc.; Jiménez and Conover 2001). More research needs to be focused on understanding raven population dynamics in sagebrush ecosystems, and how to reduce the utility of anthropogenic subsidies (food and nesting structure) for ravens.

LITERATURE CITED

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence.

Springer Science, New York, New York, USA.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

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

Aubry, L. M., E. Cam, D. N. Koons, J. -Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80: 375–383.

Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission Fauna Service, Portland, USA.

Boarman, W. I. 1993. When a native predator becomes a pest: a case study. Pages 191–206 in S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. Conservation and resource management. Pennsylvania Academy of Science, Philadelphia, USA.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, California, USA.

Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). Pages 1–31 *in* A. Poole and F. Gill, editors. The birds of North America, No. 476. The birds of North America, Philadelphia, Pennsylvania, USA.

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.

Bruggers, D. J. 1988. The behavior and ecology of the common raven in northeastern Minnesota. Dissertation, University of Minnesota, Minneapolis, USA.

Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, New York, New York, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model 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. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

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.

Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

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. O. Spencer, Jr., and D. J. Delehanty. 2007. Efficacy of CPTH-treated egg baits for removing ravens. Human-Wildlife Conflicts 1:224–234.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

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

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

Cote, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11:395–405.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Scientist 33:224–227.

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

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Fiske, I., and R. B. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

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

Gregg, M. A., 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.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian

Biology, University of California Press, Berkeley, USA.

Heath, B., R., Straw, S. H. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Wyoming Game and Fish Department, Completion Report, Cheyenne, USA.

Heinrich, B. 1988. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven (*Corvus corax*). Behavioral Ecology and Sociobiology 23:141–156.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

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

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Iles, D. T. 2012. Drivers of nest success and stochastic population dynamics of the common eider (*Somateria mollissima*). Thesis, Utah State University, Logan, USA.

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29:62–69.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institution, Washington, D. C., USA.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis, South Dakota State University, Brookings, USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

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

Knight, R. L., and M. W. Call. 1980. The common raven. Bureau of Land Management, Technical Note No. 344. Bureau of Land Management, Denver, Colorado, USA.

Kristan, W. B., III, and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoise. Ecology 84:2432–2443.

Larsen, K. H., and J. H. Dietrich. 1970. Reduction of a raven population on lambing grounds with DRC-1339. Journal of Wildlife Management 34:200–204.

Linz, G. M., C. E. Knittle, and R. E. Johnson. 1992. Home range of breeding common ravens in costal southern California. Southwestern Naturalist 37:199–202.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Manzer, D. L., 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.

Marzluff, J. M., and B. Heinrich. 1991. Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. Animal

Behavior 42:755–770.

Mezquida, E. T., S. J. Slater, and C. W. Benkman. 2006. Sage-grouse and indirect interactions: potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

Patterson, R. L. 1952. The sage grouse of Wyoming. Sage Books, Denver, Colorado, USA.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149, Berkeley, California, USA.

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.

Royle, J. A., D. K. Dawson, and S. Bates, 2004. Modeling abundance effects in distance sampling. Ecology 85:1591–1597.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

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

106:363–376.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

Thomas, L., S. T. Buckland, K. P. Burnham, D. R. Anderson, J. L. Laake, D. L. Borchers, S. Strindberg. 2002. Distance sampling. Pages 544–552 *in* A.H. El-Shaarawi, and W. W. Piegorsch, editors. Encyclopedia of environmetrics. John Wiley and Sons, Chichester, England.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, R. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

U. S. Fish and Wildlife Service. 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 75:13909–14014.

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

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

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

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120–138.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Zheng, B. 2000. Summarizing the goodness of fit of generalized linear models for longitudinal data. Statistics in Medicine 19:1265–1275.

Table 4-1. Summary of minimum, maximum, and mean distance (m) to nearest neighbor by location type (nest or random) reported by year. Data were collected in southwestern and south-central Wyoming, USA during 2008–2011.

Year	Location Type	*n*	Min	Mean	Max	SD
	Nest	63	241	2194	11812	2671
2008	Random	152	1000	2026	7216	1308
	Nest	85	103	1724.5	7195	1624
2009	Random	172	1000	2138	7073	1091
	Nest	83	107	2009	10011	2313
2010	Random	162	1031	2493	6136	1016
	Nest	109	124	1766	10086	1970
2011	Random	174	1061	2599	8450	1230

Table 4-2. Raven removal was conducted by USDA/APHIS Wildlife Services in southwest and south-central Wyoming during 2007–2011. Total number of removal events at raven foraging and roost sites around removal study sites. Number of removal events at landfills near removal study sites reported in parenthesis. Removal events quantified as the maximum number of events within 3 and 6 months prior to the last point count (sage-grouse nest or random) within a given year.

Year	Number removal events 3 months	Number removal events 6 months
2007	16 (0 landfill)	16 (0 landfill)
2008	6 (0 landfill)	7 (0 landfill)
2009	30 (6 landfill)	44 (6 landfill)
2010	33 (13 landfill)	40 (15 landfill)
2011	16 (1 landfill)	27 (8 landfill)

Table 4-3. Means and standard errors (SE) of variables used to model USDA/APHIS/Wildlife Services (WS) raven removal. Data were collected from 407 and 593 point count locations in removal and non-removal study sites, respectively, in southwestern and south-central Wyoming, USA during 2008–2011.

	Removal study sites		Non-removal study sites	
Variable description	mean	SE	mean	SE
Nearest (km) WS removal event within prior 3 mon	15.8	0.4	39.7	1.0
Nearest (km) WS removal event within prior 6 mon	14.5	0.4	39.3	1.0
Total # WS removal events within 7 km during prior 3 mon	0.2	0.0	0.0	0.0
Total # WS removal events within 7 km during prior 6 mon	0.2	0.0	0.0	0.0
Total # WS removal events within 15 km during prior 3 mon	1.6	0.2	0.0	0.0
Total # WS removal events within 15 km during prior 6 mon	2.1	0.2	0.0	0.0
Total # WS removal events within 25 km during prior 3 mon	3.9	0.2	1.0	0.1
Total # WS removal events within 25 km during prior 6 mon	5.7	0.3	1.3	0.1

# WS removal events at landfills within 25 km during prior 3 mon	2.4	0.2	0.1	0.0
# WS removal events at landfills within 25 km during prior 6 mon	3.3	0.3	0.1	0.1
# WS removal events within 7 km during prior 3 mon	0.2	0.0	0.0	0.0
# WS removal events within 7 km during prior 6 mon	0.2	0.0	0.0	0.0
# WS removal events within 15 km during prior 3 mon	1.3	0.1	0.0	0.0
# WS removal events within 15 km during prior 6 mon	1.6	0.1	0.0	0.0
# WS removal events within 25 km during prior 3 mon	2.2	0.2	0.9	0.1
# WS removal events within 25 km during prior 6 mon	3.3	0.2	1.2	0.1

Table 4-4. Means and standard errors (SE) of variables used to model sage-grouse nest daily survival rate (DSR). Data were collected from 121 and 220 sage-grouse nests at raven removal and non-removal study sites, respectively, in southwestern and south-central Wyoming, USA during 2008–2011.

	Removal study sites		Non-removal study sites	
Variable description	mean	SE	mean	SE
Max height of nest shrub (cm)	61.8	1.8	60.8	1.3
Average canopy cover of nest shrub (cm)	109.6	3.5	113.7	4.7
Total shrub cover (%) within 5 m	42.1	1.3	45.0	1.0
Sagebrush cover (%) at within 5 m	36.0	1.3	37.0	1.0
Average total shrub height (cm) within 5 m	40.3	1.4	39.2	0.9
Average sagebrush height (cm) within 5 m	41.6	1.7	39.9	1.1
Grass cover (%) within 5 m	15.8	1.4	17.4	1.1
Perennial grass cover (%) within 5 m	12.1	0.8	15.5	0.7
Average perennial grass height (cm) within 5 m	21.5	0.9	23.0	0.6
Forb cover (%) within 5 m	6.9	0.7	8.6	0.6
Bare ground cover (%) within 5 m	29.2	1.6	21.9	1.0
Litter cover (%) within 5 m	38.3	1.8	36.9	1.3
Horizontal visual obstruction (dm)	3.2	0.2	3.3	0.1
Raven density at the study site-level (no./ km^2) within	0.2	0.2	0.11	0.1

550 m of random locations				
Site-specific change in raven density (no./km^2) within 550 m of random locations calculated as the change in raven density within a study site relative to 2008	-0.1	0.0	0.0	0.0
Raven density (no./km^2) within 550 m of a sage-grouse nest while sage-grouse on nest	0.1	0.0	0.1	0.0
Raven occupancy (0, 1) within 550 m of a sage-grouse nest during last nest check with hen on nest	N/A	N/A	N/A	N/A
Sage-grouse <1 or ≥1 year at time of capture (AGE)	N/A	N/A	N/A	N/A

Table 4-5. Multinomial-Poisson mixture models assessing the effect of year, year trend, and point count type (sage-grouse nest or random) on raven densities using 'distsamp' in R. Models were analyzed separately for removal and non-removal study sites and then compared with Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (w_i). Standard distance sampling data were collected at 250 m discrete distance intervals during May to early-Aug. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA (n = 121 and 220 nests and n = 287and 373 random point count locations for removal and non-removal study sites, respectively) during 2008–2011.

Models	k	ΔAIC_c	w_i	Deviance
Removal study sites				
Year+point count type+year×point count type[a]	10	0.00	0.65	3326.24
Year+point count type	7	1.24	0.35	3333.76
Year trend+point count type+year trend×point count type	6	24.79	0.00	3359.38
Year	6	25.33	0.00	3359.92
Year trend+point count type	5	31.11	0.00	3367.76
Year trend	4	51.16	0.00	3389.86
Point count type	4	63.05	0.00	3401.76
Null	2	90.08	0.00	3430.82
Non-removal study sites				
Year+point count type[b]	7	0.00	0.45	2721.74

Year trend+point count type	5	1.57	0.20	2727.40
Year+point count type+year×point count type	10	2.25	0.15	2717.80
Year trend+point count type+year trend×point count type	6	2.92	0.10	2726.70
Point count type	4	3.05	0.10	2730.90
Year	6	13.41	0.00	2737.20
Year trend	4	16.72	0.00	2744.58
Null	2	18.43	0.00	2748.32

[a] AIC_c = 3346.80

[b] AIC_c = 2735.93

Table 4-6. Parameter estimates of raven density with *P*-values and 95% confidence intervals (CI) from top AIC$_c$ selected multinomial-Poisson mixture models using ‘distsamp’ in R. Raven densities were modeled with random locations as the reference. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA (*n* = 121 and 220 nests and *n* = 287 and 373 random point count locations for removal and non-removal study sites, respectively) during May to early-Aug, 2008–2011.

					95% CI	
Variable	Estimate[a]	SE	*Z*	*P*	Lower	Upper
Removal study sites						
Intercept	-0.46	0.13	-3.40	<0.001	-0.72	-0.19[*]
Year 2009	-0.12	0.11	-1.12	0.26	-0.34	0.09
Year 2010	-0.94	0.14	-7.00	<0.001	-1.21	-0.68[*]
Year 2011	-0.57	0.12	-4.71	<0.001	-0.80	-0.33[*]
Point count type[a]	-0.82	0.26	-3.13	0.002	-1.33	-0.31[*]
Year 2009×point count type [a]	-0.22	0.42	-0.53	0.60	-1.04	0.60
Year 2010×point count type [a]	-0.01	0.47	-0.02	0.99	-0.93	0.92
Year 2011×point count type [a]	0.60	0.32	1.90	0.06	-0.02	1.22
Non-removal study sites						
Intercept	-1.74	0.26	-6.80	<0.001	-2.24	-1.24[*]
Year 2009	0.51	0.20	2.59	0.01	0.12	0.90[*]

Year 2010	0.41	0.20	2.03	0.04	0.01	0.80[*]
Year 2011	0.53	0.20	2.72	0.007	0.15	0.91[*]
Point count type[a]	-0.48	0.13	-3.74	<0.001	-0.73	-0.23[*]

[*] Denotes a 95% confidence interval that does not include zero.

[a] Point count type (nest or random locations) with random point count locations coded as the reference category.

Table 4-7. Multinomial-Poisson mixture models assessing the effect of removal event variables on raven densities using ‘distsamp’ in R. Models were analyzed separately for removal and non-removal study sites and then compared with Akaike’s information criterion (adjusted for small sample sizes; AIC$_c$) and Akaike weights (w_i). Only the top 10 models for removal and non-removal study sites were reported. Removal event variables used in modeling include removal distance, total removal events, removal events at landfills, and removal events other than at landfills. Removal events were analyzed at 7 km, 15 km, and 25 km. The temporal scale (3 or 6 months prior to nest fate or last point count at a random location) of each model is denoted in parenthesis. Standard distance sampling data were collected at 250 m discrete distance intervals during May to early-Aug. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA (n = 407 and n = 593 for removal and non-removal study sites, respectively) during 2008–2011.

Models	k	ΔAIC$_c$	w_i	Deviance
Removal study sites				
Removal 15k+removal dist+landfill removal (6 month)[a]	6	0.00	1.00	3335.84
Removal 25k+removal dist+landfill removal (6 month)	6	29.36	0.00	3365.20
Removal 15k+landfill removal (3 month)	5	30.04	0.00	3367.92
Removal 15k+removal dist+ landfill removal (3 month)	6	30.52	0.00	3366.34
Removal 25k+landfill removal (6 month)	5	31.58	0.00	3369.48
Removal 7k+removal dist+landfill removal (6 month)	6	32.95	0.00	3368.78

Landfill removal (6 month)	4	37.55	0.00	3377.50
Removal 7k+landfill removal (6 month)	5	39.10	0.00	3377.00
Removal 25k+landfill removal (3 month)	5	50.35	0.00	3388.24
Removal 25k+removal dist+landfill removal (3 month)	6	52.27	0.00	3388.10
Non-removal study sites				
Removal 25k (6 month)[b]	4	0.00	0.44	2733.32
Removal 25k+landfill removal (6 month)	5	0.99	0.27	2732.26
Removal 25k+removal dist+landfill removal (6 month)	6	2.73	0.11	2731.96
Removal 25k (3 month)	4	3.57	0.07	2736.88
Total removal 25k (6 month)	4	4.91	0.04	2738.22
Removal 25k+landfill removal (3 month)	5	5.10	0.03	2736.38
Total removal 25k+removal dist (6 month)	5	6.98	0.01	2738.26
Removal 25k+removal dist+landfill removal (3 month)	6	7.09	0.01	2736.32
Total removal 25k (3 month)	4	7.57	0.01	2740.88
Total removal 25k+removal dist (3 month)	5	9.61	0.00	2740.88

[a] $AIC_c = 3348.04$

[b] $AIC_c = 2741.38$

Table 4-8. Generalized linear models assessing daily survival rate (DSR) of sage-grouse nests using Program MARK. Variables used in modeling include sage-grouse age (AGE), year, year trend, study site type (removal or non-removal), raven occupancy (raven occupancy) and density (raven density) at the sage-grouse nest level, and raven density (landscape raven density) and site-specific change in density of ravens at the study site-level. Models were compared with Akaike's information criterion (adjusted for small sample sizes; AIC$_c$) and Akaike weights (w_i). Data were collected from 121 and 220 sage-grouse nests at removal and non-removal study sites, respectively. Sage-grouse were located in eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA during 2008–2011.

Models	*k*	ΔAIC$_c$	w_i	Deviance
Raven occupancy+site-specific change in raven density[a]	3	0.00	0.25	811.58
Raven occupancy	2	0.39	0.20	813.97
Site-specific change in raven density	2	2.07	0.09	815.66
Null	1	2.14	0.09	817.72
Year	4	3.10	0.05	812.67
Year+study site type+year×study site type	8	3.11	0.05	804.67
Year trend	2	3.54	0.04	817.12
Nest-level raven density	2	3.63	0.04	817.22
Study site type	2	3.64	0.04	817.22
AGE	2	3.69	0.04	817.27

Landscape raven density	2	4.14	0.03	817.72
Year trend+study site type+year trend×study site type	4	4.15	0.03	813.73
Year+study site type	5	4.77	0.02	812.34
Year trend+study site type	3	4.94	0.02	816.52

[a] AIC_c = 817.59

Table 4-9. Generalized linear models assessing sage-grouse nest daily survival rate (DSR) using Program MARK. Variables used in modeling include sage-grouse nest level (raven occupancy) and site-specific change in raven density (Δ site-level raven; site-level raven), max nest shrub height, average nest shrub canopy cover, Robel visual obstruction, total shrub cover, average total shrub height, grass cover, forb cover, bare ground cover, litter cover, and average perennial grass height. Models were compared with Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (w_i). A fully saturated spatiotemporal model was included to assess goodness-of-fit; the fully saturated model included all microhabitat variables, year and study site type (removal and non-removal). Data were collected from 121 and 220 sage-grouse nests at removal and non-removal study sites, respectively. Sage-grouse were located in eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA during 2008–2011.

Models	k	ΔAIC_c	w_i	Deviance
Raven occupancy+Δ site-level raven+perennial grass height	4	0.00	0.12	809.54
Raven occupancy+Δ site-level raven	3	0.04	0.12	811.58
Raven occupancy+Δ site-level raven+visual obstruction	4	0.33	0.11	809.87
Raven occupancy+Δ site-level raven+bare ground	4	1.56	0.06	811.10
Raven occupancy+Δ site-level raven+forb cover	4	1.76	0.05	811.30
Raven occupancy+Δ site-level raven+total shrub height	4	1.77	0.05	811.31

Raven occupancy+Δ site-level raven+grass cover	4	1.81	0.05	811.35
Raven occupancy+Δ site-level raven+total shrub cover	4	1.85	0.05	811.39
Raven occupancy+Δ site-level raven+nest shrub cover	4	1.87	0.05	811.41
Raven occupancy+Δ site-level raven+litter	4	1.99	0.05	811.53
Raven occupancy+Δ site-level raven+nest shrub height	4	2.01	0.05	811.55
Null	1	2.18	0.04	817.72
Visual obstruction	2	2.26	0.04	815.80
Perennial grass height	2	3.25	0.02	816.80
Bare ground	2	3.59	0.02	817.14
Total shrub height	2	3.78	0.02	817.32
Forb cover	2	3.98	0.02	817.53
Nest shrub cover	2	4.00	0.02	817.54
Nest shrub height	2	4.03	0.02	817.57
Total shrub cover	2	4.12	0.02	817.66
Grass cover	2	4.12	0.02	817.67
Litter	2	4.17	0.02	817.72
Spatiotemporally saturated	15	18.93	0.00	806.38

[a] AIC$_c$ = 817.55

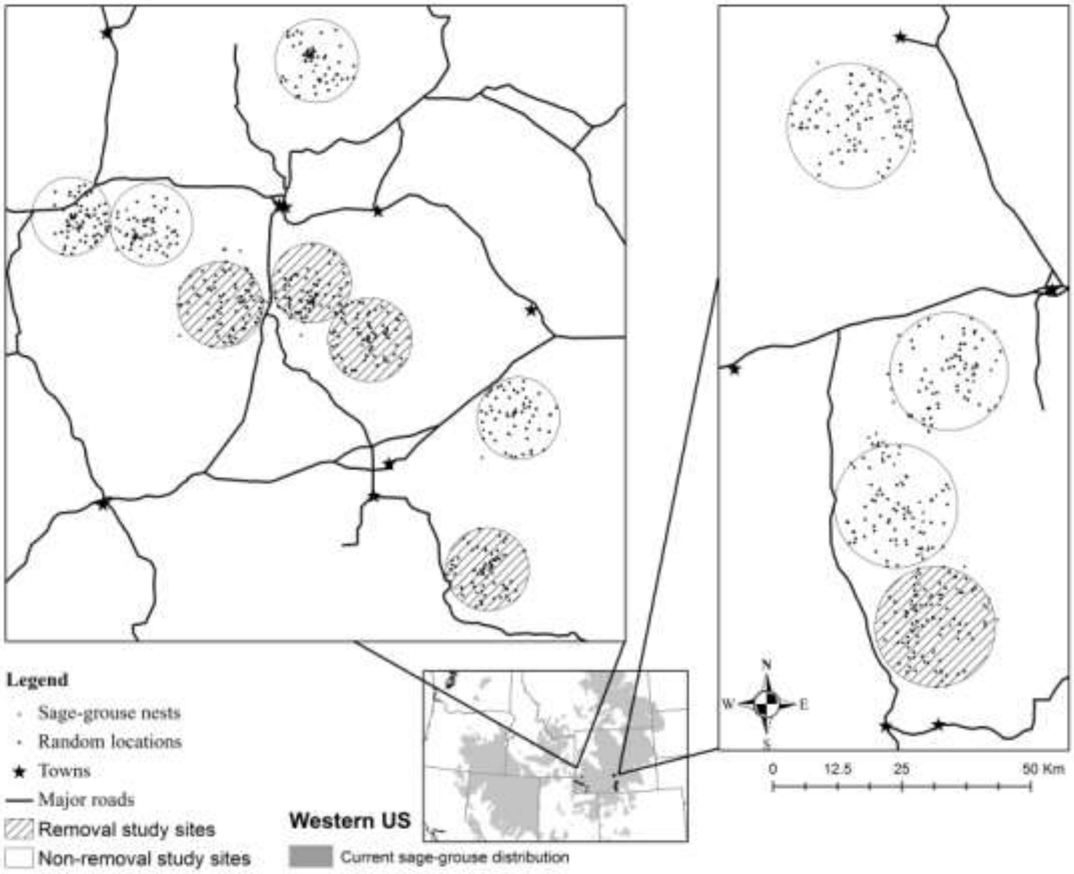


Figure 4-1. Location map of southern Wyoming depicting eight 16-km diameter and four 24-km diameter study sites, southwestern and south-central, Wyoming, USA, 2008–2011. Magnified sections correspond on left to southwest and on right to south-central Wyoming. Map includes locations of 2008–2011 sage-grouse nests, random locations, landfills, towns, and major roads.

