

PHOTOCOPY AND USE AUTHORIZATION

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at Idaho State University, I agree that the library shall make it freely available for inspection. I further state that permission for extensive copying of my thesis for scholarly purposes may be granted by the Dean of Graduate Studies and Research, Dean of my academic division, or by the University Librarian. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature _____

Date _____

GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*)
NEST PREDATION AND INCUBATION BEHAVIOR

By

Peter Samuel Coates

A dissertation
submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology
Idaho State University
May 2007

© 2007

Peter Samuel Coates

All Rights Reserved

COMMITTEE APPROVAL

To the Graduate Faculty:

The members of the committee appointed to examine the dissertation of Peter Samuel Coates find it satisfactory and recommend that it be accepted.

David J. Delehanty
Major Advisor

Charles R. Peterson
Committee Member

Richard S. Inouye
Committee Member

Jack W. Connelly
Committee Member

Daniel P. Ames
Graduate Faculty Representative

ACKNOWLEDGMENTS

First and foremost, I thank my beautiful, loving, and soon-to-be wife, Kristen. Your unconditional help in the field and expertise in revising papers helped bring this project to fruition. Also, your patience, advice, and motivating conversations encouraged me to pursue and complete my goals, especially during frustrating times. Kristen, you really helped me to succeed in this process, and I love you for that.

I am grateful to all of my family, especially Peter and Sue, my parents, and Jennifer, my sister. Thank you for believing in me and continually giving me generous words of encouragement. John, I also thank you for your support and taking interest in my research and other aspects of biology, which led to many lengthy, thought-provoking discussions that improved my overall understanding. I am grateful to the late Jack Walters, a good friend and dedicated birder. I was fortunate to have Jack volunteer time and knowledge. He inspired me to study birds, as a naturalist, through observations in nature.

I give special thanks to Dr. David Delehanty, my major advisor and good friend. Dave, this dissertation would not have been possible without your guidance, ideas, and excellent editorial comments. I benefited greatly from your dedication to my research, years of encouragement, and your thoughts about science. Our discussions in the past 8 years have significantly deepened my understanding of ecology, animal behavior, and natural history.

I am grateful to Drs. Jack Connelly, Charles Peterson, Richard Inouye, and Daniel Ames for serving as my graduate committee and providing me with helpful reviews and advice. I appreciate Jack's invaluable expertise in sage-grouse biology and management

providing me with knowledgeable feedback. Also, I thank Chuck for his open door policy fostering many fruitful discussions about evolution, ecology, and statistics. Terri Peterson made exceptional contributions to the statistical analyses.

I am grateful to the many technicians (field and lab) and volunteers for their hard work and patience. In particular, I appreciate the unfaltering reliability and dedication of Chris Simms, Ron Troy, Joey Warwick, and Noa Sparks. Their dedication included many hours of spotlighting and chasing grouse during the middle of the night, even during adverse weather conditions. We had many good times out there! Numerous graduate students provided useful feedback, which helped bring this dissertation to fulfillment, including Scott Cambrin, Brad Lowe, Pamela O'Hearn, Nicole Turek, and Josh Schultz. I especially thank Chris Jenkins, my good friend and a fellow Ph.D. candidate, for allowing me to frequently bounce new ideas, which led to discussions that advanced my understanding of wildlife, science, academia, and the politics of it all.

Nevada Department of Wildlife (NDOW) funded a portion of this research. I am grateful to many NDOW personnel who were involved in this study, namely, Sean Espinosa, Kari Martin, Sid Eaton, Larry Gilbertson, and San Stiver. I thank Jack Spencer, U. S. Department of Agriculture/Wildlife Services (USDA/WS), for providing expertise in field techniques and reviewing previous drafts and Robert Beach (USDA/WS) for insightful discussions and literature on raven behavior. I also thank David Musil, Idaho Department of Fish and Game, for allowing me to video-monitor nesting sage-grouse in Idaho. Personnel from U. S. Department of Interior, Bureau of Land Management assisted in capturing and radio-marking grouse. Numerous landowners were kind enough to openly allow me to conduct research on their property. Particularly, I am appreciative

of the Boise family for their utmost hospitality, friendship, and support in wildlife research.

Jack H. Berryman Institute and Idaho National Laboratory/Bechtel provided funding. I also thank the Graduate Student Research and Scholarship Committee and the Department of Biological Sciences (ISU) for numerous awards including a GK-12 National Science Foundation Fellowship, Research and Teaching Assistantships, and research grants. Additional funding was generously donated by sportsmen and conservation organizations, namely, Safari Club International (Idaho, Desert, and Northern Nevada Chapters), Carson Valley Chukar Club, Wildlife and Habitat Improvement of Nevada, Sportsmen for Fish and Wildlife, and Nevada Chukar Foundation.

TABLE OF CONTENTS

| | |
|---|------|
| PHOTOCOPY AND USE AUTHORIZATION | i |
| COMMITTEE APPROVAL | iv |
| ACKNOWLEDGMENTS | v |
| LIST OF FIGURES | xi |
| LIST OF TABLES | xv |
| ABSTRACT | xvii |
| PREFACE | 1 |
| PRERFACE LITERATURE CITED | 10 |
| | |
| CHAPTER 1: | |
| IDENTIFICATION OF GREATER SAGE-GROUSE NEST PREDATORS | |
| AND DEPREDATION SIGN USING CONTINOUS VIDEO- | |
| MONITORING | 17 |
| ABSTRACT..... | 17 |
| INTRODUCTION | 18 |
| STUDY AREA | 20 |
| METHODS..... | 21 |
| Video-Monitoring | 23 |
| Statistical Analyses | 25 |
| RESULTS | 26 |
| Raven Encounters | 26 |
| Badger Encounters | 27 |
| Cow Encounters | 28 |
| Rodent Encounters | 29 |
| Snake Encounters..... | 30 |
| DISCUSSION | 30 |
| MANAGEMENT IMPLICATIONS | 37 |
| LITERATURE CITED | 48 |

**CHAPTER 2:
GREATER SAGE-GROUSE INCUBATION RHYTHMS AND THE
EFFECTS OF AGE, TIMING OF INCUBATION, PREDATORS, HABITAT,
AND CLIMATE.....56**

ABSTRACT56

INTRODUCTION57

STUDY AREA59

METHODS.....61

 Videography61

 Vegetation Measurements.....62

 Index of Raven Abundance.....63

 Statistical Analyses64

Modeling incubation constancy and recess duration65

RESULTS68

 Patterns of Incubation Rhythms.....68

Incubation Constancy68

Incubation Recesses68

 Incubation Constancy Models69

 Incubation Recess Models71

DISCUSSION73

LITERATURE CITED.....99

**CHAPTER 3:
EFFICACY OF CPTH-TREATED EGG BAITS FOR REMOVING
COMMON RAVENS106**

ABSTRACT106

INTRODUCTION107

STUDY AREA.....110

METHODS.....110

 Raven Surveys.....110

 CPTH Application112

 Statistical Analyses115

RESULTS115

DISCUSSION116

| | |
|--|------------|
| LITERATURE CITED..... | 125 |
| CHAPTER 4: | |
| GREATER SAGE-GROUSE NEST SUCCESS IN RELATION TO AGE, PREDATORS, AND HABITAT, AND EFFECTS OF RAVEN REMOVAL.... | 130 |
| ABSTRACT | 130 |
| INTRODUCTION | 131 |
| STUDY AREA | 135 |
| METHODS | 136 |
| Video-Monitoring | 137 |
| Vegetation Measurements | 138 |
| Predator Surveys | 139 |
| Statistical Analyses | 141 |
| <i>Modeling sage-grouse nest success</i> | 142 |
| RESULTS | 145 |
| Raven Removal..... | 145 |
| Sage-grouse Nest Success Models..... | 147 |
| Microhabitat and Predator Relationships..... | 148 |
| DISCUSSION | 150 |
| LITERATURE CITED..... | 171 |