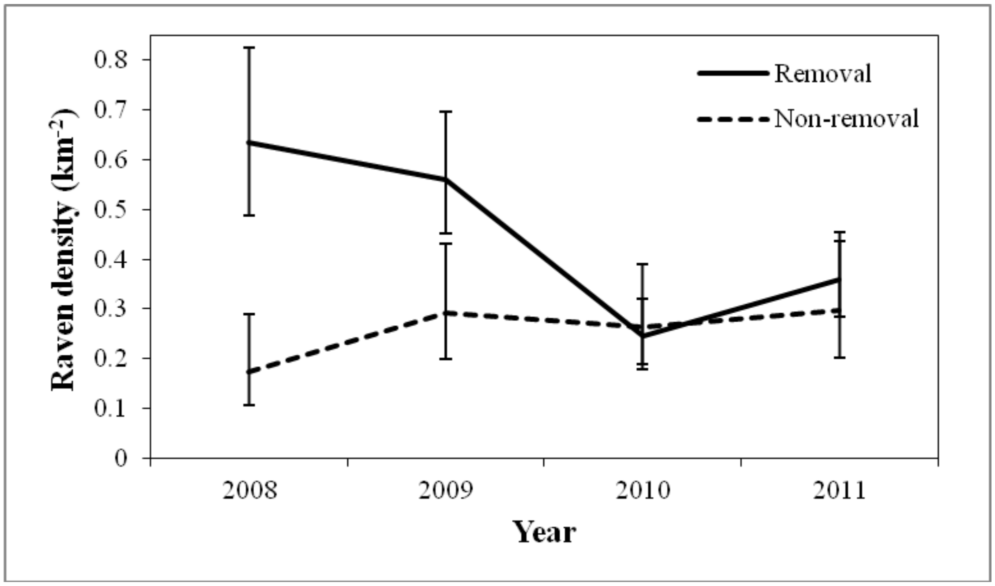


Figure 4-2. Raven density (no./km^2) estimates by year, 2008–2011, from the top AIC$_c$ selected multinomial-Poisson mixture models for removal and non-removal study sites. Estimates of raven density were modeled from 287 and 373 random locations in removal and non-removal study sites, respectively. Error bars indicate 95% confidence intervals. Data were collected from four 16-km and one 24-km removal study sites and four 16-km and three 24-km non-removal study sites in southwestern and south-central, Wyoming, USA.

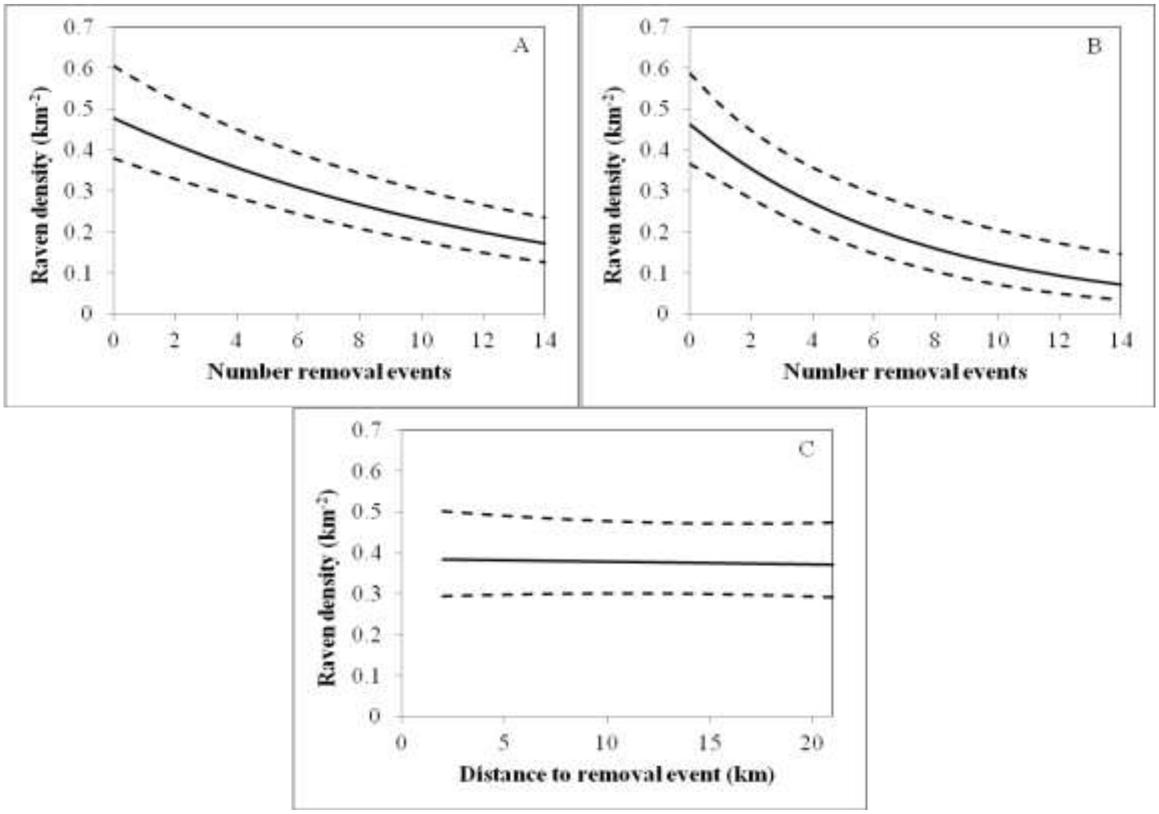


Figure 4-3. Predictions of raven density (no./km^2) from the top AIC$_c$ selected multinomial-Poisson mixture model of USDA/APHIS/Wildlife Services (WS) removal events at removal study sites with 95% confidence intervals. Predicted effects of the number of landfill (A; within 25 km) and non-landfill (B; within 15 km) based removal events conducted by WS and the effect of distance to nearest removal event (C). All variables calculated within six months of the fate of a sage-grouse nest or last recorded point count at a random location. Data were collected from four 16-km and one 24-km study sites in southwestern and south-central, Wyoming, USA (*n* = 121 sage-grouse nests and *n* = 287 random locations), 2008–2011.

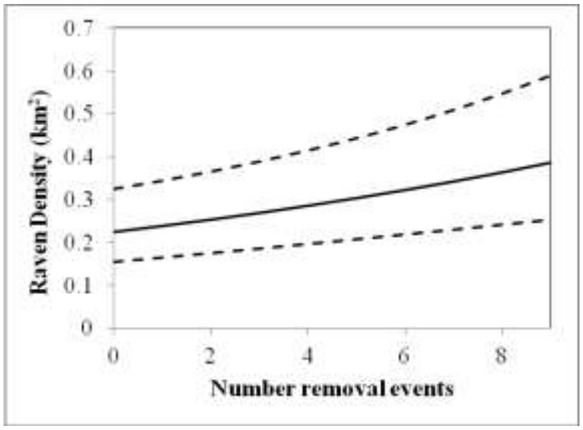


Figure 4-4. Predictions of raven density (no./km^2) from the top AIC$_c$ selected multinomial-Poisson mixture model of USDA/APHIS/Wildlife Services (WS) removal events at non-removal study sites with 95% confidence intervals. Predicted effects of the number of removal events conducted by WS between 15 and 25 km and within six months of the fate of a sage-grouse nest or last recorded point count at a random location. Data were collected from four 16-km and three 24-km study sites in southwestern and south-central, Wyoming, USA (*n* = 220 sage-grouse nests and *n* = 373 random locations), 2008–2011.

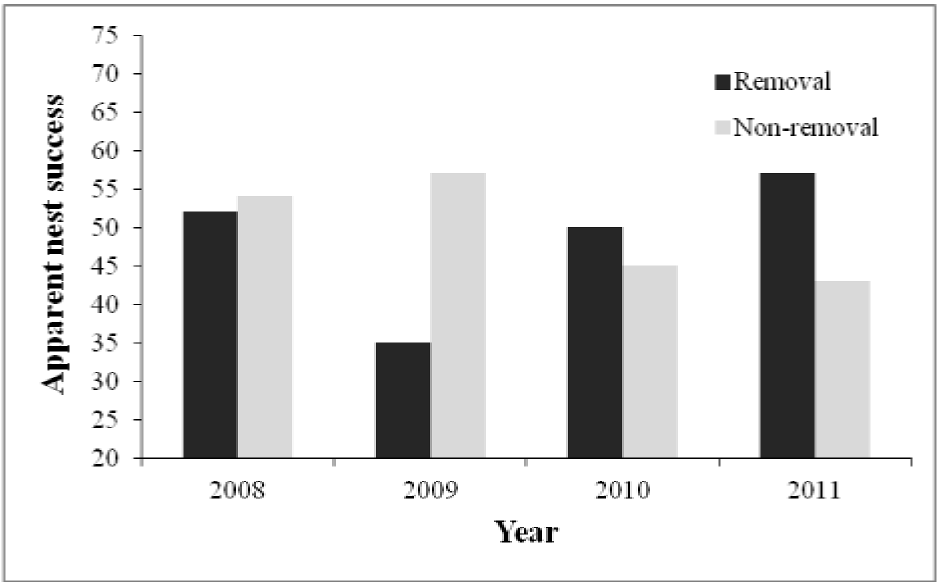


Figure 4-5. Apparent nest success (%) of 341 sage-grouse nests found in removal and non-removal study sites. Apparent nest success was calculated as the number of hatched nests divided by the total number of nests found. Removal study sites had 23, 28, 28, and 42 nests in 2008–2011, respectively. Non-removal study sites had 41, 57, 55, and 67 nests found during 2008–2011, respectively. Data were collected from four 16-km and one 24-km removal study sites and four 16-km and three 24-km non-removal study sites in southwestern and south-central, Wyoming, USA.

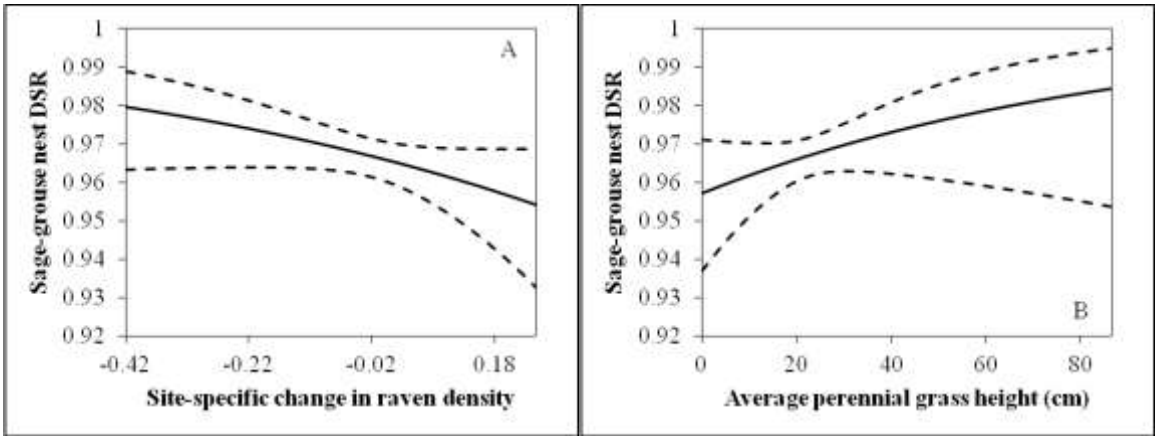


Figure 4-6. Predictions of daily survival rate (DSR) of sage-grouse nests from the top AIC$_c$ selected generalized linear model using Program MARK at removal and non-removal study sites with 95% confidence intervals. Predicted effects of site-specific change in raven density (no./km^2) at a study site relative to 2008 (A) and average perennial grass height within 5 m (B) on sage-grouse nest DSR. Raven variables calculated within EDR (550 m) of 'distsamp'. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA (*n* = 341 sage-grouse nests), 2008–2011.

CHAPTER 5

GREATER SAGE-GROUSE NEST SUCCESS IN RELATION TO CORVIDS, PROXIMITY TO ANTHROPOGENIC AND LANDSCAPE FEATURES, AND MICROHABITAT IN SOUTHERN WYOMING

ABSTRACT Nest success of greater sage-grouse (*Centrocercus urophasianus*: hereafter “sage-grouse”) has been well studied, but the effects of anthropogenic and landscape features on nest success have not been evaluated simultaneously with the potential effects of predators. Depredation of sage-grouse nests can be an influential factor limiting their productivity, and most failed sage-grouse nests are depredated by predators. Black-billed magpies (*Pica hudsonia*: hereafter “magpie”) and common ravens (*Corvus corax*: hereafter “raven”) have been verified with video as predators of ground nests, and the negative effect of ravens on the nest success of sage-grouse has been well documented. I collected nest success data from 341 sage-grouse nests in eight study sites (16 km diameter each) and four study sites (24 km diameter each) in southern Wyoming, USA during 2008–2011. I used the nest survival model in Program MARK to evaluate the effects of 4 covariate sets including corvid densities (nest-level and study site-level), anthropogenic features, landscape features, and microhabitat on sage-grouse nest success. Interactions between study site-level corvid densities (raven and magpie independently) and variables within all other covariate sets were also assessed. I tested the hypothesis that the negative effects of corvids would be amplified in areas closer to potential perches and areas with subsidized food resources. I did not find any evidence that anthropogenic

features or magpies had a negative impact on sage-grouse nest success. I found that nest success was positively correlated with rugged habitat measured at 1-km radius ($TRI_{1.0}$), and negatively impacted by the presence of ravens. My results highlight the necessity to assess habitat and predator community dynamics concurrently when designing management plans.

INTRODUCTION

Several studies have suggested that quantity and condition of breeding habitat is the most important factor that dictates the productivity of sage-grouse (Connelly et al. 1994, Braun 1998, Schroeder and Baydack 2001, Connelly et al. 2011, Hagen 2011). However, even in excellent sage-grouse habitat, most greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") nests are lost to predators such as red fox (*Vulpes vulpes*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), black-billed magpies (*Pica hudsonia*: hereafter "magpie"), and common ravens (*Corvus corax*: hereafter "ravens"; Willis et al. 1993, Gregg et al. 1994, Heath et al. 1997, Holloran 1999, Connelly et al. 2004, Baxter et al. 2007). Sage-grouse are a species of conservation concern, because their distribution and abundance in western North America has declined over the last century (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004), and many factors have been attributed to this decline including predation, habitat loss, and habitat fragmentation (Braun 1998).

Johnson and Braun (1999) and Taylor et al. (2012) found, that along with chick and adult survival, nest success was an important demographic parameter for population growth of sage-grouse. Nest success in relation to predator communities has not been the focus of sage-grouse research and conservation. However, nest success related to predator communities was not likely to have been a problem during pre-European settlement, because sage-grouse co-evolved with the predator communities present in sagebrush ecosystems (Schroeder et al. 1999, Schroeder et al. 2001). There are currently no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult; Hagen 2011, Connelly et al. 2011). Thus, Hagen (2011) suggested that in general predation is not limiting sage-grouse populations; he also indicated that predators may only negatively affect sage-grouse populations in fragmented habitats and areas with human-subsidized predator populations. However, these areas of habitat fragmentation and areas with human-subsidized predator populations have drastically increased in the recent past (Leu et al. 2008); mostly via human endeavors in sagebrush steppe. For example, red fox and common raccoon (*Procyon lotor*) have increased in abundance in sage-grouse habitat, especially near human activities (Connelly et al. 2000, Baxter et al. 2007, Hagen 2011), and densities of ravens have increased in Wyoming and throughout the historic range of sage-grouse (Larsen and Dietrich 1970, Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Sauer et al. 2011).

Increased habitat fragmentation has brought a range of new stresses to sage-grouse including increased predation rates (Schroeder and Baydack 2001, Connelly et al. 2004). Corvids, specifically ravens and magpies, have been known to utilize fragmented habitats with anthropogenic structures and features that provide subsidized food resources (anthropogenic features for ease of discussion; Andrén 1992, Vander Haegen 2002). For example, Bui et al. (2010) found that higher raven occupancy of the landscape was correlated with a greater frequency of failed sage-grouse nests around Jackson and Pinedale, Wyoming. Bui et al. (2010) suggested that increased raven occupancy could have been attributed to increased availability of nest structure for ravens from anthropogenic structures in sagebrush habitat; over half of their study was located in an intensely developed natural gas field. Videos have verified that magpies and ravens are predators of ground nests (Vander Haegen et al. 2002); they found that both species depredated nests in fragmented habitat more often than intact shrubsteppe habitat (magpies especially utilized fragmented habitat). Furthermore, passerine nest success in fragmented habitat was shown to be lower than intact shrubsteppe habitat (Vander Haegen et al. 2002). In addition to the direct negative effect of corvid abundance on sage-grouse nest success, there are potentially additive impacts of anthropogenic features on sage-grouse nest success, such as increased hunting efficiency, increased number of nesting structures, and increased carrying capacity of corvids within sage-grouse breeding habitat. Sources of perch and nesting structure for corvids include oil and gas related structures, residential houses (on buildings or in trees associated with houses), communication towers, and power lines (Engel et al. 1992, Knight and Kawashima 1993, Trost 1999, Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010); whereas, sources of reliable food subsidies include residential houses, campgrounds, landfills, and roads, which provide road-kill, dead livestock, and garbage (Knight and Call 1980, Boarman 1993, Knight and Kawashima 1993, Boarman et al. 1995, Trost 1999, Kristan et al. 2004, Marzluff and Neatherlin 2006).

Corvid depredation of sage-grouse nests has been implicated as a potential factor limiting sage-grouse productivity, especially in fragmented habitats (Batterson and Morse 1948, Willis et al. 1993, Gregg et al. 1994, Schroeder and Baydack 2001, Vander Haegen 2002, Coates and Delehanty 2010, Bui et al. 2010). Yet, it is unclear why anthropogenic features affect corvid depredation of sage-grouse nests.

Connelly et al. (2011) recommended that conservation efforts for sage-grouse should include research to quantify predator communities in relation to sage-grouse demographic rates (including nest success) and potential additive effects of predators and anthropogenic features. Increased size of corvid populations, especially ravens, in areas with subsidized resources has been anecdotally documented in southwest and south-central Wyoming associated with human activities (e.g., livestock and natural gas development; R. J. Merrell, United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services, personal communication), and raven abundance has increased in Wyoming during the past decade, 2001–2010 (Sauer et al. 2011). Thus, I recorded corvid densities associated with sage-grouse nesting and brood-rearing areas from 2008–2011 to determine if corvids were important sage-grouse nest predators. I hypothesized that sage-grouse nest success would be lower in areas and years with greater abundance of corvids, specifically, ravens and magpies. In addition, I hypothesized that this effect would be intensified in areas closer to potential perches and areas with food subsidies, such as oil and gas structures, power lines, houses, roads, towns, and landfills. To test these hypotheses, I assessed sage-grouse nest success in relation to sage-grouse exposure to corvids, potential perches, and proximity to areas associated with human provided food subsidies. As secondary objectives, I evaluated the potential effects of landscape features and microhabitat in relation to corvid abundance. Similar to anthropogenic features, landscape features could be used as perches or nest structure by raptors, or could be areas with higher productivity that attract predators. Thus, I hypothesized that sage-grouse nest success would be lower in areas closer to forested and riparian habitat, rougher topography, and lower microhabitat quality.

STUDY AREA

My study was conducted in southwest and south-central Wyoming. I had 12 circular study sites, eight were 16 km in diameter and four were 24 km in diameter. Study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured based on results found by Holloran and Anderson (2005). Study sites in south-central Wyoming were 24 km, because sage-grouse were captured at several nearby leks over a larger area. Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming. During 2007–2011, raven control (lethal removal) efforts of varying intensity were carried out by USDA/APHIS/Wildlife Services (WS) near five of the 12 study sites for the protection of livestock.

Removal and non-removal study sites had similar topographic features, weather, and vegetation. Elevation ranged from 1,950 m to 2,600 m among removal study sites and 1,925 m to 2,550 m among non-removal study sites. Most of the land within all of the study sites was federally owned and administered by the U.S. Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in two of the removal study sites and four of the non-removal study sites.

The landscape at all study sites was dominated by sagebrush (*Artemisia* spp.); Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and dwarf sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included arrowleaf balsamroot (*Balsamorhiza sagittata*), buckwheat (*Eriogonum* spp.), common yarrow (*Achillea millefolium*), dandelion (*Taraxacum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), lupine (*Lupinus* spp.), sego lily (*Calochortus nuttallii*), and wild onion (*Allium* spp.). Common grass species included: bluegrasses (*Poa* spp.), bluebunch wheatgrass (Ps*eudoroegneria* *spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in any of the study sites.

METHODS

Sage-grouse Capture and Monitoring

From 2008 to 2011, I monitored sage-grouse hens during the nesting season (late-April to mid-July). Hens were captured, radio-collared, and released in April of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, MN, USA). I aged sage-grouse hens as yearlings or adults by examining outer primaries (Patterson 1952).

Between May 1 and July 15, I located hens weekly with VHF receivers (Communications Specialists, R-1000, Orange, CA, USA) and 3-way Yagi antennas (Communications Specialists, Orange, CA, USA). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. I used handheld global positioning system (GPS) units (eTrex, Garmin Inc., Olathe, KS) to record hen locations. Location accuracy on the GPS ranged from 2–8 m.

Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until the nest hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least 1 egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation).

Corvid Variables

Between 1 May and 1 August of each year, I conducted point count surveys at sage-grouse nests and random locations within each study site to compare corvid densities. Ravens and magpies were quantified separately, but will be referred to as corvids for ease of discussion. To avoid disturbing an incubating hen, nest point counts were conducted 100–200 m away from a sage-grouse nest but within a line-of-sight of that sage-grouse nest. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap 10.0 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest ReGAP landcover data from 2008 (Lennartz 2007). Random locations were designated to be >1,000 m apart; however, random selection led to average nearest neighbor distances among random point count locations of >2,000 m (Chapter 2). I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. I generated a new set of random locations each year to avoid spatial autocorrelation; thus, random locations among years were independent.

I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all corvids observed during point counts and recording each corvid's distance from the observer (when standing at the center of the point count location). I recorded distance as the distance from the observer to where a corvid was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with corvids being attracted to or flushed away from an observer. When a corvid was displaced from the center of a point count location as an observer approached (6% of all detected birds), I recorded distance from that corvid to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). This was done when the approach of an observer resulted in a corvid moving away from the center of the point count location. A 1500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, California) in conjunction with a GPS was used to estimate distances directly or to validate visually estimated distances.

Observers were trained and tested in corvid and raptor identification before conducting point counts. Point counts were 10 min in length, and I conducted them during daylight hours on a weekly basis at each study site. I visited each point count location 1 to 8 times with most locations visited ≥3 occasions. I did not survey for corvids in inclement weather (i.e., when raining or wind speeds greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed

2% of detections within truncated observation distances. Nest point counts were performed after nests were initially located; thus, nest point counts were conducted in May to early-July. I performed random point counts May to 1 August each year.

I intermixed the sampling of nest and random point counts within each study site. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week (i.e., each individual point count location regardless of type—nest or random—was conducted at a different time of day each week and by a different observer as best as possible). The observers conducting point counts within a particular study site changed each year.

All corvid variables were calculated from the raw count data within effective detection radii (EDR; 600 m for ravens and 300 m for magpies) estimated with DISTANCE, version 6.0 release 2 (Thomas et al. 2010) as specified in Chapter 2. The raw densities were weighted by the number of visits to each point count location. Raven and magpie study site-level variables were individually calculated from random point count locations. Sage-grouse nest-level corvid abundance was calculated from point counts at sage-grouse nests within species-specific EDRs as 1) raven density (number/km^2 and hereafter “nest-level raven density”) or magpie density (number/km^2 and hereafter “nest-level magpie density”) at the nest and 2) occupancy (0 or 1) of at least 1 raven or 1 magpie during the last nest check when the sage-grouse hen was still on her nest (hereafter: “raven occupancy” or “magpie occupancy”). I did not include both nest-level raven density and raven occupancy in any model, because nest-level raven density and raven occupancy were measured at the same spatiotemporal scale. Study site-level corvid densities were calculated at each study site by averaging the raven or magpie densities at all random locations. I had noted through observation that relative changes in corvid densities within many study sites had positive or negative effects on nest success of sage-grouse. I attributed this phenomenon to the possibility of corvids being more or less effective predators on sage-grouse nests depending on the study site due to overall characteristics of a particular study site (combination of individual corvid behavior, topographic roughness, large scale cover, anthropogenic development, etc.). In addition to study site-level raven densities, I calculated site-specific change in corvid density—from random point count locations—as the increase or decrease in landscape corvid density (annual density) relative to the corvid density in a particular study site at the beginning of the study (2008). Thus, site-specific change in corvid density was 0 for all study sites in 2008. The site-specific change in corvid density variables were intended to look at relative change in risk of depredation within each study site (i.e., does site specific increase or decrease of corvid densities effect nest success of sage-grouse). Thus, site-specific change in corvid densities were not quantifying the effect of the exact density of corvids on nest success of sage-grouse among all study sites. Rather, they were assessing site-specific change in exposure to corvids.

Anthropogenic and Landscape Feature Variables

I calculated sage-grouse proximity to anthropogenic features that could be used as a perch by corvids, a nest structure by ravens, or had the potential to generate food subsidies that were provided by humans (e.g., road-kill, dead livestock, and garbage) with

ArcMap 10.0. Anthropogenic structures that were >2 m in height were considered available for perching or nesting by corvids. I quantified the distance from sage-grouse locations to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings), major road, all roads, communication tower, house, town, landfill, and power line for each sage-grouse nest. Most (>95%) oil and gas structures were energy wells. Ongoing energy development was occurring in half of my study sites, which required me to assess the dates that energy related structures and roads were added or removed from the landscape. In distance calculations, I only included oil and gas structures and roads that were physically on the ground when each sage-grouse nest was located. I obtained information on oil and gas structures, including date construction started on the structure and date when wells were plugged and abandoned (date structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; 2012). I verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture [USDA] 2010). Aerial imagery from NAIP was produced by the USDA on a 3-year rotation; thus, I used WOGCC data and on the ground GPS units to map energy development that occurred after August 2009. However, energy development reported to WOGCC after August 2009 had better reporting of location, spud date, and plug abandon date. I used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, houses, towns, and landfills within a 5-km buffer around study sites; roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units. Major roads included paved, improved gravel roads, and railroads; whereas, all roads included major roads and all unimproved 4-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around study sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power line mapping. Neither sage-grouse nor corvids were likely to discriminate between many of the different types of anthropogenic structures; thus, I created 2 anthropogenic structure variables that represented the nearest 1) distance to either an oil and gas structure, communication tower, or house (DIST_WCH); and 2) distance to either an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from sage-grouse nests to individual types of anthropogenic structures. I report means and standard errors (SE) for distances to anthropogenic feature variables for successful and unsuccessful nests (Table 5-1).

Similar to anthropogenic features, landscape features could be used as perches or nest structures by corvids or could be areas with higher productivity that attract predators. For example, magpies have been associated with riparian habitats for food availability and nesting (Trost 1999). Thus, I used ArcMap 10.0 to calculate the distance from every sage-grouse nest to forest (deciduous and conifer stands) and riparian habitats. Tree stands and riparian habitat were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007), and verified with NAIP imagery from 2009. Topography with greater surface roughness has the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that provide vantage points similar to perches, and sage-grouse have been found to avoid rougher topography during nesting (Jensen 2006, Doherty et al. 2010). For sage-grouse nests, I used ArcMap 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion; TRI variables were developed using a moving window analysis at 0.27-km, 0.54-km, 1-km, and 3-km radii (0.23 km^2, 0.92 km^2, 3.14 km^2, and 28.26 km^2 scales, respectively). Riley et al. (1999) created TRI to describe the roughness of landscapes, and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map; the index is then averaged over a user defined area. I report means and standard errors (SE) for distances to landscape feature variables for successful and unsuccessful nests (Table 5-1).

Microhabitat Variables

I sampled vegetation at sage-grouse nests in late-May to early-July 1 to 2 weeks after sage-grouse nests hatched or failed. I recorded the maximum height and the average canopy cover of the nest shrub. I quantified vegetation within 5 m surrounding sage-grouse nests by orienting 2 vegetation transects—each 10 m in length—at the cardinal directions and intersecting at a sage-grouse nest. Vegetation transects were conducted to measure average total shrub cover—including antelope bitterbrush, greasewood, rabbitbrush, sagebrush, Saskatoon serviceberry, and snowberry (Canfield 1941). Average percent cover of shrubs was calculated by dividing the total shrub intercepted line length (cm) by the total line length (2000 cm) and then multiplying by 100. Gaps <3 cm were not recorded (Wambolt et al. 2006), and no section of shrub cover was measured more than once. I averaged the height of shrubs that intersected the vegetation transect for average total shrub height; shrub heights excluded inflorescences. I calculated percent cover of grass, perennial grass, forbs, bare ground, and litter in six cover classes (1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%; Kirol et al. 2012) by averaging 9, 20-cm × 50-cm quadrats placed along vegetation transects at 2 m, 4 m, 5 m, 6 m, and 8 m (Daubenmire 1959). Perennial grass height was measured by recording the maximum grown height (droop height) excluding flowering stalks within 1 m of the 9 quadrats. The lowest visible 5-cm section of a Robel pole—that was placed in the center of a sage-grouse nest—was recorded to provide an index of general line-of-sight obstruction (hereafter "visual obstruction"; Robel et al. 1970). I recorded Robel pole readings from 1 m off the ground and 5 m away at the 4 cardinal directions and averaged these values to report 1 visual obstruction measurement per site. I report means and standard errors (SE) for vegetation variables used in models for successful and unsuccessful nests (Table 5-1).

Data Analyses

I analyzed daily survival rate (DSR) of sage-grouse nests by fitting generalized linear models of DSR using maximum likelihood in Program MARK (White and Burnham 1999). I evaluated the effect of a nesting sage-grouse's age (AGE), study site-level corvid densities, site-specific change in corvid densities, nest-level corvid occupancy or density, anthropogenic features, landscape features, and microhabitat on sage-grouse nest DSR. Modeling of sage-grouse nest DSR was conducted with an information theoretic approach (Anderson 2008). I compared models with Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002). I employed sequential AIC_c modeling of covariate sets, which was suggested by Arnold (2010) as an appropriate approach for identifying and ranking the most parsimonious models. Non-informative covariates (85% confidence intervals [CIs] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top AIC_c selected models among covariate sets (Arnold 2010).

Four covariate sets were evaluated sequentially, and consisted of 1) nest-level and site-specific change in corvid densities, 2) anthropogenic features, 3) landscape features, and 4) microhabitat variables. I evaluated the effect of a sage-grouse's age (AGE) on sage-grouse nest DSR within the sage-grouse corvid abundance covariate set. I included site-specific change in corvid densities × anthropogenic feature variables, site-specific change in corvid densities × landscape feature variables, and site-specific change in corvid densities × microhabitat as pairwise interactions within each respective covariate set. Pairwise interactions with site-specific change in corvid densities were included to assess whether negative effects of site-specific change in corvid densities were intensified in areas closer to potential perches or corvid nest structure, in areas closer to human provided food subsidies, or in areas with poorer quality microhabitat. I did not include DIST_WCH or ANTH with any other anthropogenic structure variable, because DIST_WCH and ANTH were derived from a combination of distance from sage-grouse nests to energy wells, communication towers, houses, and power lines. The best variable describing the effect of anthropogenic structures on sage-grouse nest DSR was determined through AIC$_c$ selection within the anthropogenic feature covariate set. I compared models with individual TRI variables measured at 0.27 km, 0.54 km, 1 km, and 3 km radii with AIC$_c$ to choose the best spatial scale for the TRI variable to be used in the landscape feature covariate set; the TRI variable scale with the lowest AIC$_c$ was used in all further modeling. As the final modeling step, I compared all top AIC$_c$ selected models from every covariate set (models within 2 AIC$_c$ of the top model within each covariate set) among each other and as additive models with combinations of all 4 covariate sets. I based my inference on models within 2 AIC$_c$ of the top selected model (Burnham and Anderson 2002). I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any model (r >0.65) as determined with a Pearson's correlation matrix. In this situation I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤5, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

In addition to AIC$_c$ model comparison, I implemented a spatiotemporal modeling strategy to evaluate general trends in sage-grouse nest DSR in relation to site-specific change in corvid densities, anthropogenic features, landscape features, and microhabitat. A spatiotemporal strategy was implemented because many variables describing raven abundance and sage-grouse nest survival were exclusive to a given year or type of study site (removal or non-removal). I assessed goodness-of-fit of top AIC$_c$ selected models by computing a ratio of Zheng's (2000) proportional reduction of deviance (RDR) for covariate models to spatiotemporally saturated models (maximum proportional reduction in deviance; Iles 2012), which has been considered appropriate for generalized linear models (Zheng 2000, Aubry et al. 2011). Deviance reduction for each spatiotemporally saturated model and top AIC_c selected models were calculated relative to null models (time and study site invariant):

$$D_{int} = 1 - (\text{deviance}_{interest}/\text{deviance}_{null}) \quad (1)$$

$$D_{sat} = 1 - (\text{deviance}_{saturated}/\text{deviance}_{null})$$

$$\text{RDR} = D_{int} / D_{saturated} \quad (2)$$

thus, the ratio gives an assessment of a covariate model's relative ability to explain spatiotemporal processes effecting sage-grouse nest DSR. The ratio is 1 for the spatiotemporally saturated model and 0 for the null model (Iles 2012). I compared the top AIC_c selected models of sage-grouse nest DSR to a spatiotemporally saturated model with RDR. The saturated model for sage-grouse nest DSR included year; type of study site; max nest shrub, average total shrub, and average perennial grass heights; average nest shrub, total shrub, grass, forb, bare ground, and litter cover; visual obstruction; distance to town, landfill, energy well, communication tower, house, power line, all road, and riparian and forested habitat; and the top selected TRI variable.

Spatial autocorrelation violates the independence assumption for generalized linear models. Thus, I created an inverse weighted distance matrix to assess spatial autocorrelation among sage-grouse nests, where nest locations >12 km apart were not considered to be correlated. This distance was used to directly relate to the radius of my

24-km diameter study sites; however, 12 km was also larger than the home range size of breeding ravens (0.3–45.8 ravens/km^2; Boarman and Heinrich 1999). Furthermore, I treated all sage-grouse nests within 12km of each other, regardless of year, as correlated with the degree of correlation related to the distance among nests. I used function ‘moran.test’ in package SPDEP version 0.5-46 in R to calculate Moran’s *I* for Pearson residuals of top AIC$_c$ selected generalized linear models of sage-grouse nest success.

RESULTS

I found 341 sage-grouse nests (170 hatched [50.0%], 5 abandoned [1.5%], and 166 failed [48.5%]). Average annual DSR for all sage-grouse nests was estimated at 0.968 (± 0.003 SE) from Program MARK, which yielded an estimated 40% (95% CI = 34% to 48%) nest survival using a 28-day incubation period. This estimate differed from the apparent nest success of 49.9%, and highlighted the necessity to account for nests that were depredated or abandoned before I found them by using the nest survival model in Program MARK. To assess the effect of corvid abundance on sage-grouse nest success, I conducted 3,842 point count surveys during 2008–2011 at 1,001 total point count locations with 341 sage-grouse nest locations and 660 random locations. I counted 559 ravens and 121 magpies within species-specific EDR (600 m and 300 m, respectively). Spatial autocorrelation was not a problem for the top AIC$_c$ selected sage-grouse nest DSR model (Moran’s *I*: $P > 0.5$).

Nest-level raven occupancy negatively affected sage-grouse nest success, but I did not find any effects of magpies on nest success of sage-grouse (parameter estimates for magpie occupancy and site-level magpie density had 85% CI that overlapped 0). No anthropogenic variable described differences in sage-grouse nest DSR (parameter estimates with 85% CI that overlapped 0). I found that $TRI_{1.0}$ (1-km radius) from the landscape feature covariate set described sage-grouse nest DSR best. Thus, the top AIC_c selected model included raven occupancy and $TRI_{1.0}$ (Table 5-2, Fig 5-1), which had $w_i = 0.26$ and RDR = 0.37. The second AIC_c ranked model had $w_i = 0.25$ and $\Delta AIC_c = 0.01$. I will only discuss the top model for parsimony, because the second AIC_c ranked model was a more complicated version of the top model. The parameter estimate of $TRI_{1.0}$ was positively associated with sage-grouse nest DSR (0.02; 95% CI = 0.01 to 0.04; Table 5-3), which indicated that sage-grouse had better nest success in more rugged terrain. The parameter estimate of raven occupancy (-0.45; 95% CI = -0.89 to -0.02) was negatively associated with sage-grouse nest DSR (Table 5-3).

DISCUSSION

Nest success of sage-grouse was negatively impacted by the presence and abundance of ravens (nest-level and site-level; Chapter 4). I did not find any evidence that magpies had a negative impact on sage-grouse nest success regardless of microhabitat characteristics near the nest or proximity to anthropogenic or landscape features. Similar to Aldridge and Boyce (2007) and Kirol (2012), I did not find any significant correlations between nest success and proximity to anthropogenic development, and there was no evidence of interactive effects between microhabitat or anthropogenic or landscaped features and corvid densities. Although the landscape features that I assessed represented riskier habitat, I found that nest success was positively correlated with relatively rugged habitat measured within 1 km from nests ($\mathrm{TRI}_{1.0}$). My sage-grouse nest success results suggest that sage-grouse nesting in areas with elevated raven populations may have suppressed nest success. The best sage-grouse nest success model had RDR = 0.37, which indicated that a large proportion of spatiotemporal variability in sage-grouse nest success was not accounted for in my models. Thus, there may have been variability in sage-grouse nest DSR among study sites related to factors such as weather or different predator communities. The positive correlation between rugged terrain and increased nest success of sage-grouse was counterintuitive because Kirol 2012 found that rugged terrain was negatively correlated with adult hen survival, which is the most important factor affecting sage-grouse population growth (Taylor et al. 2012).

Corvids have been found to use anthropogenic structures as perches and nesting structure (Trost 1999, Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010). Several studies have demonstrated that sage-grouse avoided habitat with man-made features, such as oil and gas infrastructure, while nesting (Holloran 2005, Kaiser 2006, Aldridge and Boyce 2007, Holloran et al. 2010, Kirol 2012). Man-made structures are potential perches, nest structure, or provide reliable food subsidies for corvids. I did not find any sage-grouse study that found a direct decrease in sage-grouse nest success in relation to proximity to potential perches. However, sharp-tailed grouse (*Tympanuchus phasianellus*) nest success was correlated to the distance from potential perch sites for corvids and raptors (i.e. nests that were >75 m away from a potential perch were more successful; Manzer and Hannon 2005). Kirol (2012) and I (Chapter 3) found that sage-grouse avoided oil and gas wells while nesting. Sage-grouse may be avoiding man-made structures to reduce risk of nest depredation and predation from corvids and raptors (i.e., sage-grouse may treat anthropogenic features as riskier areas); anthropogenic features do not directly cause any depredations of sage-grouse nests, but anthropogenic features are likely stressors that elevate predation risk in previously suitable habitat. Thus, I hypothesized that sage-grouse nest success would be lower near anthropogenic features and that this effect would be amplified when there was also greater values of site-specific change in corvid densities. However, I did not find support for this hypothesis, because neither independent anthropogenic feature variables nor anthropogenic features in conjunction with site-specific change in corvid densities had an effect on sage-grouse nest success. This indicates that anthropogenic features do not necessarily predict riskier habitat either because sage-grouse avoidance of anthropogenic features masked any effects on nest success or anthropogenic disturbance was not greater than a potential threshold. Proximity to an anthropogenic feature may not be indicative of lower nest success, but rather the quantity of anthropogenic features in close proximity.

In Chapter 4, I did not look at interactive effects of site-specific change in raven density with aspects of habitat (including microhabitat), because I was interested in evaluating direct effects of ravens on sage-grouse nest success in the context of reduction of raven density as a management tool. Simultaneous comparison of the main effects of raven and microhabitat vegetation variables in Chapter 4 was intended to account for differences among study sites in relation to sage-grouse nest-site selection. Thus, differences in nest success could be attributed to local and landscape scale raven abundance. It was possible that the microhabitat at a nest site impacted a nest’s success (Holloran et al. 2005, Moynahan et al. 2007) in fragmented habitat.

The negative effect of ravens on the nest success of sharp-tailed and sage grouse has been well documented (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010, Chapter 4). Coates and Delehanty (2010) found that sage-grouse nests were more likely to be depredated by a raven when nesting in relatively lower total shrub cover (50 m^2 scale), but sage-grouse nests in relatively high visual obstruction (presumably higher total shrub cover) were more likely to be depredated by a badger. This indicates that microhabitat conditions near a sage-grouse nest have different effects on nest success depending on the predator composition of an area, and the presence of different types of predators may induce changes in sage-grouse behavior associated with habitat usage. For instance, sage-grouse reduced time off of their nests when nesting in areas with high abundances of ravens (Coates and Delehanty 2008), which may reduce a sage-grouse’s risk of nest depredation. Sometimes visual predators find nests of ground-nesting birds, including sage-grouse, by watching hens leave or return to nests (Manzer and Hannon 2005, Coates 2007). Sage-grouse also predominately choose nest sites in vegetation cover at the microhabitat scale (Connelly et al. 2004). Several studies have reported that sage-grouse select nest sites based on a preference for different microhabitat characteristics, such as: sagebrush density (Wallestad and Pyrah 1974, Connelly et al.

2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005, Kirol et al. 2012), and grass cover (Kaczor 2008, Kirol et al. 2012). Sage-grouse living in areas with different predator compositions, such as avian or mammalian predators, may prefer different types of vegetation cover (Connelly et al. 2004, Coates and Delehanty 2010). Thus, I hypothesized that higher percent concealment cover and vegetation height (microhabitat characteristics) would have a greater positive effect on nest success when there was higher corvid abundance (interactive effect). However, I did not find any evidence of interactive effects of microhabitat variables and site-specific change in corvid densities on sage-grouse nest success. Interactive mechanisms effecting sage-grouse nest success between predators and habitat characteristics are difficult to detect, but are commonly cited as potential factors effecting nest success; thus, there clearly needs to be more research before conclusions are made.

Magpies have been found to depredate sage-grouse nests (Holloran and Anderson 2003), and magpies have been found to be effective nest depredators in fragmented habitats (Andrén 1992, Vander Haegen et al. 2002). I found a slight negative effect of magpie occupancy (parameter estimate -0.25; 95% CI: -1.27 to 0.77) on sage-grouse nest success, but the magpie occupancy model in the corvid covariate set was below the null model. Thus, I did not find any evidence for increased depredation of sage-grouse nests in areas with greater values of site-specific change in magpie density. Magpie populations may have been too stable to detect direct negative effects of magpie abundance on sage-grouse nest success (i.e., there may not have been enough temporal variation in the values of site-specific change in magpie density to detect differences in sage-grouse nest success). Sage-grouse may have reduced the risk of nest depredation by magpies by not nesting near areas used by magpies (see Chapter 2). Magpies are known to be associated with riparian areas but also forage in sagebrush habitats (Trost 1999). In Chapter 3, I also found that sage-grouse placed their nests away from riparian habitat; therefore, sage-grouse may avoid magpies and the habitat that most frequently has magpies. However, this could also indicate that sage-grouse and magpies select different habitat (differential habitat selection). Within the range of proximity to riparian habitat where sage-grouse nested, the proximity of a sage-grouse's nest to riparian habitat did not affect nest success. Sage-grouse nest success may not have had detectible negative effects from proximity to riparian habitat, because sage-grouse placement of nests was beyond a threshold distance from riparian habitat.

The only landscape feature predictive of sage-grouse nest success was $TRI_{1.0}$, and sage-grouse hens nesting in more rugged habitat at a relatively large scale (1-km radius) were more likely to succeed. I hypothesized that rugged terrain would be riskier habitat and high corvid densities would intensify this effect, because hilltops, knolls, and cliff edges associated with rugged terrain would act as perches for corvids. In addition, moderately rugged terrain may be correlated to greater risk of predation from olfactory predators (mammalian predators), which have been known to hunt in areas such as drainage bottoms. Thus, rugged terrain would correlate with greater exposure to nest depredation from corvids and mammalian predators. Contrary to my hypothesis, I found a positive effect of $TRI_{1.0}$ (Table 5-3). Two potential explanations for this finding include

1) rugged topography may provide some refugia from visual predators (e.g., ravens and magpies), because topographic features such as slight depressions may decrease the effective distance that a corvid can detect a sage-grouse on the ground; and 2) rugged terrain creates atmospheric turbulence, and higher turbulence decreases an olfactory predator's ability to detect prey (Conover 2007). However, Conover et al. (2010) found that sage-grouse use nest locations that hide their nests from visual but not olfactory predators. Even though sage-grouse do not generally nest in locations that provide concealment from olfactory predators, sage-grouse that tend to nest in more rugged topography may experience less nest depredation by olfactory predators. The relationship of topography related to corvid and mammalian depredation of sage-grouse nests was beyond the scope of my study, and more research is needed before conclusions can be drawn about the impact of interactions between landscape features and predator community dynamics on sage-grouse nest success.

MANAGEMENT IMPLICATIONS

A diverse array of generalist predators have encroached into sagebrush steppe habitats throughout the western United States. These generalist predators have been able to sustain elevated populations by capitalizing on structural and forage resources associated with habitat fragmented by humans. Thus, their densities are not limited by the density of a particular species of prey (Schroeder and Baydack 2001, Evans 2004, Manzer and Hannon 2005, Coates 2007). Ravens, magpies, red foxes, and coyotes are generalist predators that use different hunting strategies to obtain prey, and they can suppress the breeding success of ground-nesting birds (Evans 2004). These factors produce complex predator community dynamics that interact with prey species behavior including selection of available habitat. For this reason, management agencies need to understand how interactions among anthropogenic and landscape features, microhabitat, and the predator community relate to sage-grouse demographic rates (e.g., nest success). The aspects of habitat (anthropogenic and landscape features) that present riskier areas for prey species are confounded by the predator composition that reside in those areas. For example, the effect of concealment cover on nest success of sage-grouse can be dependent upon the species of predator near nests (Coates and Delehanty 2010). Likewise, it was unclear how rugged topography related to the risk of nest depredation. Prey species select habitat that reduces the risk of predation; however, selecting nesting habitat that provides them some protection against one predator species may increase their vulnerability to another predator species. Thus, selection of habitat to protect against visual predators may force sage-grouse to nest in riskier habitats with respect to mammalian predators. However, sage-grouse have been found to select habitat that provides concealment from visual and not olfactory predators (Conover et al. 2010). It is imperative to understand the anthropogenic and landscape feature and predator community conditions that reduce sage-grouse exposure to all predators while nesting. My results highlight the necessity to assess habitat and predator community dynamics concurrently when designing management plans.