LIST OF FIGURES

- 1.1. Greater sage-grouse study area in northeastern Nevada during 2002-2005. Filled circles represent lek routes where nests were monitored using videography. A public landfill was located approximately 7 km from the northernmost site.....43
- 1.2. Video images of sage-grouse nests in northeastern Nevada. (a) Image of incubating grouse. (b) Raven depredation that resulted in no diagnostic egg remains. (c) Badger perforating egg shell and sucking out egg contents. (d) Eggshells following badger depredation (from c) left in nest bowl, which resulted in holes on the side of eggs (arrow), (e) Badger removing eggs from nest bowl. (f) Eggshell fragments of badger depredation (from e) which were fragmented and the nest destroyed. Image taken with a 35-mm camera following badger depredation to show eggshells that were outside nest bowl. Arrow indicates where nest bowl was located.....44
- 1.3. Time of predation by badgers ($n = 7$) and ravens ($n = 9$) at natural, video-recorded sage-grouse nests in northeastern Nevada during 2002-2005. An additional raven encounter was reported in the text but the time was not recorded. Time of 0:00 indicates midnight. Dots represent time of first appearance of predators during predation events. Shaded areas indicate approximate nocturnal hours based on average sunrise and sunset times during dates of predation events.....45
- 1.4. Video images of sage-grouse unsuccessfully defending nest against ravens in northeastern Nevada. Seven eggs were depredated within the first egg was taken 9.4 minutes before image (a). All consecutive video images are approximately one second apart. (a) Grouse moves away from nest bowl exposing the last egg (arrow). (b) Raven attempts to pick up the egg from nest bowl. (c) Raven withdraws without taking the egg. (d) Grouse attacks raven with feathers extended from across the nest bowl (arrows). Clutch size was seven and ravens took all eggs. The grouse appeared to attack on several occasions but another raven, opposite of attack, removed eggs from nest46

| | |
|--|----|
| 1.5. Video images of Wyoming ground squirrels attempting to perforate intact sage-grouse eggs at two natural nests in northeastern Nevada. (a-b) Ground squirrel inspected each egg and appeared to use incisors to attempt to perforate eggshell of three eggs. (c-d) Ground squirrel repeatedly biting at an intact egg (arrows) for 98 seconds. This nest was previously partially depredated by a raven. Ground squirrel was not successful at perforating sage-grouse egg and the grouse abandoned single remaining egg following raven depredation. No ground squirrels ($n = 23$) successfully opened eggs | 47 |
| 2.1. Bimodal distribution of incubation recesses ($n = 1,037$) in relation to sunset, noon, and sunrise by greater sage-grouse in northeastern Nevada during 2002-2005. Zero represents sunrise, noon, and sunset. Peak frequency of recesses of age classes pooled occurred 30 min before sunrise and at sunset. Vertical striped pattern (▨) represents civil and nautical twilight periods. Dotted pattern (▩) represents crepuscular period. Horizontal striped pattern (≡) represent approximate timing of raven depredations, (a) 0622-0842 ($n = 6$), (b) 1359-1404 ($n = 1$), (c) 1754-1831, ($n = 2$). Raven depredations averaged 70.8 ± 24.8 min..... | 92 |
| 2.2. Differences in the number of recesses among yearlings ($n = 11$) and adults ($n = 32$) in relation to the day of incubation of greater sage-grouse in northeastern Nevada during 2002-2005. Trend lines were calculated from repeated-measures each day of incubation..... | 93 |
| 2.3. Ordinal date (days elapsed between 01 Jan and day of incubation) in relation to incubation constancy (%) and recess duration (min) of greater sage-grouse ($n = 43$) in northeastern Nevada during 2002-2005. Points along x-axis are repeated-measures and represent mean values at each date. Bars indicate standard errors..... | 94 |
| 2.4. Interaction between age (yearling, $n = 11$; adult, $n = 32$) and day of incubation (quadratic) in relation to incubation constancy (%) and recess duration (min) of greater sage-grouse in northeastern Nevada during 2002-2005. Points along x-axis are repeated-measures and represent mean values at each day of incubation. Bars indicate standard errors | 95 |

| | |
|---|-----|
| 2.5. Visual obstruction at nest in relation to incubation constancy (%) of greater sage-grouse ($n = 37$) in northeastern Nevada during 2002-2005. Points and bars represent mean and standard error values, respectively..... | 96 |
| 2.6. Recess duration (min) of greater sage-grouse ($n = 43$) in relation to maximum ambient temperature in northeastern Nevada during 2002-2005. Points and bars represent mean and standard error values, respectively..... | 97 |
| 2.7. Indices of raven abundance (number counted per 10 km) in relation to recess duration (min) of greater sage-grouse ($n = 36$) in northeastern Nevada during 2002-2005. Points and bars represent mean and standard error values, respectively..... | 98 |
| 3.1. Indices of common raven (<i>Corvus corax</i>) abundance in relation to days of treatment using CPTH (3-chloro-p-toluidine hydrochloride), which was injected into chicken egg baits and placed in the environment for consumption by ravens every 7 days in northeastern Nevada during 2002-2005. Surveys were conducted between late-March and mid-June, which encompassed the treatment period. Notice change in scale of raven abundances in 2005..... | 123 |
| 3.2. Indices of common raven (<i>Corvus corax</i>) abundance at 3 control sites (no CPTH, 3-chloro-p-toluidine hydrochloride, treatment) in northeastern Nevada during 2004 (▲) and 2005 (●). Days of surveys were conducted from late-March to mid-June encompassing CPTH treatment that was carried out at the treatment site located 22, 37, and 53 km distance away from control sites 1, 2, and 3, respectively. Notice change in scale of ravens densities among sites..... | 124 |
| 4.1. Logistic response curves predicting the probability of greater sage-grouse nest success in relation to (a) distance from common raven removal area and (b) indices of raven abundance in northeast Nevada, 2002-2005. Dots represent observations of individual nests, 0 = failed nests and 1 = successful nests. Arrows represent points of inflection on response curve, which is associated to a 50% probability of nesting successfully. The point of inflection was approximately (a) 29.5 km from the raven removal route and (b) 7.3 counted per 10 km..... | 168 |

| | |
|--|-----|
| 4.2. Logistic response curves predicting the probability of raven and badger depredation in relation to indices of abundance and activity, respectively, and microhabitat characteristics in northeast Nevada, 2002-2005. Dots represent observations of individual nests, 0 = successful nests and 1 = depredated nests by species of interest. Arrows represent points of inflection on response curves, which are associated to a 50% probability of species of predator depredating nests..... | 169 |
| 4.3. Percent of greater sage-grouse nests ($n = 79$) that were successful or failed in relation to age class in northeastern Nevada, 2002-2005..... | 170 |

LIST OF TABLES

| | |
|--|----|
| 1.1. Number of sage-grouse nests by fate and camera exposure across years in northeastern Nevada during 2002-2005. Percentages of nest fates of camera and no-camera nests by year are in parentheses..... | 40 |
| 1.2. Nest and egg remains at depredated greater sage-grouse nests that were video-recorded using infrared, miniaturized cameras and video recorders to identify nest predators and depredation sign in northeastern Nevada, 2002-2005..... | 41 |
| 1.3. Number of encounters and behavior of rodents at sage-grouse nests monitored using infrared miniaturized cameras to identify nest predators and behavior in northeastern Nevada, 2002-2005..... | 42 |
| 2.1. Explanatory variables used in mixed model analyses of incubation constancy and recess duration of greater sage-grouse in northeastern Nevada during 2002-2005 | 87 |
| 2.2. Mixed models explaining incubation constancy of greater sage-grouse in relation to predators, age of grouse, timing of incubation, climate, and microhabitat variables in northeastern Nevada, during 2002-2005 | 88 |
| 2.3. Mixed models explaining duration of recess of greater sage-grouse in relation to predators, age of grouse, timing of incubation, climate, and microhabitat variables in northeastern Nevada, during 2002-2005 | 89 |
| 2.4. Relative importance of explanatory variables used to model incubation constancy and recess duration of greater sage-grouse in northeastern Nevada during 2002-2005..... | 90 |
| 2.5. Explanatory microhabitat variables used to model incubation constancy and recess duration in northeastern Nevada during 2004-2005..... | 91 |
| 3.1. Linear regression analyses of common raven (<i>Corvus corax</i>) densities throughout the nesting season of sharp-tailed grouse and sage-grouse at the treatment site, consisting of egg baits treated with CPTH (3-chloro-p- | |