LITERATURE CITED

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

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer Science, New York, New York, USA.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

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

Aubry, L. M., E. Cam, D. N. Koons, J. -Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80:375–383.

Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission Fauna Service, Portland, USA.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the 72nd North American Wildlife and Natural Resources Conference 72:258–269.

Boarman, W. I. 1993. When a native predator becomes a pest: a case study. Pages 191–206 *in* S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. Conservation and resource management. Pennsylvania Academy of Science, Philadelphia, USA.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, USA.

Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). Pages 1–31 *in* A. Poole and F. Gill, editors. Birds of North America, No. 476. Birds of North America, Philadelphia, Pennsylvania, USA.

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.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model 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. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

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.

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., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

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

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer.

1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

Conover, M. R. 2007. Predator–prey dynamics: the use of olfaction. Taylor and Francis, Boca Raton, Florida, 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. Condor 112:331–336.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Scientist 33:224–227.

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

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

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

Gregg, M. A., 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.

Hanser, S. E., M. Leu, S. T. Knick, and C. L. Aldridge. 2011. Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Heath, B., R., Straw, S. H. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Wyoming Game and Fish Department, Completion Report, Cheyenne, USA.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., and S. H. Anderson. 2003. Direct identification of northern sage-grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.

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

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Iles, D. T. 2012. Drivers of nest success and stochastic population dynamics of the common eider (*Somateria mollissima*). Thesis, Utah State University, Logan, USA.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis, South Dakota State University, Brookings, USA.

Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Thesis, University of Wyoming, Laramie, USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

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

Knight, R. L., and M. W. Call. 1980. The common raven. Bureau of Land Management, Technical Note No. 344. Bureau of Land Management, Denver, Colorado, USA.

Knight, R. L., and J. Y. Kawashima. 1993. Responses of ravens and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266–271.

Kristan, W. B. III, W. I. Boarman, and J. J. Crayon. 2004. Diet composition of common ravens across the urban-wildland interface of the West Mojave Desert. Wildlife Society Bulletin 32:244–253.

Jensen, B. M. 2006. Migration, transition range, and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis, University of Wyoming, Laramie, USA.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institution, Washington, D. C., USA.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage grouse population. Conservation Biology 13:77–84.

Lammers, W. M., and M. W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Larsen, K. H., and J. H. Dietrich. 1970. Reduction of a raven population on lambing grounds with DRC-1339. Journal of Wildlife Management 34:200–204.

Lennartz, S. 2007. USGS Gap Analysis Program (GAP) species distribution model. Sanborn Map Corporation. Portland, Oregon, USA.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Manzer, D. L., 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.

Marzluff, J. M., and E. A. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. Biological

Conservation 130:301–314.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

Patterson, R. L. 1952. The sage grouse of Wyoming. Sage Books, Denver, Colorado, USA.

Prather, P. R., and T. A. Messmer. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

Ralph, C. J., 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, Berkeley, California, USA.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

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.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

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*). *In* A. Poole and F. Gill, editors. Birds of North America. Birds of North America, Philadelphia, Pennsylvania, USA.

Slater, S. J., and J. P. Smith. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

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.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, R. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Trost, C. H. 1999. Black-billed magpie (*Pica hudsonia*). *In* A. Poole and F. Gill, editors. Birds of North America, No. 398. Philadelphia, Pennsylvania, USA.

Vander Haegen, W. M., M. A. Schroeder, and R. M. DeGraaf. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. Condor 104:496–506.

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

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

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

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Wyoming Oil and Gas Conservation Commission (WOGCC). 2012. WOGCC homepage. [Online.] Available at http://wogcc.state.wy.us.

Zheng, B. 2000. Summarizing the goodness of fit of generalized linear models for longitudinal data. Statistics in Medicine 19:1265–1275.

Table 5-1. Means and standard errors (SE) of variables used to model sage-grouse nest daily survival rate (DSR) for successful and unsuccessful nests. Data were collected from 341 sage-grouse nests at eight 16-km and four 24-km diameter study sites in southwestern and south-central Wyoming, USA during 2008–2011.

	Successful		Unsuccessful	
Variable description	Mean	SE	Mean	SE
Max height of nest shrub (cm)	60.34	1.47	61.90	1.48
Average canopy cover of nest shrub (cm)	112.62	5.93	111.90	2.72
Total shrub cover (%) within 5 m	43.47	1.21	44.38	1.02
Average total shrub height (cm) within 5 m	38.90	1.10	40.34	1.07
Grass cover (%) within 5 m	20.31	1.11	19.88	1.17
Perennial grass cover (%) within 5 m	14.17	0.70	14.32	0.86
Average perennial grass height (cm) within 5 m	22.81	0.83	22.15	0.65
Forb cover (%) within 5 m	7.90	0.65	8.06	0.62
Bare ground cover (%) within 5 m	25.46	1.24	23.50	1.26
Litter cover (%) within 5 m	36.96	1.46	37.76	1.52
Horizontal visual obstruction (dm)	3.12	0.13	3.34	0.12
Site-level raven density (no./km^2) within 550 m of random locations	0.15	0.13	0.15	0.13
Site-specific change in raven density (no./km^2) within 550 m of random locations calculated as the	-0.04	0.01	-0.02	0.01

change in raven density within a study site relative to 2008				
Site-level magpie density (no./km^2) within 550 m of random locations	0.14	0.19	0.16	0.20
Site-specific change in magpie density (no./km^2) within 550 m of random locations calculated as the change in raven density within a study site relative to 2008	-0.09	0.02	-0.10	0.02
Raven occupancy (0, 1) within 550 m of a sage-grouse nest during last nest check with hen on nest	N/A	N/A	N/A	N/A
Magpie occupancy (0, 1) within 300 m of a sage-grouse nest during last nest check with hen on nest	N/A	N/A	N/A	N/A
Sage-grouse <1 or ≥1 year old at time of capture (AGE)	N/A	N/A	N/A	N/A
Distance (km) from sage-grouse nest to nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings)	5.71	0.39	5.00	0.33
Distance (km) from sage-grouse nest to nearest major road including paved roads, railroad, and improved gravel roads	1.41	0.10	1.33	0.09

Distance (km) from sage-grouse nest to nearest road including paved roads, railroad, improved gravel roads, and unimproved 4-wheel drive roads	0.34	0.02	0.33	0.02
Distance (km) from sage-grouse nest to nearest communication tower	10.16	0.63	10.04	0.63
Distance (km) from sage-grouse nest to nearest residential house	7.41	0.43	7.49	0.47
Distance (km) from sage-grouse nest to nearest overhead line (transmission or distribution power lines, or telephone line)	7.93	0.39	8.11	0.39
Distance (km) from sage-grouse nest to nearest anthropogenic perch (ANTH; oil and gas structure, communication tower, residential house, or power lines)	3.11	0.18	2.97	0.18
Distance (km) from sage-grouse nest to nearest town	3.46	0.19	3.27	0.19
Distance (km) from sage-grouse nest to nearest landfill	23.77	0.59	24.14	0.52
Distance (km) from sage-grouse nest to nearest oil and gas structure, communication tower, or residential house (DIST_WCH)	28.16	0.82	28.07	0.70
Distance (km) from sage-grouse nest to nearest	2.61	0.24	3.15	0.28

forested habitat including deciduous and conifer stands				
Distance (km) from sage-grouse nest to nearest riparian habitat	1.70	0.11	1.55	0.10
Topographic ruggedness index within 0.27-km radius (0.23 km^2 scale)	19.66	1.03	16.36	0.80
Topographic ruggedness index within 0.54-km radius (0.92 km^2 scale)	19.68	0.93	16.70	0.73
Topographic ruggedness index within 1-km radius (3.14 km^2 scale)	20.63	0.86	17.66	0.69
Topographic ruggedness index within 3-km radius (28.26 km^2 scale)	22.00	0.72	21.33	0.63

Table 5-2. Generalized linear models assessing sage-grouse nest daily survival rate using Program MARK. Variables used in modeling included sage-grouse nest-level occupancy and site-specific change in corvid densities (study site-level), anthropogenic and landscape features, and microhabitat. Models were compared with Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (w_i). A fully saturated spatiotemporal model was included to assess goodness-of-fit; the saturated model included year; study site type; distance to town, landfill, energy well, communication tower, house, power line, all road, and riparian and forested habitat; topographic ruggedness at 1 km radius ($TRI_{1.0}$) variable; and all microhabitat variables.

Models	k	ΔAIC_c	w_i	Deviance
Raven occupancy, $TRI_{1.0}$ [a]	3	0.00	0.26	806.51
Raven occupancy, site-level raven, $TRI_{1.0}$	4	0.10	0.25	804.61
$TRI_{1.0}$	2	1.76	0.11	810.27
Raven occupancy, site-level raven, forest distance, $TRI_{1.0}$	5	1.81	0.11	804.31
Site-level raven, $TRI_{1.0}$	3	2.10	0.09	808.61
Raven occupancy, forest distance	3	2.57	0.07	809.08
Raven occupancy, site-level raven, forest distance	4	3.60	0.04	808.10
Raven occupancy, site-level raven	3	5.07	0.02	811.58
Forest distance	2	5.31	0.02	813.82
Raven occupancy	2	5.46	0.02	813.97

Site-level raven	2	7.15	0.01	815.66
Null	1	7.21	0.01	817.72
Fully saturated	25	25.13	0.00	787.36

[a] $AIC_c = 812.51$

Table 5-3. Parameter estimates with 95% confidence intervals (CI) from the top AIC$_c$ selected generalized linear model (see Table 5-2) assessing sage-grouse nest daily survival rate (DSR) using Program MARK. Sage-grouse nest-level raven (raven occupancy) was recorded as raven occupancy during last nest check with sage-grouse on her nest, and topographic ruggedness index at 1 km radius (TRI$_{1.0}$) was quantified as the difference in elevation among adjacent pixels of a digital elevation map.

			95% CI	
Variable	Estimate[a]	SE	Lower	Upper
Intercept	3.02	0.17	2.69	3.34[*]
Raven occupancy	-0.45	0.22	-0.89	-0.02[*]
TRI$_{1.0}$	0.02	0.01	0.01	0.04[*]

[*] Denotes a 95% confidence interval that does not include zero.

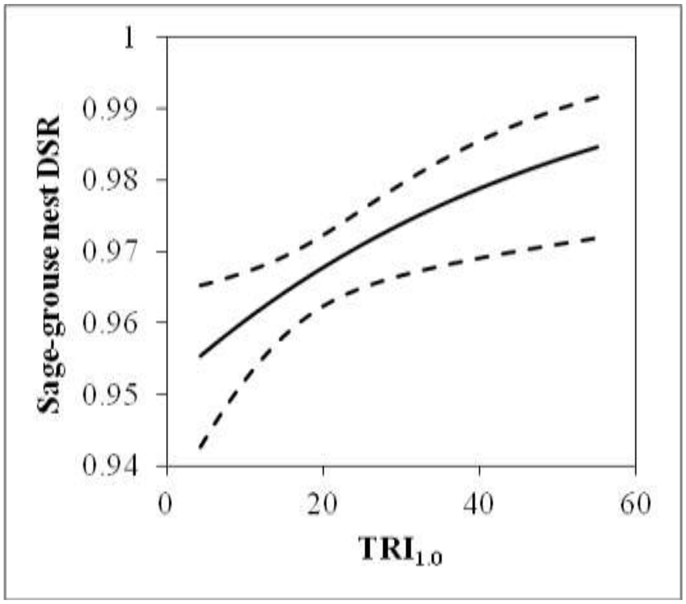


Figure 5-1. Predictions of daily survival rate (DSR) of sage-grouse nests from the top AIC$_c$ selected generalized linear model using Program MARK with 95% confidence intervals. Predicted effects of topographic ruggedness calculated at 1 km radius (TRI$_{1.0}$) on DSR of sage-grouse nests. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA (*n* = 341 sage-grouse nests), 2008–2011.

CHAPTER 6

GREATER SAGE-GROUSE HEN SURVIVAL: EFFECTS OF RAPTORS, ANTHROPOGENIC AND LANDSCAPE FEATURES, AND HEN BEHAVIOR

ABSTRACT Survival of breeding-age hens is the most important demographic parameter driving greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") populations. Effects of anthropogenic and landscape features on survival of sage-grouse hens have not been evaluated in the context of predator communities. In addition, management agencies would benefit from more information on the effects of parental investment and anti-predation strategies on sage-grouse survival. During 2008–2011, I collected survival data for 427 sage-grouse hens at 12 study sites (eight 16-km diameter sites and four 24-km diameter sites) in southern Wyoming, USA. Between 1 May and 31 August each year, there were 132, 162, 156, and 165 hens monitored, respectively. Cox proportional hazard (Cox PH) models were used to assess the effects of four covariate sets including: raptor densities, anthropogenic features, landscape features, and sage-grouse behavior on sage-grouse hen survival. Cox PH models were analyzed in two separate steps; 1) parental investment analysis and 2) anti-predation strategy analysis. Data for the parental investment analysis included 3,523 survival intervals with 380 nests and 162 broods; whereas, data for the anti-predation strategy analysis included 2,304 survival intervals from non-reproductive sage-grouse hens. I found that sage-grouse summer survival was correlated with landscape features that represented riskier habitat, especially risk of predation from raptors. Breeding season survival of sage-grouse was negatively associated with proximity to trees (deciduous and coniferous), topographic ruggedness at a 0.27 km scale ($TRI_{0.27}$), and site-specific change in golden eagle (*Aquila chrysaetos*) density (site-specific change in golden eagle density was calculated as the increase or decrease in study site-level golden eagle density [annual density] relative to the raptor density in a particular study site at the beginning of the study [2008]). However, site-specific change in golden eagle density was negatively associated with sage-grouse survival only when taking $TRI_{0.27}$ into context (interactive effect). This interaction indicated that the negative effect of both site-specific change in golden eagle density and $TRI_{0.27}$ was dampened in areas with higher $TRI_{0.27}$ and greater values of site-specific change in golden eagle density. My sage-grouse survival results indicated that survival of non-reproductive hens was greater than brooding or nesting hens. Hens that stayed in intermediate-size flocks and yearling hens had higher survival than hens in small or large flocks and hens >2 years old. Topographic ruggedness in conjunction with site-specific change in golden eagle density had a dynamic effect on sage-grouse survival, which illustrates the importance of considering predator communities in tandem with habitat components.

INTRODUCTION

Survival of breeding age birds in direct relation to predator communities has not been a main focus of greater sage-grouse (*Centrocercus urophasianus*: hereafter “sage-grouse”) research. Survival related to predator communities was not likely to have been a problem during pre-European settlement because sage-grouse co-evolved with the predator communities present in sagebrush ecosystems (Schroeder et al. 1999, Schroeder et al. 2001). There are currently no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult; Connelly et al. 2011). Thus, Hagen (2011) indicated that predators may only be negatively affecting sage-grouse populations in fragmented habitats and areas with human-subsidized predator populations. However, these areas of habitat fragmentation and areas with human-subsidized predator populations have drastically increased in the recent past (Leu et al. 2008). For example, red fox (*Vulpes vulpes*) and common raccoon (*Procyon lotor*) have increased in abundance in sage-grouse habitat, especially near human activities (Connelly et al. 2000b, Baxter et al. 2007, Hagen 2011). In addition, golden eagles (*Aquila chrysaetos*) use anthropogenic structures as perches and nesting structure (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010).

Recent research has indicated that sage-grouse hen survival may be the most important demographic parameter driving sage-grouse productivity (Johnson and Braun 1999, Taylor et al. 2012). Taylor et al. (2012) found that sage-grouse hen survival was the most influential demographic rate on population growth, and Johnson and Braun (1999) found that adult and juvenile sage-grouse survival were the most limiting demographic parameters for a population in northern Colorado. This should not be surprising, because sage-grouse are relatively long-lived ground-nesting birds with low productivity (Connelly et al. 2000b, Holloran et al. 2005, Connelly et al. 2011). Thus, many aspects of recruiting new individuals into a population are connected to sage-grouse hens (i.e., nest success and chick survival). Juvenile survival may also be partially connected to learned behaviors from when an individual sage-grouse was a chick (Thompson 2012).

Sage-grouse hens have been known to have high annual survival (48–78% in Wyoming; Holloran 2005, Connelly et al. 2011) with the breeding season having the lowest seasonal survival rate for sage-grouse hens (Connelly et al. 2000a). There has been little published on seasonal survival estimates for female sage-grouse (Connelly et al. 2011); however, Connelly et al. (2000a) found that 52% of sage-grouse hen mortalities occurred in spring and summer. Sage-grouse are a species of conservation concern because their distribution and abundance in western North America have declined over the last century (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004); many factors have been attributed to this decline including predation, habitat loss, and habitat fragmentation (Braun 1998). Research designed to evaluate potential factors affecting summer survival of sage-grouse in relation to predators and habitat quality will help guide management practices. Furthermore, low productivity of sage-grouse in combination with increased predation rates in fragmented habitats has the potential to decrease or extirpate local sage-grouse populations.

Increasing levels of human development in sage-grouse habitat have brought a range of new stresses to sage-grouse from habitat fragmentation to predation (Connelly et al. 2004, Doherty et al. 2010, Kirol 2012). Potentially additive impacts of human development on sage-grouse survival include increased hunting efficiency of raptors (perches), number of nesting structures, and carrying capacity of generalist predators.

Sources of perch and nesting structure for raptors include oil and gas structures, residential houses, communication towers, power lines, trees, and rugged terrain.

Although raptors have been reported to prey on sage-grouse, raptor densities have not been directly correlated to sage-grouse survival rates or population growth. Golden eagles have been suggested as the major sage-grouse predator (Willis et al. 1993, Connelly et al. 2000a, Danvir 2002, Dahlgren 2006, Mezquida et al. 2006), and high golden eagle abundance was associated with decreased sage-grouse survival (Danvir 2002). However, no sage-grouse study has directly related site-specific densities of raptors to sage-grouse hen survival. I recorded raptor densities associated with sage-grouse nesting and brood-rearing areas from 2008–2011 to determine if raptors were important sage-grouse predators and impact sage-grouse hen survival during the summer. I hypothesized that sage-grouse hen survival would be greater in areas and years with fewer raptors, specifically, golden eagles, *Buteo* hawks (*Buteo* spp.), and northern harriers (*Circus cyaneus*; hereafter “harrier”). In addition, I hypothesized that this effect would be intensified in areas closer to potential perches, such as oil and gas structures, power lines, houses, trees, and rougher topography. To test these hypotheses, I assessed sage-grouse hen survival in relation to sage-grouse exposure to raptors, potential raptor perches, and proximity to areas associated with natural or human provided food subsidies. As secondary objectives, I evaluated differences between yearling and adult sage-grouse hen survival, and the effect of sage-grouse hen behavior (parental investment, weekly movement, and flock size) in relation to survival. I hypothesized that lower parental investment, shorter weekly movements, and an optimal flock size would increase hen survival.

STUDY AREA

My study was conducted in southwest and south-central Wyoming. I chose 12 circular study sites, each 16 or 24 km in diameter (eight study sites of 16-km diameter and four study sites of 24-km diameter). Study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured based on results found by Holloran and Anderson (2005). Study sites in south-central Wyoming were 24 km in diameter, because sage-grouse were captured at several nearby leks over a larger area. Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming. Elevation of study sites ranged from 1,925 m – 2,550 m. Most of the land within all of the study sites was federally owned and administered by the Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in six (50%) of the study sites; well density within study sites averaged 0.12 ± 0.22 (SD) wells km^{-2} (range = 0.0–0.64 wells km^{-2}).

The landscape at all study sites was dominated by sagebrush (*Artemisia* spp.);

Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and dwarf sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included arrowleaf balsamroot (*Balsamorhiza sagittata*), buckwheat (*Eriogonum* spp.), common yarrow (*Achillea millefolium*), dandelion (*Taraxacum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), lupine (*Lupinus* spp.), sego lily (*Calochortus nuttallii*), and wild onion (*Allium* spp.). Common grass species included: bluegrasses (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in any of the study sites.

METHODS

Sage-grouse Capture and Monitoring

From 2008 to 2011, I monitored sage-grouse hen survival during late spring and summer (May through August). Hens were captured, radio-collared, and released in April of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003) and fitted them with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, MN, USA). Collars were equipped with motion-sensors (pulse rate of transmitter increased after 8 hours without bird movement), which allowed me to detect mortalities from a distance. I aged sage-grouse hens at the time of capture as yearlings or >2 years of age by examining outer primaries feathers (Patterson 1952).

I visually located hens weekly with VHF receivers (Communications Specialists, R-1000, Orange, CA, USA) and 3-way Yagi antennas (Communications Specialists, Orange, CA, USA) to locate and monitor nests. To assess the effects of parental investment on survival, I classified sage-grouse hen status as nesting, brooding, or non-reproductive each week (hen status was a surrogate for differences in parental investment). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. After 1 July, I continued to visually locate brooding hens weekly; whereas, non-reproductive hens were visually located bi-weekly. Brood hens were identified by either visually detecting chicks or observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, or clucking). I classified a sage-grouse hen as a brood hen if there was evidence of at least 1 chick with that hen. A non-reproductive hen was a hen that never nested, her nest failed, or her brood failed. I reclassified a brooding hen as non-reproductive when I did not detect evidence of a brood during 2 consecutive telemetry visits. The reproductive status of an individual sage-grouse hen was re-assessed every time a hen was visually located. I documented sage-grouse hen survival with telemetry equipment from a distance when a visual location was not possible, and telemetry signal from a distance was used as often as possible to identify mortality dates; thus, a live or dead signal for most sage-grouse was obtained >1 per week. I used handheld global positioning system (GPS) units (eTrex, Garmin Inc., Olathe, KS, USA) to record hen locations. Location accuracy on the GPS ranged from 2–8 m.

Sage-grouse Behavior Variables

I used visual sage-grouse locations to record minimum flock size and minimum weekly movements. Both of these metrics were collected as indicators of exposure to predation. The minimum flock size each week was recorded as the number of adult sage-grouse near (within ~50 m^2) a radio-collared hen including the radio-collared hen. I considered this count a minimum flock size, because there were probably individuals that were not detected during each count. Flock size was averaged across all visits for each individual hen during a summer. Movement distances between a sage-grouse's sequential locations were calculated using Geospatial Modeling Environment version 0.7.1.0 (Spatial Ecology LLC, Marshfield, WI, USA) and ArcMap version 10.0 (ESRI Inc., Redlands, CA, USA). I standardized movement distance between sequential visits to minimum weekly movement distances by dividing each distance between telemetry

locations by the number of days that had elapsed between telemetry locations,
I then averaged all weekly movement distances for each sage-grouse. This produced a minimum distance, because sage-grouse movements between telemetry locations were unknown.

Raptor Variables

From May 1 – August 1 of each year, I conducted point count surveys at random locations within each study site to compare raptor densities. Random locations were selected in habitat considered to be available to sage-grouse hens during the summer within each study site. To restrict random locations to available nesting habitat, I used ArcMap 10.0 to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest ReGAP landcover data from 2008 (Lennartz 2007). Random locations were designated to be ≥1000 m apart, but average nearest neighbor distances among random point count locations was >2000 m after random selection. I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. I generated a new set of random locations each year to avoid spatial autocorrelation; thus, random locations among years were independent.

I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all raptors observed during point counts and recording each raptor’s distance from the observer (when standing at the center of the point count location). Observers recorded the distance from the observer to where a raptor was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with raptors being attracted to or flushed away from an observer. When a raptor was displaced from the center of a point count location as an observer approached (6% of all detected birds), I recorded distance from that raptor to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). A 1500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, CA, USA) in conjunction with a GPS was used to estimate distances directly or to validate visually estimated distances.

Observers were trained and tested in raptor identification before conducting point counts. Point counts were 10 minutes in length, and we conducted them during daylight hours on a weekly basis at each study site. We visited each point count location 1–8 times with most locations visited ≥3 occasions. We did not survey for raptors in inclement weather (i.e., when raining or wind speeds were greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed to 2% of detections within truncated observation distances. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week. The observers conducting point counts within a particular study site changed each year.

I calculated average annual densities of raptors at the study site-level (number / 100 km^2). All raptor variables were calculated from the raw count data within Program DISTANCE estimated effective detection radii (EDR) as specified in Chapter 2. Study site-level density of golden eagles, *Buteo* hawks, and harriers were individually calculated within species-specific EDRs (1000 m, 450 m, and 350 m, respectively) of each random point count location within a study site (see Chapter 2 for further details). I had noted through observation that relative changes in raptor densities within many study sites had positive or negative effects on survival of sage-grouse. I attributed this phenomenon to the possibility of raptors being more or less effective predators on sage-grouse depending on the study site due to overall characteristics of a particular study site (combination of individual raptor behavior, topographic roughness, large scale cover, anthropogenic development, etc.). In addition to study site-level raptor densities, I calculated site-specific change in raptor densities—from random point count locations—as the increase or decrease in study site-level raptor density (annual density) relative to the raptor density in a particular study site at the beginning of the study (2008). Thus, site-specific change in raptor density was 0 for all study sites in 2008. These site-specific change in raptor density variables were intended to look at relative change in risk of predation within each study site (i.e., does site specific increase or decrease of raptor densities effect survival of sage-grouse). Thus, site-specific change in raptor densities were not quantifying the effect of the exact density of raptors on survival of sage-grouse among all study sites. Rather, they were assessing site-specific change in exposure to raptors.

Anthropogenic and Landscape Feature Variables

I calculated sage-grouse proximity to anthropogenic features that could be used as perch or nest sites by raptors or could provide food subsidies with ArcMap 10.0.

Anthropogenic structures that were >2 m in height were considered available for perching or nesting by raptors. I quantified the distance from sage-grouse locations to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings), major road, all roads, communication tower, house, and power line for each sage-grouse location. Most (>95%) oil and gas structures were energy wells. Ongoing energy development was occurring in half of my study sites, which required me to assess the dates that energy related structures and roads were added or removed from the landscape.

In distance calculations, I only included oil and gas structures and roads that were physically on the ground when each sage-grouse was located. I obtained information on oil and gas structures, including date construction started on the structure and date when wells were plugged and abandoned (date structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; 2012). I verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture [USDA] 2010). Aerial imagery from NAIP is produced by the USDA on a 3-year rotation; thus, I used WOGCC data and on the ground GPS units to map energy development that occurred after August 2009. However, energy development reported to WOGCC after August 2009 had better reporting of location, spud date, and plug abandon date.

I used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, and houses within a 5-km buffer around study sites; roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units. Major roads included paved, improved gravel roads, and railroads; whereas, all roads included major roads and all unimproved 4-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around study sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power line mapping.

Neither sage-grouse nor raptors were likely to discriminate between many different types of anthropogenic structures. Thus, I created 2 anthropogenic structure variables that represented the nearest 1) distance to either an oil and gas structure, communication tower, or house (DIST_WCH); and 2) distance to either an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from sage-grouse locations to individual types of anthropogenic structures. I report means and standard errors (SE) for distances to anthropogenic feature variables (Table 6-1).

Similar to anthropogenic features, landscape features could be used as perches or nest structure by raptors, or could be areas with higher productivity that attract predators. Thus, I used ArcMap 10.0 to calculate the distance from every sage-grouse location to forested (deciduous and conifer stands) and riparian habitats. Stands of trees and riparian habitat were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007), and verified with NAIP imagery from 2009. Topography with greater surface roughness has the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that provide vantage points similar to perches. For every sage-grouse location, I used ArcMap 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion; TRI variables were developed using a moving window analysis at 0.27-km ($TRI_{0.27}$), 0.54-km ($TRI_{0.54}$), 1-km (TRI_1), and 3-km (TRI_3) radii (0.23-km^2, 0.92-km^2, 3.14-km^2, and 28.26-km^2 scales, respectively). Riley et al. (1999) created TRI to describe the roughness of landscapes, and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map; the index is then averaged over a user defined area. I report means and standard errors (SE) for distances to landscape feature variables in Table 6-1.

Data Analyses

I analyzed sage-grouse hen survival with the Anderson-Gill formulation of the Cox proportional hazard (Cox PH) model using function ‘coxph’ in package SURVIVAL version 2.36-14 in R (R 2.14.2, www.r-project.org, accessed 15 Apr 2012). Cox PH models are robust semi-parametric models that are commonly used to analyze time-to-event data (Cox 1972), such as survival obtained from telemetry. The risk of mortality (hazard ratio [$h(t|x_t)$]) is a function of the non-parametric baseline hazard ($h_0(t)$) and the parametric covariates (x’s) affecting survival (Hosmer and Lemeshow 1999) with the Cox PH equation expressed as:

$$h(t|x_t) = h_0(t) \times \exp(\beta_1 x_{i1} + \beta_2 x_{i} + \beta_k x_{ik}) \tag{1}$$

Coefficient values were expressed as mortality hazard; thus, positive values would be associated with greater risk of mortality and lower survival.

Data can be left censored for individuals entering the study at different times and right censored for individuals that did not die during the study. In Cox PH models, fixed (time-independent; average exposure for an individual) and time-dependent (exposure of individual during each survival interval) covariates can be fit to assess their effect on survival (Hosmer and Lemeshow 1999). The baseline hazard is allowed to vary with time in Cox PH, and time-dependent variables are included by constructing time intervals for each unique individual (Therneau and Grambsch 2000). However, covariates in Cox PH models are assumed to have proportional mortality hazard over time (proportional hazard assumption; Hosmer and Lemeshow 1999). Thus, I used function ‘cox.zph’ in package SURVIVAL in R (Therneau and Grambsch 2000) to test the proportional hazard assumption for each covariate in all models; the proportionality of each covariate was validated with $P > 0.05$ for each covariate.

In addition, I calculated dfbetas (statistic that measures the scaled change in each parameter estimate by iteratively deleting each observation) and generated leverage plots to evaluate if there were any influential observations; no observations were omitted as a result of high influence. I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any Cox PH model (r >0.65) as determined with a Pearson’s correlation matrix; thus, I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤5, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

I constructed time intervals for each individual sage-grouse hen by calculating the day that corresponded to halfway between each time that I located a sage-grouse. Unless mortality date could be more accurately assessed by evidence from a carcass, mortality date was estimated as the time equal to halfway between the last date the hen was known to be alive and the date mortality was detected. During each year, time was started at $t = 0$ upon the first visual location of each sage-grouse hen that was relocated at least 2 weeks after radio-collaring. I did not include survival data collected directly after radio-collaring, because survival may have been affected by trapping stress or the bird adjusting to the collar (Winterstein et al. 2001); this excluded 4 birds from analyses. There were approximately 110 days of exposure time for each sage-grouse per summer (i.e., summer survival was assessed from $t = 0$ to $t = 110$, which corresponded to 1 May to 31 August).

I included study site-level raptor densities and site-specific change in raptor densities as fixed variables (average exposure to raptors over a summer), and anthropogenic and landscape feature variables as time-dependent variables (calculated from all sage-grouse locations where the hen was visually located). Study site-level raptor densities and site-specific change in raptor densities were defined as fixed variables, because raptor variables were quantified as annual densities (across an entire summer) at the study site-level. Anthropogenic and landscape features were incorporated as time-dependent variables, because the effect of these variables on survival was likely different depending on the bird’s location relative to these features, which changed as the bird moved through its environment over time. The distance to houses and forested habitat were highly correlated ($r > 0.65$), and distance to forested habitat fit the data better than distance to houses; thus, I included distance to forested habitat in modeling instead of distance to houses. However, distance to houses was incorporated into the DIST_WCH and ANTH variables.

Modeling of sage-grouse survival was conducted with an information theoretic approach (Anderson 2008). I compared Cox PH models with Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002) with function 'aictab' in package AICCMODAVG version 1.25 in R. I employed sequential AIC_c modeling of covariate sets, which was suggested by Arnold (2010) as an appropriate approach for identifying and ranking the most parsimonious models. Non-informative covariates (85% confidence intervals [CI] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top AIC_c selected models among covariate sets (Arnold 2010). I classified models within 2 AIC_c of the null model as being non-competitive (Burnham and Anderson 2002); thus, any model <2 AIC_c of the null was omitted from further analyses. Four covariate sets were evaluated sequentially: 1) raptor variables, 2) anthropogenic features, 3) landscape features, and 4) sage-grouse behavior. Cox PH models with raptor variables were compared as single variable models for each raptor species individually with AIC_c to choose which type (study site-level or site-specific change in density) of raptor variable fit the data best; thus, the raptor variable type with the lowest AIC_c was used in all further modeling. I evaluated the effect of a sage-grouse's age (AGE) on survival within the sage-grouse behavior covariate set. I included raptor variables × anthropogenic structure variables and raptor variables × landscape feature variables as pairwise interactions within anthropogenic and landscape feature covariate sets. Pairwise interactions with raptor variables were included to assess whether negative effects of raptor variables were intensified in areas closer to potential perches or nest structure or in areas closer to natural or human provided food subsidies. I did not include DIST_WCH or ANTH with any other anthropogenic structure variable, because DIST_WCH and ANTH were derived from a combination of distance from sage-grouse locations to energy wells, communication towers, houses, and power lines. The best variable describing the effect of anthropogenic structures on survival was determined through AIC_c selection within the anthropogenic feature covariate set. I compared Cox PH models with individual TRI variables measured at 0.27-km, 0.54-km, 1-km, and 3-km radii with AIC_c to choose the best spatial scale for the TRI variable to be used in the landscape feature covariate set; the TRI variable scale with the lowest AIC_c was used in all further modeling. As the final modeling step, I compared all top AIC_c selected models from every covariate set (models within 2 AIC_c of the top model within each covariate set) among each other and as additive models with combinations of all 3 covariate sets. I based my inference on Cox PH models within 2 AIC_c of the top selected model (Burnham and Anderson 2002).

The effects of sage-grouse behavior on survival in relation to raptors and anthropogenic and landscape features had to be analyzed as 2 separate Cox PH analysis steps. The sequential modeling procedure described above was applied to both the Cox PH analysis steps. In “Step 1” (parental investment analysis), I evaluated parental investment (hen status) with raptors and anthropogenic and landscape features by using all sage-grouse locations (nesting, brooding, and roosting locations). However, I excluded potential anti-predation behaviors (average weekly movement and average flock size) from Step 1 model building, because all variables that potentially described an anti-predation behavior were constant for 2 of 3 of the parental investment categories (nesting and brooding). In “Step 2” (anti-predation strategy analysis), I used non-reproductive locations to evaluate the effects of weekly movements and average flock size with raptors and anthropogenic and landscape features on sage-grouse survival. Average flock size was compared as a linear and quadratic variable in the sage-grouse behavior covariate set to assess the possibility of an optimal flock size. In Step 2, I included an interaction between average flock size and AGE to assess if yearling sage-grouse in larger flocks had higher survival.

In addition to AIC_c model comparison, I implemented a spatiotemporal modeling strategy to evaluate general trends in sage-grouse hen survival in relation to raptor variables, anthropogenic features, landscape features, and sage-grouse behavior. A spatiotemporal strategy was implemented to Cox PH model evaluation because many variables describing sage-grouse survival were exclusive to a given year or study site. I assessed goodness-of-fit of the top Cox PH models by computing a ratio of Zheng’s (2000) proportional reduction of deviance (RDR) for covariate models to spatiotemporally saturated models (maximum proportional reduction in deviance; Iles 2012), which has been considered appropriate for Cox PH models (Zheng 2000, Aubry et al. 2011). Deviance reduction for each spatiotemporally saturated model and top covariate models of interest were calculated relative to null models (time and study site invariant):

$$D_{int} = 1 – (deviance_{interest}/deviance_{null}) \tag{2}$$

$$D_{sat} = 1 – (deviance_{saturated}/deviance_{null})$$

$$RDR = D_{int} / D_{saturated} \tag{3}$$

thus, the ratio gives an assessment of a covariate model's relative ability to explain spatiotemporal processes effecting sage-grouse survival. The ratio is 1 for the spatiotemporally saturated model and 0 for the null model (Iles 2012). I compared the top AIC$_c$ selected Cox PH models of sage-grouse survival from Step 1 and 2 to a spatiotemporally saturated model with RDR. The saturated model for sage-grouse survival included year; study site; distance to energy well, communication tower, house, power line, all road, and tree stand; the top selected TRI variable; and distance to riparian habitat.

Although I could not test for spatial autocorrelation in Cox PH analyses, raptor densities derived from distance sampling techniques are robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My raptor sampling was designed to count the greatest proportion of raptors within a study site each week while not counting the same raptor more than once per week as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a study site in one day reduced the possibility of double-counting individual raptors during that week's visit. Counting the same individual raptor during different weeks, regardless of the particular point count location, was properly scaled by accounting for survey effort. Replication of point counts by sampling multiple weeks was done to increase the proportion of raptors detected as suggested by Thomas et al. (2010). Furthermore, study site-level and site-specific change in raptor densities were averaged by study site and year; thus, the lowest unit of measurement was at the study site-level annually. Time-dependent variables for Cox PH analyses were not subject to spatial autocorrelation, because Cox PH treats each time interval as a separate observation (Hosmer and Lemeshow 1999).

RESULTS

During 2008–2011, I captured 427 sage-grouse hens that were included in my Cox PH analyses because they were available to monitor (i.e., they did not go missing or die within 2 weeks of radio-collaring). Fifty, 76, and 69 sage-grouse hens survived into a subsequent year, 2009, 2010, and 2011, respectively; thus, there were 132, 162, 156, and 165 sage-grouse hens in 2008, 2009, 2010, and 2011, respectively. From 1 May – 31 August, I found 88 sage-grouse hen mortalities (22 nesting, 19 brooding, and 47 non-reproductive sage-grouse), which yielded apparent summer survival estimates of 81–89% annually. There were 3,523 time intervals for analyzing survival (402 nesting, 817 brooding, and 2,304 non-reproductive locations). I monitored 380 nesting sage-grouse and 162 brooding sage-grouse. The proportional hazards assumption was not violated for any model within 2 AIC_c of the top selected model.

To evaluate the effect of raptor densities on sage-grouse survival, I conducted 2,948 point count surveys during 2008–2011 at 660 total random point count locations. I counted 252 golden eagles, 138 *Buteo* hawks, and 57 harriers within species-specific EDRs (see Chapter 2). Neither study site-level nor site-specific change in golden eagle, *Buteo* hawk, and harrier densities had an individual effect on sage-grouse summer survival (all main effects of raptor variables had 85% CIs that overlapped 0). Variables describing site-specific changes in raptor densities fit the data better than landscape densities of raptors; thus, I used site-specific change in raptor densities in interactive models.

I found that landscape variables and sage-grouse behavior variables described summer sage-grouse survival best for both the parental investment and anti-predation analyses. I found that TRI at the 0.27-km radius ($TRI_{0.27}$) fit the data best for all analyses. No anthropogenic variable described differences in summer survival of sage-grouse hens (parameter estimates had 85% CI that overlapped 0) for either the parental investment or anti-predation analyses. In the parental investment analysis, I found that the top AIC_c selected Cox PH model included AGE, sage-grouse hen status (nesting, brooding, or non-reproductive), and site-specific change in golden eagle density × $TRI_{0.27}$ (Table 6-2), which had $w_i = 0.96$ and RDR = 0.82. The anti-predation strategy analysis had 3 models within 2 AIC_c (Table 6-2). However, the top 2 AIC_c ranked models had $w_i = 0.38$ and $w_i = 0.32$, respectively, and the third AIC_c ranked model had $w_i = 0.17$ (Table 6-2); thus, I will only discuss the top 2 models. Both top AIC_c ranked models included average flock size, quadratic effect of flock size, AGE, AGE × average flock size, distance to forested habitat, and $TRI_{0.27}$ (Table 6-2). In addition, I found that the top AIC_c ranked model for the anti-predator strategy analysis included the site-specific change in golden eagle density × $TRI_{0.27}$ interaction and had RDR = 0.98 (Table 6-2). Whereas, the simpler second AIC_c ranked model for the anti-predator strategy analysis had RDR = 0.90. The near 1 values of RDR for all top AIC_c selected models indicated that a high proportion of the maximum explainable deviance for sage-grouse summer survival was accounted for in my top selected models.

Topographic ruggedness index at 0.27 km radius was the landscape feature variable that most consistently explained sage-grouse summer survival. I found that higher $TRI_{0.27}$ values were correlated with lower sage-grouse summer survival (Tables 6-3 and 6-4). In the anti-predator analysis, there was support for lower survival of sage-grouse closer to forested habitat at non-reproductive locations from all top AIC_c ranked models from the anti-predator strategy analysis (Tables 6-2 and 6-4, Fig. 6-1). Parameter estimates for distance to forested habitat were -0.15 (0.08 SE; 95% CI = -0.31 to 0.02) and -0.15 (0.08 SE; 95% CI = -0.31 to 0.01) for the top and second AIC_c ranked models, respectively (Table 6-4).

Even though raptor densities (study site-level and site-specific change) by themselves did not describe sage-grouse survival, I found that the interaction between site-specific change in golden eagle density and $TRI_{0.27}$ was highly explanative of sage-grouse summer survival (Tables 6-3 and 6-4). Site-specific change in golden eagle density was negatively associated with sage-grouse summer survival only when taking $TRI_{0.27}$ into context. When site-specific change in golden eagle density was relatively high and sage-grouse were in areas with more rugged terrain, I found that the negative effect of site-specific change in golden eagle density and $TRI_{0.27}$ were dampened (Fig. 6-

2). The site-specific change in golden eagle density × $TRI_{0.27}$ parameter estimate was -0.01 (0.00 SE; 95% CI = -0.01 to -0.00) and -0.01 (0.00 SE; 95% CI = -0.02 to -0.00) for the parental investment analysis and anti-predation analyses, respectively (Tables 6-3 and 6-4).

For variables describing the effect of sage-grouse behavior on sage-grouse summer survival, I found that non-reproductive sage-grouse had marginally higher survival than nesting (parameter estimate 0.45 [0.27 SE]; 95% CI = -0.09 to 0.99) or brooding (parameter estimate 0.51 [0.28 SE]; 95% CI = -0.04 to 1.07) sage-grouse hens in the parental investment analysis (Table 6-3). In the anti-predation strategy analysis, I found that non-reproductive adults that flocked in intermediate numbers had higher survival (Table 6-4, Fig. 6-3A); thus, sage-grouse hens in small flocks (by themselves or another hen) and large flocks had lower summer survival. Average flock size parameter estimates were -0.55 (0.18 SE; 95% CI = -0.89 to -0.20) with quadratic 0.03 (0.01 SE; 95% CI = 0.01 to 0.05) for the top AIC_c ranked model, and -0.55 (0.18 SE; 95% CI = -0.90 to -0.21) for the second AIC_c ranked model with the same quadratic parameter estimate as the top AIC_c ranked model. All top AIC_c ranked Cox PH models included AGE. However, yearling sage-grouse hens had higher survival (parameter estimate -0.69 [0.30 SE]; 95% CI = -1.27 to -0.11) in the parental investment analysis, but marginally lower survival (parameter estimates: top model = 1.26 [0.78 SE]; 95% CI = -0.28 to 2.80; and second model = 1.23 [0.78 SE]; 95% CI = -0.28 to 2.80) in both of the top AIC_c selected models from the anti-predation strategy analysis when a yearling hen was in a flock of <3 birds (Table 6-4, Fig. 6-3B). In the anti-predation strategy analysis, I also found the AGE × average flock size interaction term was marginally significant for the top 2 AIC$_c$ selected models, which indicated that yearlings that on average chose to flock in greater numbers had greater survival (interaction parameter estimates: top model = -0.86 [0.48 SE]; 95% CI = -1.80 to 0.08; and second model = -0.87 [0.48 SE]; 95% CI = -1.81 to 0.07).

DISCUSSION

I found that sage-grouse summer survival was negatively correlated with landscape features that represented riskier habitat, especially risk of predation from raptors. Breeding season survival of sage-grouse was negatively impacted by proximity to trees (deciduous and coniferous) and greater values of TRI$_{0.27}$ and site-specific change in golden eagle density (study site relative change in golden eagle density among years). Kirol (2012) also found that terrain roughness was negatively correlated with sage-grouse summer survival in south-central Wyoming. His study indicated that proximity to anthropogenic features had no effect on sage-grouse survival, and I found no evidence of an interactive effect between anthropogenic features and raptor densities. My results also suggest that survival was greater for non-reproductive hens, hens that stayed in intermediate size flocks, and yearling hens. The best sage-grouse survival models had RDR = 0.82 to 0.98, which indicated that a large proportion of spatiotemporal variability in sage-grouse survival was accounted for in my models. My apparent late spring and summer survival rate was 79%, which was within estimated annual survival rates in Wyoming (Connelly et al. 2011). Thus, landscape features in conjunction with site-specific change in golden eagle density and sage-grouse behavior had dynamic effects on survival.

It was possible that distance variables associated with time intervals for mortalities were biased due to a predator moving a sage-grouse carcass. However, I did not find summer mortalities with evidence of drastic predator movements (>1 km), and sage-grouse carcasses were typically found close to the last location where the sage-grouse was known to be alive. For example, sage-grouse killed while nesting were found on average 0.38 km from their nest, and only 2 of 22 (9%) were found >1 km away from their nest. The average distance from sage-grouse nest to mortality location (0.38 km) was within the 0.54 km diameter of the $TRI_{0.27}$ variable, and topographic ruggedness variables at 0.27 km, 0.54 km, 1 km, and 3 km radii all had a negative effect on sage-grouse survival.