toluidine hydrochloride), and three control sites located 22, 37 and 53 km from the treatment site in northeastern Nevada during 2002-2005. *P* represents probability values from regression analyses. Asterisks (*) represent significant change in raven densities through time ($\alpha = 0.05$).....122

| | |
|--|-----|
| 4.1. Explanatory variables characterizing predators, age of grouse, and microhabitat used in an information theoretic approach to model nest success and used in exact regression models to predict probability of depredation by each predator species of greater sage-grouse to in northeastern Nevada during 2002-2005..... | 161 |
| 4.2. Logistic models explaining nest success of greater sage-grouse in relation to predators, age of grouse, and microhabitat variables in northeastern Nevada, during 2002-2005..... | 162 |
| 4.3. Relative importance of estimated parameters from logistic regression models of nest success of greater sage-grouse in northeastern Nevada during 2002-2005..... | 163 |
| 4.4. Parameter estimates and 95% CI describing relationships between probability of greater sage-grouse nest depredation by common raven and explanatory variables measured in northeastern Nevada in 2002-2005. Videography was used to identify predator..... | 164 |
| 4.5. Parameter estimates and 95% CI describing relationships between probability of greater sage-grouse nest depredation by American badger and explanatory variables measured in northeastern Nevada using videography to identify predator during 2002-2005..... | 165 |
| 4.6. Comparison of means (independent t-tests) of microhabitat variables of sage-grouse nests that were unambiguously confirmed to have been depredated by ravens or badgers in northeastern Nevada during 2002-2005..... | 166 |
| 4.7. Pearson's correlation describing relationships between predator indices in relation to nest sites and nest microhabitat characteristic in northeastern Nevada during 2002-2005..... | 167 |

ABSTRACT

The greater sage-grouse (*Centrocercus urophasianus*) is a sagebrush obligate species. It has declined in distribution and abundance substantially since Euro-American settlement of western North America. Although nest predation is a natural component of sage-grouse reproduction, habitat changes may interact with predator communities and incubation behavior leading to sage-grouse population declines. I used continuous videography at natural sage-grouse nests to document fine-scale incubation rhythms, identify predators, and record predation behavior in northeastern Nevada. An information-theoretic modeling approach was used to relate factors that characterized habitat, timing of incubation, and predators to nest success and incubation rhythms. I also experimentally reduced local raven numbers to measure the effects of raven reduction on sage-grouse nest success. Females exhibited relatively high incubation constancy (96%) and employed a bimodal distribution of incubation recess that peaked during morning and evening twilight. Common ravens (*Corvus corax*) and American badgers (*Taxidea taxus*) were confirmed destroying nests. Raven depredations were mostly crepuscular. Yearling sage-grouse nests failed more than those of adults, and yearling recesses were longer, more frequent, and occurred during times of greater daylight than those of adults. Recess duration, nest failure, and probability of raven-caused depredation were positively related to raven abundance. Compared to adults, yearlings appeared to face greater trade-offs between foraging and concealing eggs. Raven reduction increased sage-grouse nest success, but badgers appeared to partially compensate for removal. Nest herbaceous understory was positively related to incubation constancy. This likely was due to the effects of understory at nests on parental energy savings by reducing parent

heat loss. I detected differences in nest habitat characteristics between nests depredated by ravens and badgers, such as shrub canopy cover, herbaceous understory, and forb biomass. Canopy cover was inversely related to raven depredation. Thus, habitat characteristics appeared to interact with predator composition and abundance increasing the probability of sage-grouse nest failure. Ravens are generalist predators now occurring in high abundance in North America and forage within degraded sage-grouse nest habitat. Ravens appear to influence incubation behavior and depredation rates and in some areas may negatively influence sage-grouse productivity. In human-altered landscapes, these negative effects may be substantial.