Previous research has shown that most sage-grouse mortalities in the spring and summer can be attributed to predation (Connelly et al. 2011), but other possible sources of mortality include collisions with vehicles, fences, and power lines (Braun 1998, Connelly et al. 2000a, Connelly et al. 2004, Beck et al. 2006); and West Nile virus (Naugle et al. 2004, Walker et al. 2007b, Walker and Naugle 2011). I did not find evidence of any sage-grouse colliding with a fence or power line (no carcasses near fences or under power lines). West Nile virus was not likely to have killed many birds in this study, because West Nile virus was not known to be prominent in my study sites during this study (Walker and Naugle 2011). In addition, mortalities from West Nile virus usually occur July to mid-September (Walker et al. 2007b, Walker and Naugle

2011), and I only found 17 of the 88 mortalities after 5 July. Sage-grouse survival has been documented to be lowest from March to June and relatively higher after July (Connelly et al. 2000a, Connelly et al. 2011, Walker and Naugle 2011); thus the timing of mortalities in my study coincides with typical sage-grouse summer survival.

Golden eagle, *Buteo* hawk, and harrier densities (study site level or site-specific change) did not independently predict sage-grouse survival. Raptor populations may have been too stable over time for me to detect direct negative effects of raptor abundance on sage-grouse survival. However, I found moderate support for lower sage-grouse survival when sage-grouse were exposed to a greater density of golden eagles within a study site (site-specific change in golden eagle density) while simultaneously taking $TRI_{0.27}$ into account (site-specific change in golden eagle density × $TRI_{0.27}$; Tables 6-3 and 6-4), and high values of $TRI_{0.27}$ negatively affected sage-grouse survival. Marzluff et al. (1997) found that golden eagles in sagebrush habitat selected areas with more rock outcrops and cliffs in southern Idaho. I hypothesized that rugged terrain would be riskier habitat and high raptor densities would intensify this effect because hilltops, knolls, and cliff edges associated with rugged terrain would act as perch or nesting structure for raptors. Thus, rugged terrain would correlate with greater exposure to predation from raptors. Contrary to my hypothesis, I found that the negative effect of $TRI_{0.27}$ and site-specific change in golden eagle density was dampened by the combination of greater rugged terrain and greater values of site-specific change in golden eagle density (Tables 6-3 and 6-4). Two potential explanations for this finding include; 1) rugged topography may provide some refugia from visual predators (e.g., golden eagles), because topographic features such as slight depressions may decrease the effective distance that a raptor can detect a sage-grouse on the ground; and 2) greater abundance of golden eagles in rugged topography (risky habitat) may competitively exclude other predators. Golden eagles and coyotes are known to be the top predators in sagebrush ecosystems (Mezquida et al. 2006, Hagen 2011), and presence of golden eagles may reduce the hunting efficiency of mammalian predators. I found that nesting and brooding sage-grouse selected locations with lower topographic ruggedness compared to the landscape at random in Chapter 3, which has been verified by other sage-grouse research (Jensen 2006, Doherty et al. 2010, Hanser et al. 2011, Kirol 2012); thus, sage-grouse avoided extremely rugged terrain. The moderately rugged topography (relative to the landscape) where sage-grouse had higher mortality may have been correlated to greater risk of predation from olfactory predators (mammalian predators), which have been known to hunt in areas such as drainage bottoms (Conover 2007).

Other landscape features such as forested and riparian habitats have the potential to pose a higher risk of predation for sage-grouse. Sage-grouse avoidance of forested habitat, especially pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.), has been documented (Doherty et al. 2010), but there has been little research looking at the impact of proximity to forested areas on sage-grouse survival. I found that proximity to trees was negatively related to the survival of non-reproductive hens; although distance from sage-grouse locations to forested habitat was an imprecise predictor (95% CI overlapped 0; Table 6-4). There has been some documentation of the negative effect of proximity to trees on sage-grouse survival, but this topic clearly needs more study. For example, Commons et al. (1999) found higher spring counts of male Gunnison sage-grouse (*Centrocercus minimus*) on leks after removal of pinyon-juniper in southwestern Colorado; they attributed this to lower densities of raptors after pinyon-juniper was removed. Nesting and early brood-rearing sage-grouse avoid riparian habitat (Doherty et al. 2010, Chapter 3), presumably due to increased risk of predation. However, I did not find a connection of low hen survival and proximity to riparian habitats.

Several studies have demonstrated that sage-grouse avoid habitat with man-made features, such as oil and gas infrastructure (Aldridge 2005, Holloran 2005, Walker et al. 2007a, Kirol 2012), power-lines (Hanser et al. 2011), and roads (Holloran 2005, Aldridge and Boyce 2007), which are potential perches or nest structure for raptors or provide reliable food subsidies. In fact, golden eagles, red-tailed hawks (*Buteo jamaicensis*), ferruginous hawks (*Buteo regalis*), and Swainson’s hawks (*Buteo swainsoni*) have been found to use power lines for perch sites and areas around power lines for foraging (Lammers and Collopy 2007, Prather and Messmer 2010 , Slater and Smith 2010). Holloran (2005) found that annual survival of adult female sage-grouse was lower in a natural gas field, and collisions with vehicles are known to cause sage-grouse mortalities (Braun 1998). Thus, I hypothesized that sage-grouse survival would be lower near anthropogenic features and that this effect would be amplified when there were also high densities of raptors. However, I did not find support for this hypothesis indicating that anthropogenic features do not necessarily predict riskier habitats or sage-grouse avoidance of anthropogenic features masked any effects on survival.

Behaviors associated with parental investment and anti-predation strategies have the potential to influence survival rates of animals. Increased experience, quantified as age, should also be positively correlated with survival. However, yearling sage-grouse have been found to have higher survival than adults ≥2 years of age (Zablan et al. 2003, Holloran 2005, Connelly et al. 2011). For example, Zablan et al. (2003) found 77% and 59% survival for yearling and adult female sage-grouse in Colorado, respectively. Connelly et al. (1993), Holloran (2005), and Moynahan et al. (2007) documented that yearling sage-grouse hens initiated nests and re-nested less often than adult hens. I found similar results with 56% and 60% apparent nest initiation for yearling and adult hens, respectively, and 11 of 14 re-nesting events were from adult hens. Adult sage-grouse hens have higher nest success compared to yearlings, which indicates that adults are more likely to have a brood (Connelly et al. 2011). I found broods with 19% and 30% of yearling and adult sage-grouse hens, respectively, and I found that sage-grouse hens that were nesting or brooding had lower survival than hens without a nest or brood (Table 6-3). Thus, yearling sage-grouse hens may have had higher survival, because they were less likely to be incubating or tending a brood. This provides some evidence that differential behavior related to parental investment may account for higher survival rates of yearling sage-grouse hens.

In contrast, Moynahan et al. (2006) found nesting sage-grouse in Montana had higher survival than non-nesting hens. They attributed their findings to better physical condition of nesters versus non-nesters, increased visibility of non-nesting hens, or both. The apparent inconsistency with Moynahan et al. (2006) and my results most likely arises from differences in analyses. Moynahan et al. (2006) compared survival of hens that had initiated a nest within a summer versus hens that did not initiate a nest within a summer. On the other hand, I allowed the nesting status (nesting, brooding, or non-reproductive) of each hen to change over time with a time-dependent Cox PH variable; thus, I assigned each mortality to a time-dependent breeding status. In light of my results, Moynahan et al. (2006) results more likely relate to the better physical condition or experience of hens that attempted to nest.

My results from the anti-predation strategy analysis suggested that survival was greater for non-reproductive hens that stayed in intermediate size flocks (Fig. 6-3A). I did not find higher survival of yearlings versus adults when comparing survival of only non-reproductive hens (i.e., the main effect of AGE was not significant; Table 6-4), and yearling hen survival was connected to average flock size (interaction AGE × average flock size; Tables 6-2 and 6-4). In fact, survival of yearling sage-grouse hens was lower than adults when yearlings were in flocks of <3 grouse on average (Fig. 6-3B, Table 6-4). However, the interaction between AGE and average flock size indicated that yearlings that chose to stay in larger groups had higher survival.

I hypothesized that sage-grouse would have higher survival in optimally sized flocks, because small and very large flocks would represent increased risk of predation. Small flocks would decrease the benefits of sentinel behavior (i.e., sage-grouse detecting a predator) and the dilution effect, and large flocks would increase a predator’s probability of detecting a flock of sage-grouse. The dilution effect predicts that an individual in a larger flock will have a lower probability of being eaten. Intermediate flock sizes would allow individual sage-grouse to benefit from the dilution effect and sentinel behavior, while avoiding detection by predators. I found support for an optimally sized flock for non-reproductive sage-grouse, which my top AIC_c selected Cox PH model predicted around 3–14 birds (Fig. 6-3A). I also predicted that increased movement distances would be negatively related to survival, because there would be a greater risk of being detected by a visual predator for hens moving greater distances. However, I did not find support for a negative effect of weekly movement distance. This may be attributed to no effect or a lack of detailed information on movements from telemetry techniques. I was only able to record minimum linear movements, which ignore daily movements within a smaller area.

Raptors including golden eagles, *Buteo* hawks, and harriers have been identified as significant threats to sage-grouse survival (Schroeder et al. 1999, Schroeder and Baydack 2001). However, I found that natural abundances of raptors, even in the presence of anthropogenic features, did not seem to adversely affect sage-grouse survival. This may be attributed to sage-grouse avoiding raptors, avoidance of risky habitats, and habitat condition; negative effects of high raptor densities may also have been masked by other spatiotemporal processes such as weather. Dinkins et al. (2012) found that nesting and brooding sage-grouse avoided raptors, and many researchers have found that sage-grouse avoid risky habitats (Aldridge 2005, Holloran 2005, Aldridge and Boyce 2007, Walker et al. 2007a, Doherty et al. 2010, Hanser et al. 2011, Kirol 2012).

MANAGEMENT IMPLICATIONS

Many authors have suggested that ground-nesting bird survival, including sage-grouse, is connected to quantity and quality of habitat, and the presence of adequate sagebrush habitat minimizes predator effects on sage-grouse survival (Connelly et al. 1994, Braun 1998, Aldridge et al. 2008, Connelly et al. 2011). I agree with this, but there needs to be careful consideration of interactive effects of anthropogenic and landscape features and predator community dynamics (risk of predation). For example, sage-grouse hens avoided conventional and natural gas wells (Kirol 2012; Chapter 3), which placed them in areas with higher $TRI_{0.27}$. In addition, areas with higher $TRI_{0.27}$ had lower sage-grouse survival, which was dampened by high densities of golden eagles. However, the overall sage-grouse survival in areas with higher $TRI_{0.27}$ was lower. This indicates that changes in sage-grouse selection of habitat in response to anthropogenic features (fragmentation of habitat) can have dynamic consequences for sage-grouse survival, especially when considering differences in predator compositions. Thus, habitat fragmentation of sagebrush habitats has complex effects on sage-grouse use of the landscape, which in turn can have complex impacts on survival.

LITERATURE CITED

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Canada.

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

Aldridge, C. L., S. E. Nielson, 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.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer Science, New York, New York, USA.

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

Aubry, L. M., E. Cam, D. N. Koons, J. -Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80:375–383.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the 72nd North American Wildlife and Natural Resources Conference 72:258–269.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

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.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

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

Commons, M. L., R. K. Baydack, and C. E. Braun. 1999. Sage-grouse response to pinyon-juniper management. Pages 238–239 *in* S. B. Monsen, and R. Stevens, editors. Proceedings, ecology and management of pinyon-juniper communities within the Interior West. United States Department of Agriculture, Forest Service, RMRS-P-9, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000a. Effects of predation and hunting on adult sage grouse (*Centrocercus urophasianus*) in Idaho. Wildlife Biology 6:227–232.

Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting of sage-grouse in southeastern Idaho. Condor 95:1041–1043.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

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

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

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

Conover, M. R. 2007. Predator−prey dynamics: the use of olfaction. Taylor and Francis, Boca Raton, Florida, USA.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B-Statistical Methodology 34:187–220.

Dahlgren, D. K. 2006. Greater sage-grouse ecology and response to experimental management of mountain big sagebrush on Parker Mountain, Utah. Thesis, Utah State University, Logan, Utah, USA.

Danvir, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, 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 74:1544–1553.

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

Gregg, M. A., 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.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Hanser, S. E., M. Leu, S. T. Knick, and C. L. Aldridge. 2011. Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

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

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Hosmer, D. W., and S. Lemeshow. 1999. Applied logistic regression. Second edition. John Wiley and Sons, New York, New York, USA.

Iles, D. T. 2012. Drivers of nest success and stochastic population dynamics of the common eider (*Somateria mollissima*). Thesis, Utah State University, Logan, USA.

Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis, University of Wyoming, Laramie, USA.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institution, Washington, D. C., USA.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Lammers, W. M., and M. W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Lennartz, S. 2007. USGS Gap Analysis Program (GAP) species distribution model. Sanborn Map Corporation. Portland, Oregon, USA.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Marzluff, J. M., S. T. Knick, M. S. Vekasy, L. S. Schueck, and T. J. Zarriello. 1997. Spatial use and habitat selection of golden eagles in southwestern Idaho. Auk 114:673–687.

Mezquida, E. T., S. J. Slater, and C. W. Benkman. 2006. Sage-grouse and indirect interactions: potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

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

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704–713.

Patterson, R. L. 1952. The sage grouse of Wyoming. Sage Books, Denver, Colorado, USA.

Prather, P. R., and T. A. Messmer. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

Ralph, C. J., 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, Berkeley, California, USA.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

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*). *In* A. Poole, and F. Gill, editors. Birds of North America. Birds of North America, Philadelphia, Pennsylvania, USA.

Slater, S. J., and J. P. Smith. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

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.

Therneau, T. M., and P. M. Gambsch. 2000. Modeling survival data: extending the Cox model. Springer-Verlag, New York, New York, USA.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, R. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Thompson, T. R. 2012. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from demographic and genetic methods. Dissertation, University of Idaho, Moscow, USA.

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

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

Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127–141 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

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

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007b. West Nile virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691–696.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Winterstein, S. R., K. H. Pollock, and C. M. Bunck. 2001. Analysis of survival data from radiotelemetry studies. Pages 352–380 *in* J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Wyoming Oil and Gas Conservation Commission (WOGCC). 2012. WOGCC homepage. <http://wogcc.state.wy.us/>. Accessed 15 January 2012.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144–154.

Zheng, B. 2000. Summarizing the goodness of fit of generalized linear models for longitudinal data. Statistics in Medicine 19:1265–1275.

Table 6-1. Descriptions, means, and standard errors (SE) of variables used to model sage-grouse survival with the Anderson-Gill formulation of the Cox proportional hazard model; means and SE were stratified by sage-grouse that survived the duration of the study and those that did not. Variables include raptor densities, anthropogenic features, and landscape features from 3,523 summer (1 May through 31 August) survival intervals. Sage-grouse behavior variables (average weekly movement and average flock size) were from non-reproductive 2,304 sage-grouse locations. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

	Survived			Mortality		
Variable description	*n*	mean	SE	*n*	mean	SE
Study site-level golden eagle density (no./100 km^2)	3435	1.91	2.73	88	2.22	2.84
Study site-level *Buteo* hawk density (no./100 km^2)	3435	6.59	7.44	88	7.66	8.42
Study site-level harrier density (no./100 km^2)	3435	7.02	8.19	88	6.41	6.92
Distance (km) from sage-grouse location to nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other	3435	7.55	0.12	88	7.38	0.62

energy extraction related buildings)						
Distance (km) from sage-grouse location to nearest major road including paved roads, railroad, and improved gravel roads	3435	1.51	0.02	88	1.71	0.13
Distance (km) from sage-grouse location to nearest road including paved roads, railroad, improved gravel roads, and unimproved 4-wheel drive roads	3435	0.33	0.01	88	0.38	0.03
Distance (km) from sage-grouse location to nearest communication tower	3435	10.13	0.13	88	10.55	0.78
Distance (km) from sage-grouse location to nearest residential house	3435	7.50	0.10	88	6.87	0.52
Distance (km) from sage-grouse location to nearest overhead line (transmission or distribution power lines, or telephone line)	3435	8.57	0.09	88	8.41	0.60
Distance (km) from sage-grouse location to nearest anthropogenic perch (ANTH; oil and gas structure,	3435	3.32	0.04	88	3.46	0.24

communication tower, residential house, or power lines)						
Distance (km) from sage-grouse location to nearest oil and gas structure, communication tower, or residential house (DIST_WCH)	3435	3.64	0.05	88	3.88	0.25
Distance (km) from sage-grouse location to nearest forested habitat including deciduous and conifer stands	3435	2.87	0.05	88	2.00	0.26
Distance (km) from sage-grouse location to nearest riparian habitat	3435	1.65	0.03	88	1.48	0.16
Topographic ruggedness index at 0.27 km radii (0.23-km^2 scale)	3435	16.48	0.19	88	21.76	1.55
Topographic ruggedness index at 0.54 km radii (0.92-km^2 scale)	3435	17.06	0.18	88	21.62	1.38
Topographic ruggedness index at 1 km radii (3.14-km^2 scale)	3435	18.01	0.17	88	21.82	1.28
Topographic ruggedness index at 3 km radii (28.26-km^2 scale)	3435	20.65	0.16	88	23.74	1.04
Average weekly sage-grouse movement distance (km)	2257	1.17	0.05	47	0.99	0.14

Average flock of sage-grouse	2257	3.71	0.06	47	2.07	0.34

Table 6-2. Model comparison of Cox proportional hazard (Cox PH) models from the parental investment and anti-predator strategy analyses. Models assessed the effects of 4 covariate sets including site-specific change in raptor densities, anthropogenic features, landscape features, and sage-grouse behavior on sage-grouse hen survival. Models were compared with Akaike's information criterion (adjusted for small sample sizes; AIC$_c$) and Akaike weights (w_i). Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA. A total of 427 sage-grouse hens were monitored during 2008–2011.

Models [a,d]	k	ΔAIC$_c$	w_i	Deviance
Parental investment				
AGE, status, GOEA×TRI$_{0.27}$ [b]	6	0.00	0.96	1039.30
GOEA×TRI$_{0.27}$	3	6.44	0.04	1051.76
AGE, status	3	13.71	0.00	1059.02
Null	0	22.83	0.00	1074.16
Fully saturated	22	24.47	0.00	1031.50
Anti-predation strategy				
Flock^2, flock×AGE, forest distance, GOEA×TRI$_{0.27}$ [c]	8	0.00	0.38	479.86
Flock^2, flock×AGE, forest distance, TRI$_{0.27}$	6	0.36	0.32	484.24
Flock^2, forest distance, GOEA×TRI$_{0.27}$	6	1.63	0.17	485.52
Flock^2, forest distance, TRI$_{0.27}$	4	2.14	0.13	490.06
Flock^2, flock×AGE	4	14.31	0.00	502.22

Flock^2	2	15.27	0.00	507.20
Forest distance, GOEA×TRI$_{0.27}$	4	21.71	0.00	509.62
Forest distance, TRI$_{0.27}$	2	22.75	0.00	514.68
Fully saturated	22	27.03	0.00	478.50
Null	0	39.04	0.00	534.96

[a] Models with interaction terms included all individual variables within the interactions.

[b] AIC$_c$ = 1051.32

[c] AIC$_c$ = 495.93

[d] Variables included in final Cox PH model selection included sage-grouse age (AGE), sage-grouse parental investment status (status), average flock size (flock), quadratic of average flock size (flock^2), site-specific change in golden eagle density (GOEA), topographic ruggedness index at 0.27-km radius (TRI$_{0.27}$), and distance to forested habitat (deciduous and conifer stands). The saturated model for sage-grouse survival included year; study site; distance to energy well, communication tower, house, power line, all road, and riparian and forested habitats; and the top selected TRI variable.

Table 6-3. Parameter estimates of sage-grouse survival (as hazard ratios—depicting risk of mortality) from top AIC$_c$ selected Cox proportional hazard model for parental investment analysis with *P*-values and 95% confidence intervals. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011. A total of 427 sage-grouse hens were monitored during 2008–2011.

					95% CI	
Variable [c]	Estimate	SE	Z	*P*	Lower	Upper
AGE	-0.69	0.30	-2.3	0.02	-1.27	-0.11*
Status brooding [a]	0.51	0.28	1.8	0.07	-0.04	1.07
Status nesting [b]	0.45	0.27	1.6	0.10	-0.09	0.99
GOEA	0.14	0.08	1.7	0.09	-0.02	0.31
TRI$_{0.27}$	0.02	0.01	2.2	0.03	0.00	0.04*
GOEA×TRI$_{0.27}$	-0.01	0.00	-2.6	0.01	-0.01	-0.00*

*Denotes a 95% confidence interval that does not include zero.

[a] Sage-grouse survival comparing brooding to non-reproductive hens.

[b] Sage-grouse survival comparing nesting to non-reproductive hens.

[c] Variables included in top AIC$_c$ selected Cox PH model include sage-grouse age (AGE), sage-grouse parental investment status (status), site-specific change in golden eagle density (GOEA), and topographic ruggedness index at 0.27-km radius (TRI$_{0.27}$).

Table 6-4. Parameter estimates of sage-grouse survival (as hazard ratios—depicting risk of mortality) from top 2 AIC$_c$ selected Cox proportional hazard models for anti-predation strategy analysis with *P*-values and 95% confidence intervals. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011. A total of 427 sage-grouse hens were monitored during 2008–2011.

					95% CI	
Variable [a]	Estimate	SE	Z	*P*	Lower	Upper
Top selected						
Flock	-0.55	0.18	-3.11	<0.01	-0.89	-0.20[*]
Flock^2	0.03	0.01	3.17	<0.01	0.01	0.05[*]
AGE	1.26	0.78	1.60	0.11	-0.28	2.80
GOEA	0.15	0.12	1.26	0.21	-0.08	0.38
TRI$_{0.27}$	0.02	0.01	1.61	0.11	-0.01	0.05
Forest distance	-0.15	0.08	-1.76	0.08	-0.31	0.02
Flock×AGE	-0.86	0.48	-1.79	0.07	-1.80	0.08
GOEA×TRI$_{0.27}$	-0.01	0.00	-2.13	0.03	-0.02	-0.00[*]
Second selected						
Flock	-0.55	0.18	-3.11	<0.01	-0.90	-0.21[*]
Flock^2	0.03	0.01	3.21	<0.01	0.01	0.05[*]
AGE	1.23	0.78	1.57	0.12	-0.31	2.76

Forest distance	-0.15	0.08	-1.79	0.07	-0.31	0.01
TRI$_{0.27}$	0.03	0.01	2.72	0.01	0.01	0.05[*]
Flock×AGE	-0.87	0.48	-1.81	0.07	-1.81	0.07

[*] Denotes a 95% confidence interval that does not include zero.

[a] Variables included in top 2 AIC$_c$ selected Cox PH models include sage-grouse age (AGE), average flock size (flock), quadratic of average flock size (flock^2), site-specific change in golden eagle density (GOEA), topographic ruggedness index at 0.27-km radius (TRI$_{0.27}$), and distance to forested habitat (deciduous and conifer stands).

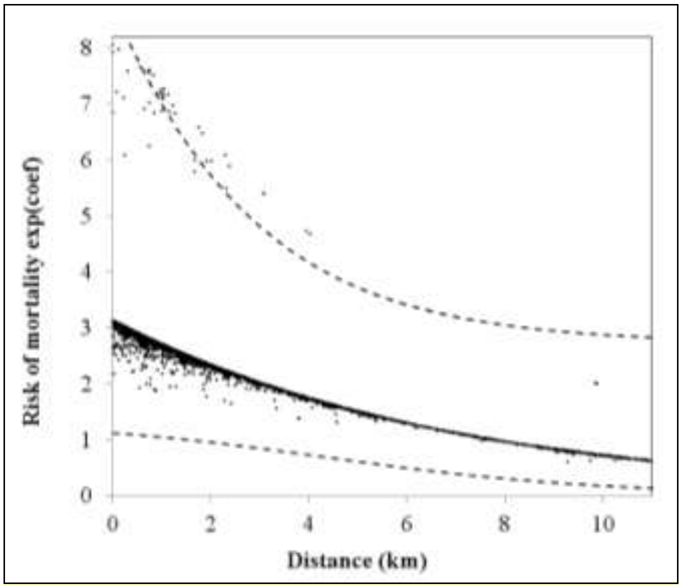


Figure 6-1. Predicted effect with 95% confidence intervals of distance to forested habitat (deciduous and conifer) on sage-grouse hen survival from the top AIC$_c$ selected Cox proportional hazard model from the anti-predation strategy analysis. Predicted effects displayed as the risk of mortality with the y-axis units plotted as exp(coefficient values). All other parameters were held at the mean value. Partial residuals were overlaid on predicted effect plots as solid points. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

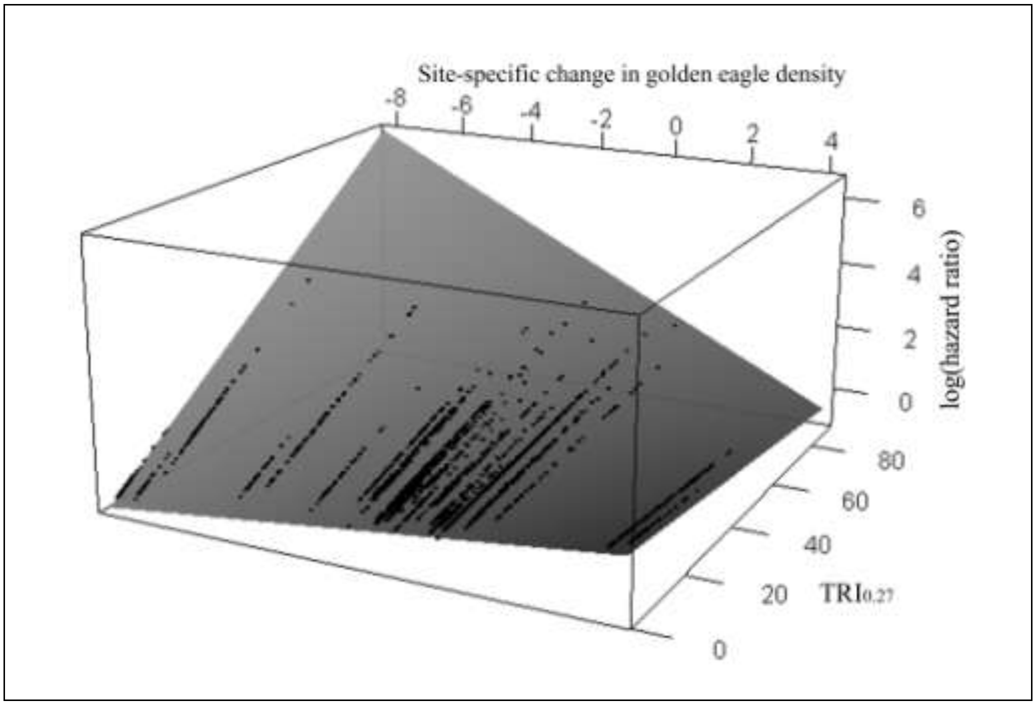


Figure 6-2. Interactive effect of site-specific change in golden eagle density and topographic ruggedness index at 0.27-km radius (TRI$_{0.27}$) on sage-grouse hen survival (as a hazard ratio—depicting risk of mortality) from the parental investment analysis. Predicted effects from the top AIC$_c$ selected Cox proportional hazard model displayed as the risk of mortality with the y-axis units plotted as exp(coefficient values). All other parameters were held at their mean value. Solid points represent observed data overlaid on the predicted surface. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

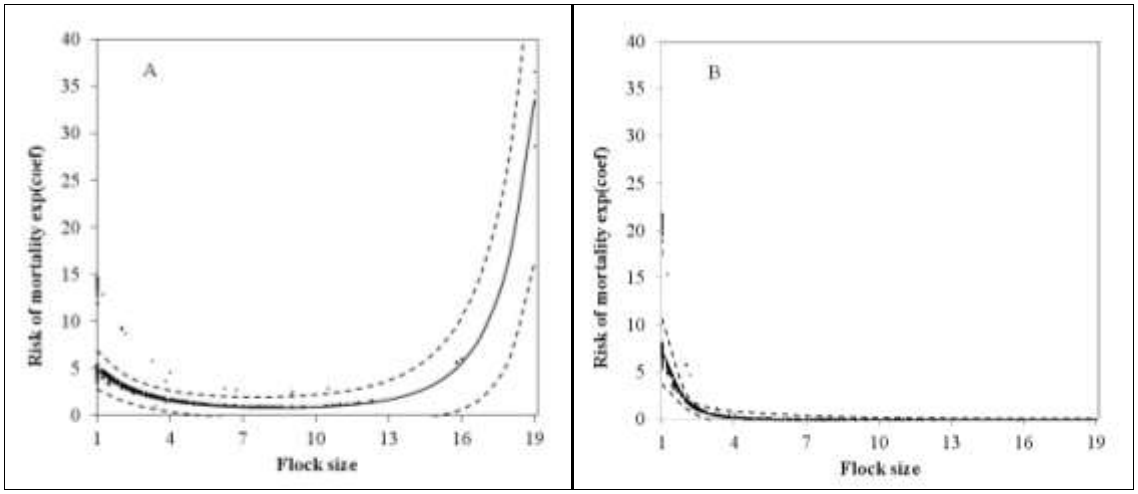


Figure 6-3. Predicted effect of average flock size of sage-grouse hens with 95% confidence intervals from the top AIC$_c$ selected Cox proportional hazard model (from the anti-predation strategy analysis) of sage-grouse hen survival. The model included a quadratic of average flock size and an interaction between flock size and sage-grouse age (adult or yearling). Predicted effects of the average flock size of sage-grouse during the summer for adult (A) and yearling (B) hens. Predicted effects displayed as risk of mortality with the y-axis units plotted as exp(coefficient values). Partial residuals were overlaid on predicted effect plots. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

CHAPTER 7

CONCLUSIONS

There has been a large volume of research on the habitat requirements and population demographic rates of greater sage-grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) throughout its range (see reviews in Connelly et al. 2004, Connelly et al. 2011). However, there has been little research assessing the influence of predator composition on habitat selection, nest success, and hen survival. Increases in avian predator densities are likely to result in higher depredation rates on sage-grouse nests and reduced chick survival (Evans 2004, Cresswell 2008). Predation has been proposed as a potential threat to sage-grouse populations (Braun 1998); however, there are no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult; Connelly et al. 2011). Hagen (2011) suggested that predation is not limiting sage-grouse populations, and management actions designed to alleviate predation, such as predator removal, may only serve to provide a short-term release of predation rates in fragmented habitats and areas with human-subsidized predator populations. Increases in the human footprint have occurred and are likely to continue throughout most of the range of sage-grouse (Leu et al. 2008), which has increased the abundance of generalist predators throughout the western United States (Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Baxter et al. 2007, Sauer et al. 2011).

In Lima’s (1998) and Cresswell’s (2008) reviews of non-lethal effects of predator-avoidance, they illustrated that presence of a predator had dramatic impacts on use of habitat by prey species. These effects were found to be as great or greater than the effects of direct predation. Thus, the presence of greater abundances of avian predators may induce changes in sage-grouse behavior associated with habitat usage and affect nest success and hen survival. Sage-grouse reduce time off of their nests when they inhabit areas near high abundances of ravens (Coates and Delehanty 2008); thus, in addition to using indirect mechanisms, sage-grouse may be using avian predator abundance directly to evaluate predation risk while nesting. In Chapter 2, I found that sage-grouse were capable of avoiding areas with relatively higher densities of small, medium, and large avian predators—specifically American kestrels (*Falco sparverius*; hereafter; “kestrels”), black-billed magpies (*Pica hudsonia*; hereafter “magpies”), common ravens (*Corvus corax*; hereafter “ravens”), golden eagles (*Aquila chrysaetos*), *Buteo* hawks, and northern harriers (*Circus cyaneus*; hereafter “harriers”)—compared to available sagebrush habitat. My results suggested that sage-grouse avoided avian predators at nest and brood locations on the basis of the size of avian predators rather than individual species identity, equivalence of all species, foraging behavior of predators, or presumed threat to sage-grouse reproductive stage. By selecting habitat with lower densities of avian predators, sage-grouse lower their exposure to avian predation and risk of reproductive failure.

Predation risk trade-offs and non-lethal predator effects, such as avoidance of risky habitats (indirect avoidance) and habitats occupied by greater density of avian predators (direct avoidance; Evans 2004, Verdolin 2006, Cresswell 2008), are mechanisms that explain the differential use of sagebrush habitat (habitat partitioning) by female sage-grouse. High densities of avian predators and close proximity to anthropogenic and landscape features—specifically oil and gas infrastructure, power lines, major roads, riparian habitat, and rugged topography—are likely to result in reduced adult survival and higher depredation rates on sage-grouse nests (Lima 1998, Evans 2004, Cresswell 2008). I found that sage-grouse hens used direct and indirect mechanisms to lower their exposure to predation and nest depredation particularly from avian predators. Sage-grouse use of habitat was negatively connected to avian predator densities with quality sage-grouse habitat presumably having lower densities of small, medium, and large avian predators. In general, sage-grouse avoided risky habitat by directly avoiding areas with higher densities of small, medium, and large avian predators and indirectly by avoiding areas close to anthropogenic and landscape features (see Chapter 3). Similar to previous research, my analyses confirmed that sage-grouse select locations farther away from anthropogenic and landscape features that could be used as perches or provide subsidized food resources for predators, which included oil and gas structures (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Holloran et al. 2010, Kirol 2012) and major roads (Holloran 2005, Aldridge and Boyce 2007) at all reproductive stages, power lines (Hanser et al. 2011) at brood locations, and riparian habitat (Doherty et al. 2010, Dzialak et al. 2011) at nest locations. I found that sage-grouse also chose flatter locations at nest-sites similar to the findings of Jensen (2006), Doherty et al. (2010), Dzialak et al. (2011), and Kirol (2012). Thus, human manipulation of habitat that structurally changes habitat and promotes greater density of avian predators may limit sage-grouse populations because habitat that has high-quality cover and forage may become functionally unavailable to sage-grouse when avian predator densities are at high levels and anthropogenic features are nearby. Habitat partitioning during vulnerable reproductive stages by female sage-grouse relative to predation risk and food availability was a means for sage-grouse hens to lower their risk of predation and nest depredation, while using habitat to meet energetic requirements of hens and chicks.

As sagebrush habitat is developed, raven occupancy and density will increase in areas adjacent to and overlapping with high-quality sage-grouse habitat. The negative effect of ravens on the nest success of grouse has been well documented (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010). For example sharp-tailed grouse (*Tympanuchus phasianellus*) in southern Alberta had 8-times greater nest success in landscapes with <3 corvids/km^2 as opposed to landscapes with high densities of corvids (Manzer and Hannon 2005). Around Jackson and Pinedale, Wyoming, Bui et al. (2010) found that higher occupancy rates of ravens were correlated with failed sage-grouse nests. Raven depredation on sage-grouse nests was a common occurrence in northeast Nevada based on infrared video cameras set up at nest sites (Coates et al. 2008), and sage-grouse nest success in northeast Nevada was related to the number of ravens per 10-km transect with nest failure rates increasing 7% with every additional raven/10 km (Coates and Delehanty 2010). My results also indicated that sage-grouse nest success was negatively impacted by the presence of ravens near sage-grouse nests (local scale) and higher raven densities at the study site level (landscape scale; see Chapter 4). This suggests that sage-grouse nesting in areas with subsidized raven populations may have suppressed nest success, which may contribute to lower sage-grouse population growth rates.

Coates (2007) studied the effect of raven removal on sage-grouse nest success at 4 study areas in Nevada—1 study area with raven removal and 3 study areas without raven removal. Raven abundance was reduced with DRC-1339 treated-egg baits (Coates 2007, Coates et al. 2007). With every 1 km increase in distance away from raven removal routes, Coates (2007) found that sage-grouse nests were 2.1% more likely to fail, and ravens were 13% more likely to be the culprit. This information provided a good indication that reduction of raven abundance by USDA/APHIS/Wildlife Services (WS) may provide a benefit for sage-grouse nesting in areas with subsidized raven populations. My study verified that WS raven management can reduce the abundance of ravens at a relatively large scale (15-km radius or 706.5 km^2), and sage-grouse nest success was correlated with reduced densities of ravens on the landscape (see Chapter 4).

The management of ravens may be a potential mitigating strategy for areas of low sage-grouse nest success. In some areas, reductions in raven density at a landscape level may increase the amount of functional habitat for sage-grouse. Coates (2007), Bui et al. (2010), and Hagen (2011) suggested that predator removal may provide a short-term release in predation rates within fragmented habitats and areas with subsidized predator populations. However, Hagen (2011) indicated that predator removal will not mitigate sage-grouse population declines throughout the range of sage-grouse. I agree that the positive effects of raven removal for sage-grouse nest success are likely short-lived gains.

In Chapter 4, I monitored WS raven management as it applied to livestock depredation; thus, targeted raven management to benefit sage-grouse may produce better results. However, identification of areas where sage-grouse may benefit from raven removal and implementation of a raven removal program targeted at benefitting sage-grouse will not be an easy task. Management of both breeding and transient ravens will be necessary, which will present many challenges. Predator removal may have a place in sage-grouse management when sage-grouse populations are subjected to high densities of ravens as an interim mitigation measure. However, low reproductive rates may persist in many areas due to compensatory predation by other predators (Coates 2007, Bui et al. 2010). Long-term solutions to reduce human-subsidized raven populations are necessary to address the growing raven and sage-grouse conflict. Reducing raven abundance may be possible through non-lethal means, such as reducing availability of supplemental food (road-kill, dead livestock, and garbage) and nesting and perching structures (oil and gas structures, power lines, telephone poles, communication towers, etc.; Jiménez and Conover 2001). More research needs to be focused on understanding raven population dynamics in sagebrush ecosystems, and how to reduce the utility of anthropogenic subsidies (food and nesting structure) for ravens.

In Chapter 5, I tested the hypothesis that the negative effects of corvids would be amplified in areas closer to potential perches and areas with subsidized food resources (anthropogenic and landscape features). I also evaluated interactive effects between corvid densities and microhabitat. Even though I found a negative effect of the abundance of ravens (nest-site or study-site scale), my results did not suggest any amplifying effect of corvid (raven or magpie) abundance with proximity to any anthropogenic or landscape feature variable. I did not find any evidence that magpies had a negative impact on sage-grouse nest success regardless of the proximity to anthropogenic and landscape features or microhabitat. Similar to Aldridge and Boyce (2007) and Kirol (2012), I did not find any significant correlations between nest success and proximity to anthropogenic development, and there was no evidence of interactive effects between anthropogenic features and corvid densities. Although the landscape features that I assessed represented riskier habitat, I found that nest success was positively correlated with relatively rugged habitat. Rugged terrain, nest-level raven occupancy, and site-level raven density had complex effects on nest success, which has been illustrated as an important factor affecting sage-grouse population growth (Johnson and Braun 1999, Taylor et al. 2012).

Recent research has indicated that sage-grouse hen survival may be the most important demographic parameter driving sage-grouse productivity (Johnson and Braun 1999, Taylor et al. 2012). Effects of anthropogenic and landscape features on survival of sage-grouse hens have not been evaluated in the context of predator communities. In addition, management agencies would benefit from more information on the effects of parental investment and anti-predation strategies on sage-grouse survival, which has not been the focus of sage-grouse research and conservation. Raptors have been identified as significant threats to sage-grouse survival, including golden eagles, *Buteo* hawks, and harriers (Schroeder et al. 1999, Schroeder and Baydack 2001, Danvir 2002). I found that sage-grouse summer survival was negatively correlated with landscape features that represented riskier habitat, especially risk of predation from raptors (see Chapter 6).

Breeding season survival of sage-grouse was negatively impacted by proximity to trees (deciduous and coniferous), more rugged terrain, and golden eagle density when terrain was less rugged. Kirol (2012) also found that terrain roughness was negatively correlated with sage-grouse summer survival in Wyoming. I found lower sage-grouse survival when sage-grouse were exposed to a high density of golden eagles while simultaneously taking topographic ruggedness into account (Chapter 6). I found that the negative effect of topographic ruggedness and golden eagle density was dampened by the combination of greater rugged terrain and high density of golden eagles. Two potential explanations for this finding include 1) rugged topography may provide some refugia from visual predators (e.g., golden eagles), because topographic features such as slight depressions may decrease the effective distance that a raptor can detect a sage-grouse on the ground; and 2) greater density of golden eagles in rugged topography (risky habitat) may competitively exclude other predators. Golden eagles and coyotes are the top predators in sagebrush ecosystems (Mezquida et al. 2006, Hagen 2011), and presence of golden eagles may partially reduce the hunting efficiency of mammalian predators. Thus, landscape features in conjunction with golden eagle density and sage-grouse behavior had dynamic effects on survival. My research also indicated that proximity to anthropogenic features had no effect on sage-grouse survival, and there was no evidence of an interactive effect between anthropogenic features and raptor densities. My sage-grouse survival results also suggest that survival was greater for hens without nests or broods, hens that stayed in intermediate size flocks, and yearling hens.

Many authors have suggested that ground-nesting bird survival, including sage-grouse, is connected to quantity and quality of habitat, and the presence of adequate sagebrush habitat minimizes predator effects on sage-grouse survival (Connelly et al. 1994, Braun 1998, Aldridge et al. 2008, Connelly et al. 2011). I agree with this, but there needs to be careful consideration of interactive effects of anthropogenic and landscape features and predator community dynamics (risk of predation). The aspects of habitat (anthropogenic and landscape features) that present riskier areas for prey species are confounded by the predator composition that reside in those areas. For this reason, management agencies need to understand how interactions among proximity to anthropogenic and landscape features, microhabitat, and the predator community relate to sage-grouse selection of habitat and demographic rates (e.g., nest success and survival). For instance, I found that areas with higher topographic ruggedness had lower sage-grouse survival, which was dampened by high densities of golden eagles. Sage-grouse hens avoided conventional and natural gas wells (Kirol 2012; see also Chapter 3), which placed them in areas with higher topographic ruggedness (natural gas development is typically in flatter areas). However, the overall sage-grouse survival in areas with higher topographic ruggedness was lower. This indicates that changes in sage-grouse selection of habitat in response to anthropogenic features (fragmentation of habitat) can have dynamic consequences for sage-grouse survival, especially when considering differences in predator compositions. Thus, habitat fragmentation of sagebrush habitats has complex effects on sage-grouse use of the landscape, which in turn can have complex impacts on survival. My results highlight the necessity to assess habitat and predator community dynamics concurrently when designing management plans.

LITERATURE CITED

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

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

Aldridge, C. L., S. E. Nielson, 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.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the North American Wildlife and Natural Resources Conference 72:258–269.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, California, USA.

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.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

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.

Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

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. O. Spencer, Jr., and D. J. Delehanty. 2007. Efficacy of CPTH-treated egg baits for removing ravens. Human-Wildlife Conflicts 1:224–234.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of

Fish and Wildlife Agencies. Unpublished Report, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

Danvir, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, Utah, USA.

Doherty, K. E. 2008. Sage-grouse and energy development integrating science with conservation planning to reduce impacts. Dissertation, University of Montana, Missoula, Montana, 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 74:1544–1553.

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 6:1–18.

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Hanser, S. E., M. Leu, S. T. Knick, and C. L. Aldridge. 2011. Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, Wyoming, USA.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis, University of Wyoming, Laramie, USA.

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29:62–69.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.

Manzer, D. L., 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 implication of coyote control on sage-grouse populations. Condor 108:747–759.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

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*). Birds of North America. Philadelphia, Pennsylvania, USA.

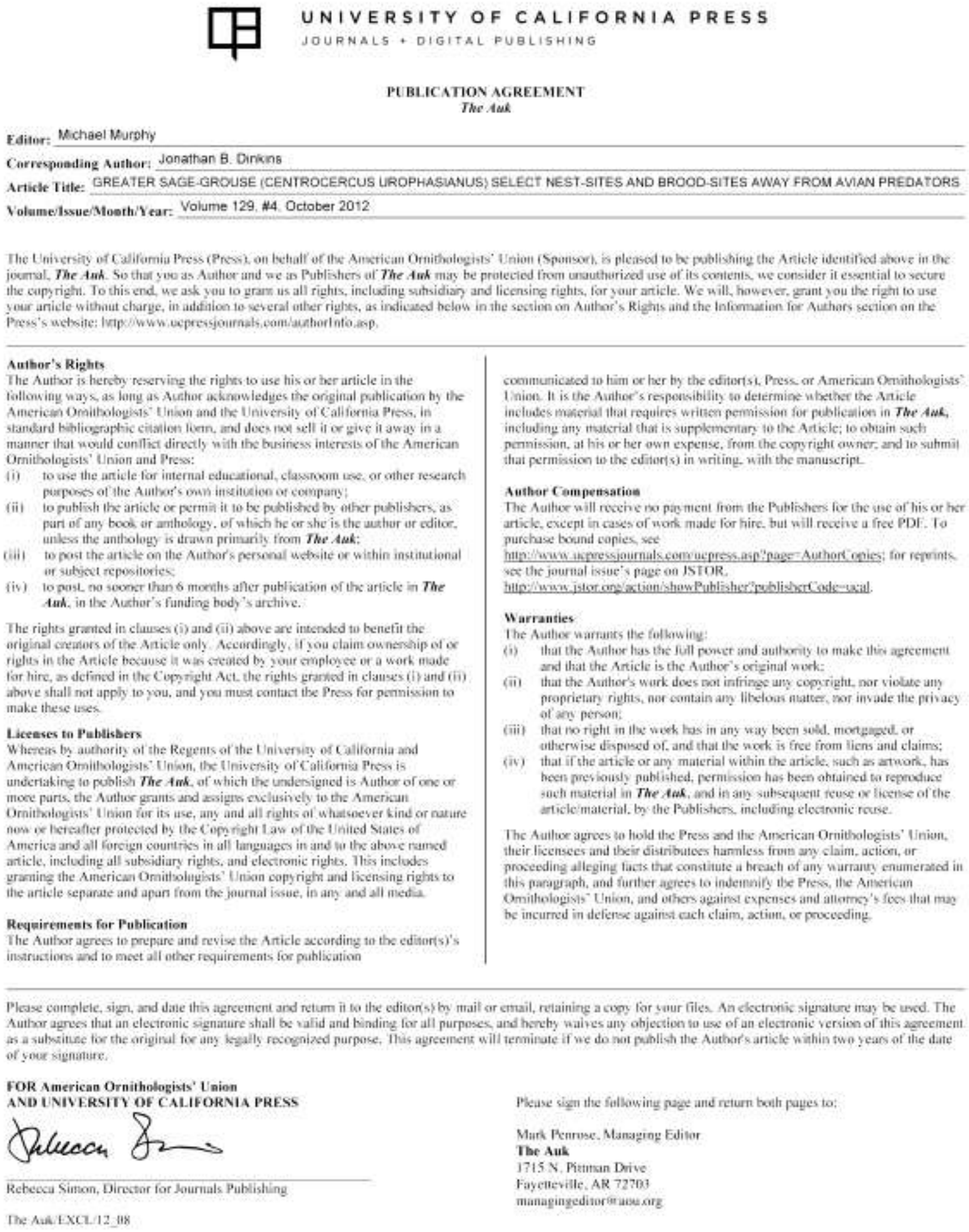
Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife

Management 76:336−347.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

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.

APPENDIX



UNIVERSITY OF CALIFORNIA PRESS
JOURNALS + DIGITAL PUBLISHING

PUBLICATION AGREEMENT
The Auk

Editor: Michael Murphy
Corresponding Author: Jonathan B. Dinkins
Article Title: GREATER SAGE-GROUSE (CENTROCERCUS UROPHASIANUS) SELECT NEST-SITES AND BROOD-SITES AWAY FROM AVIAN PREDATORS
Volume/Issue/Month/Year: Volume 129, #4, October 2012

The University of California Press (Press), on behalf of the American Ornithologists' Union (Sponsor), is pleased to be publishing the Article identified above in the journal, ***The Auk***. So that you as Author and we as Publishers of ***The Auk*** may be protected from unauthorized use of its contents, we consider it essential to secure the copyright. To this end, we ask you to grant us all rights, including subsidiary and licensing rights, for your article. We will, however, grant you the right to use your article without charge, in addition to several other rights, as indicated below in the section on Author's Rights and the Information for Authors section on the Press's website: http://www.ucpressjournals.com/authorInfo.asp.

Author's Rights

The Author is hereby reserving the rights to use his or her article in the following ways, as long as Author acknowledges the original publication by the American Ornithologists' Union and the University of California Press, in standard bibliographic citation form, and does not sell it or give it away in a manner that would conflict directly with the business interests of the American Ornithologists' Union and Press:

(i) to use the article for internal educational, classroom use, or other research purposes of the Author's own institution or company;
(ii) to publish the article or permit it to be published by other publishers, as part of any book or anthology, of which he or she is the author or editor, unless the anthology is drawn primarily from ***The Auk***;
(iii) to post the article on the Author's personal website or within institutional or subject repositories;
(iv) to post, no sooner than 6 months after publication of the article in ***The Auk***, in the Author's funding body's archive.

The rights granted in clauses (i) and (ii) above are intended to benefit the original creators of the Article only. Accordingly, if you claim ownership of or rights in the Article because it was created by your employee or a work made for hire, as defined in the Copyright Act, the rights granted in clauses (i) and (ii) above shall not apply to you, and you must contact the Press for permission to make these uses.

Licenses to Publishers

Whereas by authority of the Regents of the University of California and American Ornithologists' Union, the University of California Press is undertaking to publish ***The Auk***, of which the undersigned is Author of one or more parts, the Author grants and assigns exclusively to the American Ornithologists' Union for its use, any and all rights of whatsoever kind or nature now or hereafter protected by the Copyright Law of the United States of America and all foreign countries in all languages in and to the above named article, including all subsidiary rights, and electronic rights. This includes granting the American Ornithologists' Union copyright and licensing rights to the article separate and apart from the journal issue, in any and all media.

Requirements for Publication

The Author agrees to prepare and revise the Article according to the editor(s)'s instructions and to meet all other requirements for publication communicated to him or her by the editor(s), Press, or American Ornithologists' Union. It is the Author's responsibility to determine whether the Article includes material that requires written permission for publication in ***The Auk***, including any material that is supplementary to the Article; to obtain such permission, at his or her own expense, from the copyright owner; and to submit that permission to the editor(s) in writing, with the manuscript.

Author Compensation

The Author will receive no payment from the Publishers for the use of his or her article, except in cases of work made for hire, but will receive a free PDF. To purchase bound copies, see http://www.ucpressjournals.com/ucpress.asp?page=AuthorCopies; for reprints, see the journal issue's page on JSTOR, http://www.jstor.org/action/showPublisher?publisherCode=ucal.

Warranties

The Author warrants the following:

(i) that the Author has the full power and authority to make this agreement and that the Article is the Author's original work;
(ii) that the Author's work does not infringe any copyright, nor violate any proprietary rights, nor contain any libelous matter, nor invade the privacy of any person;
(iii) that no right in the work has in any way been sold, mortgaged, or otherwise disposed of, and that the work is free from liens and claims;
(iv) that if the article or any material within the article, such as artwork, has been previously published, permission has been obtained to reproduce such material in ***The Auk***, and in any subsequent reuse or license of the article/material, by the Publishers, including electronic reuse.

The Author agrees to hold the Press and the American Ornithologists' Union, their licensees and their distributees harmless from any claim, action, or proceeding alleging facts that constitute a breach of any warranty enumerated in this paragraph, and further agrees to indemnify the Press, the American Ornithologists' Union, and others against expenses and attorney's fees that may be incurred in defense against each claim, action, or proceeding.

Please complete, sign, and date this agreement and return it to the editor(s) by mail or email, retaining a copy for your files. An electronic signature may be used. The Author agrees that an electronic signature shall be valid and binding for all purposes, and hereby waives any objection to use of an electronic version of this agreement as a substitute for the original for any legally recognized purpose. This agreement will terminate if we do not publish the Author's article within two years of the date of your signature.

FOR American Ornithologists' Union
AND UNIVERSITY OF CALIFORNIA PRESS

Rebecca Simon, Director for Journals Publishing

The Auk/EXCL/12_08

Please sign the following page and return both pages to:

Mark Penrose, Managing Editor
The Auk
1715 N. Pittman Drive
Fayetteville, AR 72703
managingeditor@aou.org

May 21, 2013

Jonathan B. Dinkins
Department of Wildland Resources
Utah State University
Logan, UT 84322-5230

Dear Christopher P. Kirol,

I am in the process of preparing my dissertation to complete my Ph.D. in Wildlife Biology at Utah State University, and hope to finish my degree in May 2013. I am writing to request your permission to include the *Auk* article that you co-authored with myself (citation below) as a chapter in my dissertation. You will be cited as a co-author on the title page of Chapter 2 of my dissertation. Please indicate your approval of my inclusion of this article in my dissertation by signing below. If you have any questions or concerns, please feel free to contact me.

Sincerely,
Jonathan B. Dinkins

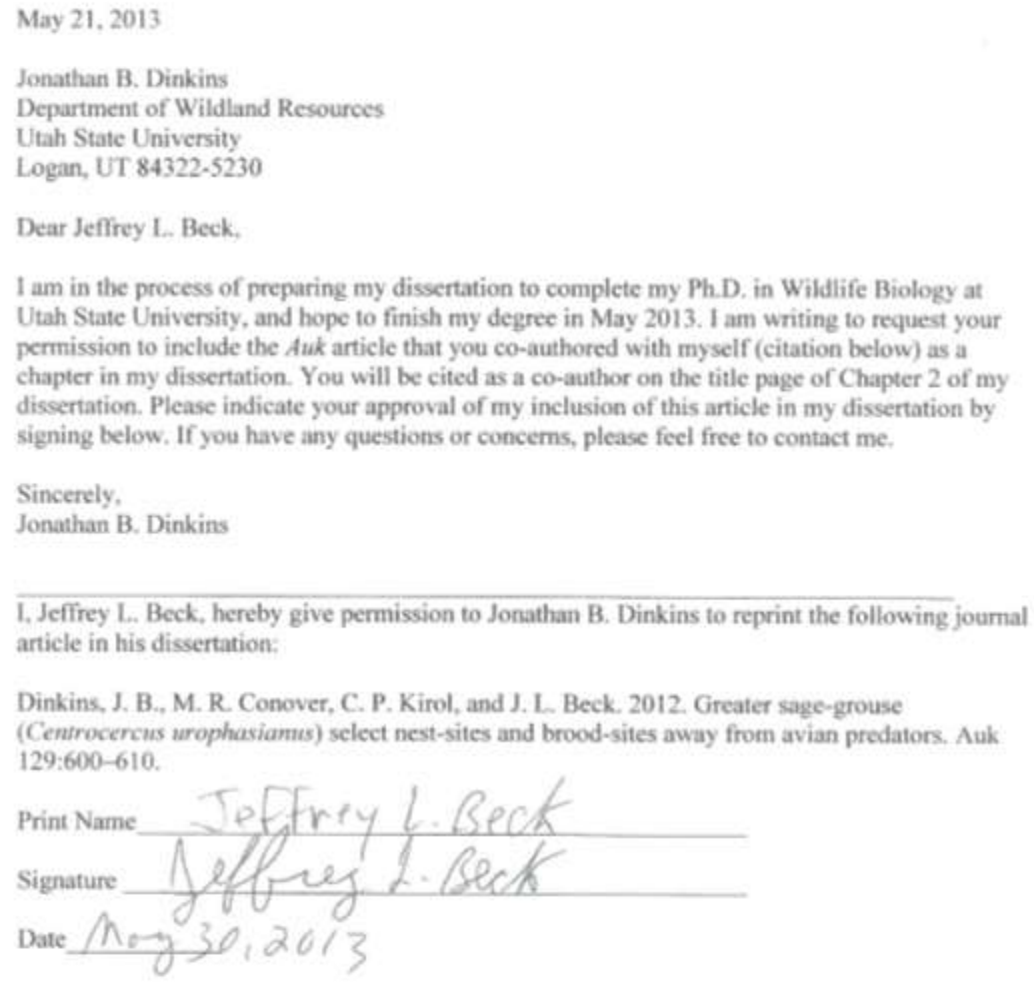
I, Christopher P. Kirol, hereby give permission to Jonathan B. Dinkins to reprint the following journal article in his dissertation:

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

Print Name Christopher Kirol

Signature

Date 5/29/13



May 21, 2013

Jonathan B. Dinkins
Department of Wildland Resources
Utah State University
Logan, UT 84322-5230

Dear Jeffrey L. Beck,

I am in the process of preparing my dissertation to complete my Ph.D. in Wildlife Biology at Utah State University, and hope to finish my degree in May 2013. I am writing to request your permission to include the *Auk* article that you co-authored with myself (citation below) as a chapter in my dissertation. You will be cited as a co-author on the title page of Chapter 2 of my dissertation. Please indicate your approval of my inclusion of this article in my dissertation by signing below. If you have any questions or concerns, please feel free to contact me.

Sincerely,
Jonathan B. Dinkins

I, Jeffrey L. Beck, hereby give permission to Jonathan B. Dinkins to reprint the following journal article in his dissertation:

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

Print Name Jeffrey L. Beck
Signature Jeffrey L. Beck
Date May 30, 2013

CURRICULUM VITAE

Jonathan B. Dinkins
(May 2012)

EDUCATION

Ph.D. **Wildlife Biology**, Utah State University, Logan, UT (expected Apr 2013)
M.F.A. **Ceramic Sculpture**, Montana State University, Bozeman, MT (May 2005)
B.S. **Biology**, University of Puget Sound, Tacoma, WA (May 2001)
B.A. **Studio Art**, University of Puget Sound, Tacoma, WA (May 2001)

WORK EXPERIENCE

- **Ph.D. Student** **(Jan 2008 – present)**
  Utah State University *Logan, UT*
  Dissertation: *Common Ravens Density and Greater Sage-Grouse Nesting Success in Southern Wyoming: Potential Conservation and Management Implications*. Conducted greater sage-grouse and raptor/corvid field research from 2008-2011. Objectives: evaluated the following: 1) sage-grouse nest-site and brood-site selection in relation to avian predators (golden eagle, red-tailed hawk, ferruginous hawk, Swainson's hawk, northern harrier, prairie falcon, American kestrel, common raven, black-billed magpie), 2) effects of natural and anthropogenic features on avian predator abundance and sage-grouse selection of habitat, 3) sage-grouse nest success in relation to corvid abundance, 4) effects of Wildlife Services (WS) raven removal for livestock on raven abundance around sage-grouse nesting habitat, 5) potential benefits for sage-grouse nest success from WS raven removal near sage-grouse nesting areas, and 6) effects of avian predator densities, proximity to natural and anthropogenic features, and sage-grouse hen behavior on sage-grouse hen survival. Duties and experience: experimental design, independently hired and supervised 1-2 field crews consisting of up to 9 technicians for each of 4 field seasons, spotlight capture and radio-telemetry of sage-grouse, sage-grouse nest monitoring, raptor surveys (point-counts), vegetation sampling, aerial telemetry in fixed-wing and helicopter, ordering materials, agency and landowner contacts, data entry, and data analysis.

- **Teaching Assistant** **(Jan 2009 – present)**
  Utah State University *Logan, UT*
  Assisted with instruction of undergraduate and graduate courses for the Wildland Resources Department at Utah State University for three semesters. Duties and experience: lectured, graded papers and tests and assisted with labs for Animal Behavior (2 semesters), Wildlife Damage Management (2 semesters;

graduate level), and Dynamics of Structured Populations (1 semester; graduate level).

- **Wildlife Technician** **(Mar – Jun 2007)**
  Big Horn Environmental *Sheridan, WY*
  Conducted wildlife surveys in the Powder River Basin of Wyoming. The work included sage-grouse, sharp-tailed grouse, raptor (red-tailed hawk, ferruginous hawk, Swainson's hawk, rough-legged hawk, peregrine falcon, prairie falcon, northern harrier, American kestrel, golden eagle, bald eagle), owl (short-eared owl, burrowing owl, long-eared owl, and great-horned owl), mountain plover, and black-tailed prairie dog surveys for habitat usage and population estimates for land management.
  <u>Duties and experience:</u> lek counts, raptor and owl nest productivity surveys, All-Topo real-time navigation, GPS, aerial and ground surveys, data entry, 4x4 driving, and land-owner contacts.

- **Research Technician** **(Jun 2006 – Dec 2007)**
  Montana State University–Bozeman *Bozeman, MT and throughout MT*
  Worked for the Montana Veterinary Entomology Lab on topics related to West Nile Virus and insect parasites.
  <u>Duties and experience:</u> designed and implemented a fish study for possible mosquito predators in coal-bed methane ponds in the Powder River Basin (Montana and Wyoming), gave presentations, wrote for publication, wildlife forensic entomology, assessed ectoparasites on American white pelicans, dissected pelicans for West Nile virus (WNv) testing, identified mosquitoes from West Nile Virus monitoring traps throughout the state of Montana, handled domestic sheep for a study assessing the prospects of an insecticide to remove sheep keds and lice, Excel, Word, PowerPoint, and R.

- **Wildlife Technician** **(Mar – Jun 2006)**
  University of Montana *Decker, MT and Sheridan, WY*
  Worked on a behavior and demography study that was assessing the effects of coal-bed methane development on greater sage-grouse.
  <u>Duties and experience:</u> spotlight capture, banding, radio-telemetry, blood collection, nest locating, nest monitoring, vegetation sampling (line-intercept, Daubenmire and Robel), ground truing of satellite habitat imagery, ATV use, driving standards on 2-track roads (4x4), GPS, compass, map-use, ArcMap, Excel, Word, and data-entry.

- **Wildlife Technician** **(May – Aug 2005)**
  Silva Environmental *Quincy, CA*
  Surveyed California spotted owls and northern goshawks on a contract for the U.S. Forest Service.
  <u>Duties and experience:</u> Surveyed spotted owls and goshawks for pair status, nesting, and reproductive success, broadcast surveying, map use, compass, owl mousing,

detection follow-ups, crew-leader responsibilities, driving 4x4 standard vehicles, ATV use, snowmobile, GPS, data entry, GPS Trackmaker, and Terrain Navigator Pro.

- **Research Assistant** **(Jun 2003 – Sep 2004)**
  US Forest Service *Bozeman, MT*
  Performed field studies throughout western Montana (the research focused on the biological control of dalmatian toadflax through insect injury from weevils and caterpillars) for the Forestry Sciences Lab in Bozeman.
  Duties and experience: worked with a small field crew, reading vegetation data with a Daubenmire quadrat, assessed insect damage, light meter readings, photosynthetic rate sampling, GPS, driving 4x4 vehicles, re-potting plants, and plant stem analysis.

- **Research Scientist** **(Apr 2001 – Jun 2002)**
  University of Washington *Seattle, WA*
  Involved in hepatic lipase studies using transgenic mice as a model of hepatic lipase's function in getting rid of unwanted cholesterol and possible prevention of atherosclerosis.
  Duties and experience: PCR, western blot, recombinant DNA (using restriction enzymes), agarose gel electrophoresis, and various mouse procedures/handling (orbital bleeding, subcutaneous and intravenous injections, anesthetic administration [ketamine and xylazine], etc.).

Peer-Reviewed Articles

Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, S. N. Frey. In Review. Effects of common raven removal on greater sage-grouse nesting success. Journal of Wildlife Management.

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

Kirol, C. P., J. L. Beck, **J. B. Dinkins**, and M. R. Conover. 2012. Greater sage-grouse nesting and brood-rearing microhabitat selection in xeric big sagebrush. Condor 114:75−89.

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. Condor 112:331−336.

Book Chapters

Conover, M. R., **J. B. Dinkins**, and M. J. Haney. In press. Impacts of weather and accidents on wildlife. *In* P. R. Krausman and J. W. Cain III, eds. Wildlife Management and Conservation. The Wildlife Society and John Hopkins University Press, Bethesda, MD.

Conover, M. R., and **J. B. Dinkins**. 2012. Managing abundant wildlife through the human dimension. Pages 177–188 *in* D. Decker, S. Riley, and B. Siemer, eds. Human Dimensions of Wildlife Management. The Wildlife Society and John Hopkins University Press, Bethesda, MD.

Press Articles

Dinkins, J. B. 2011. Common ravens and greater sage-grouse: ongoing research in Wyoming. The Communicator, Utah State University Extension 7(1):3.

Journal Editor

Assistant Editor, *Human Wildlife Interactions*. (2008-present)

Reviewer for Journals

Ecological Processes

Grants

Wyoming Land Conservation Initiative	= *$37,000*	(2012)
Southwest Sage-grouse Local Working Group	= *$33,000*	(2011)
South-central Sage-grouse Local Working Group	= *$33,000*	(2011)
Wyoming Land Conservation Initiative	= *$37,000*	(2011)
Anadarko Petroleum	= *$39,500*	(2010–2011)

Presentations

Dinkins, J. B., M. R. Conover, C. P. Kirol, and J. L. Beck. 2012. Greater sage-grouse (*Centrocercus urophasianus*) select nest-sites and brood-sites away from avian predators. The Wildlife Society 19th Annual Conference, Portland, OR.

Dinkins, J. B., M. R. Conover, C. P. Kirol, and J. L. Beck. 2012. Greater sage-grouse (*Centrocercus urophasianus*) select nest-sites and brood-sites away from avian predators. 28th Western Association of Fish and Wildlife Agencies Sage and Columbian Sharp-tailed Grouse Workshop, Steamboat Springs, CO.

Dinkins, J. B., M. R. Conover, C. P. Kirol, and J. L. Beck. 2012. Greater sage-grouse select nest-sites and brood-sites away from avian predators. Wyoming Land Conservation Initiative, WLCI Science Workshop, Rock Springs, WY.

Dinkins, J. B., M. R. Conover, C. P. Kirol, and J. L. Beck. 2012. Greater sage-grouse select nest-sites and brood-sites away from avian predators. The Wildlife Society, Utah Chapter Meeting, Springdale, UT.

Dinkins, J. B. 2011. Greater sage-grouse select nest-sites and brood-sites away from avian predators. The Wildlife Society, Wyoming Chapter Meeting, Jackson, WY.

Dinkins, J. B. 2010. Multivariate analysis to adentify where sage-grouse select nest sites. The Wildlife Society, Wyoming Chapter Meeting, Lander, WY.

Dinkins, J. B. 2008. Impacts of raven abundance on greater sage-grouse nesting success in southwest Wyoming. The Wildlife Society, Wyoming Chapter Meeting, Sheridan, WY.

Dinkins, J. B. 2008. Raven predation on sage-grouse nests. Industry and Government Conference, Rawlins, WY.

Dinkins, J. B., G. Johnson, M. Rolston, C. Pariera Dinkins. 2007. Laboratory evaluation of the predation efficacy of three fish species on immature mosquitoes. Wyoming Mosquito Management Association, Cody, WY.

Dinkins, J. B., G. Johnson, M. Rolston, C. Pariera Dinkins. 2007. Laboratory evaluation of the predation efficacy of three fish species on immature mosquitoes. Montana Mosquito and Vector Control Association, Helena, MT.

Computer Knowledge

-Mac and PC, Word, PowerPoint, Excel, PhotoShop, SAS, R (packages: lme4 [generalized linear mixed models], ncf [spatial analyses], sdep [spatial eigenvector mapping], survival [Cox proportional hazards], unmarked [distance sampling with covariate generalized linear models], nnet [multinomial logistic regression], and multivariate techniques in randomForest and rpart [principle components analysis, linear discriminant analysis, classification trees, and random forests]), GPS Trackmaker, Terrain Navigator Pro, All-Topo, ArcMap, MARK, and Program Distance

Professional Organizations

-The Wildlife Society, Wyoming Chapter	(2008-present)
-Board of Directors, Montana Raptor Conservation Center	(2006)
-Ceramics Guild, Montana State University	(2003-2005)

Fellowships

-Jack H. Berryman Institute Graduate Student Fellowship	(2010)

Scholarships/Awards

-Presidential Scholarship, Montana State University-Bozeman	(2002-2003)
-Paul and Helen Perdue Community Service Award, University of Puget Sound	(2001)
-Student Athletic Advisory Council, University of Puget Sound	(2000-2001)
-Art Department Scholarship, University of Puget Sound	(1998-2001)
-Ball Scholarship, University of Puget Sound	(1999-2000)
-Green Memorial Scholarship, University of Puget Sound	(2000-2001)
-Helen Buchanan Scholarship, University of Puget Sound	(1998-1999, 2000-2001)
-Florence Todd Scholarship, University of Puget Sound	(1999-2000)
-Hope Scholarship, Academic Merit	(1997-1998)
-Eagle Scout	(1993)