PREFACE

The greater sage-grouse (*Centrocercus urophasianus*) is a sagebrush (*Artemisia* spp.) obligate species. Sage-grouse distribution is closely associated with sagebrush distribution, particularly big sagebrush (*A. tridentata*) (Patterson 1952, Connelly and Braun 1997, Benedict et al. 2003, Schroeder et al. 2004) across western North America, primarily in the Great Basin and Interior Columbia Basin. Prior to Euro-American settlement of western North America, the potential area of sagebrush habitat for sage-grouse distribution was approximately 1,200,483 km² (Schroeder et al. 2004). Currently, sage-grouse occupy 55.7% of this area (Schroeder et al. 2004). Numbers of grouse within the current distribution are also declining (Connelly and Braun 1997, Braun 1998). Breeding numbers have been reduced by 17-47% over a period >40 years (Connelly and Braun 1997).

Habitat loss, fragmentation, and degradation are critical factors responsible for distribution and abundance declines in sage-grouse (Connelly and Braun 1997, Braun et al. 1977). Important habitat alteration factors include agricultural practices (Dalke et al. 1963, Wallestad and Pyrah 1974, Swenson et al. 1987), energy development (Aldridge 1998, Holloran 2005), roadway creation and associated development (Patterson 1952), fences (Braun 1998), livestock overgrazing (Beck and Mitchell 2000), wildfire (Nelle et al. 2000), and establishment of non-native vegetation (Knick et al. 2003). Other factors affecting grouse include infectious disease (Naugle et al. 2004) and climate (Back et al. 1987). Both recent (Connelly and Braun 1997, Schroeder et al. 2004) and historic (Patterson 1952) reports expressed concern over sage-grouse declines in distribution and numbers. This has led to multiple petitions to list the greater sage-grouse as threatened or

endangered under the U. S. Endangered Species Act and listing as endangered within other jurisdictions (Schroeder et al. 2000, Aldridge and Brigham 2003).

Maintenance of existing sage-grouse populations depends on a suite of environmental and ecological factors upon which multiple life-stages depend including factors associated with nest success (Connelly et al. 1991, Popham and Gutierrez 2003, Holloran et al. 2005), chick survival (Aldridge and Brigham 2001), annual migration (Berry and Eng 1985, Leonard et al. 2000), and adult survival (Naugle et al. 2004, Zablan et al. 2003). Nest success of birds is a natural antecedent to other important life-stages and plays a critical role in population maintenance (Martin 1993, 1995).

Nest predation is a natural component of bird reproduction and is the primary cause of reproductive failure across a wide variety of birds, and across diverse habitats and geographic locations (Ricklefs 1969, Martin 1995). Predation accounts for an estimated 79% of loss of prairie grouse nests (Bergerud 1988). Unnatural levels of nest predation may limit population growth of birds by reducing annual reproductive rates (Martin 1995, Evans 2004), particularly so for game species (Bro et al. 2006).

Nesting is reported to be the most critical life-stage in grouse productivity (Bergerud 1988) because breeding densities in subsequent years are adversely affected by high rates of nest depredation causing lower long-term productivity. Sage-grouse have been reported to have the highest nest predation rates of 9 species of North American grouse based on 82 field studies (Bergerud 1988). Thus, nest predation may be an especially important factor influencing sage-grouse population dynamics (Schroeder and Baydack 2001, Autenrieth 1981).

Many authors have measured and thoroughly described important relationships between sage-grouse nest success and habitat characteristics (Connelly et al. 1991, Gregg et al. 1994, Holloran et al. 2005), but knowledge of interactions between the predator community and specific nest habitat components is poorly developed. Predators have direct, proximate effects on nest success through their consumption of eggs. Changes in habitat, on the other hand, have indirect but long-term and important effects in that habitat alterations affect predation rates (Martin 1993, 1995, Evans 2004).

Changes in habitat can influence predation rates by influencing predator composition and abundance, as well as the ability of predators to locate nests. Interactions between changes in habitat and predation were shown to have substantial effects at the landscape level (Stephens et al. 2003) and include fragmentation of nesting areas that resulted in birds nesting in areas of reduced concealment and, seemingly, increased probability of detection by visually-cued predators. Habitat fragmentation can cause changes in diversity and density of predators (Andrén et al. 1985, Andrén and Angelstam 1988).

Reported microhabitat effects in relation to nest success of sage-grouse appear to be contradictory without first considering predator communities. For example, in some studies, nest success did not appear to vary among shrub species (Sveum et al. 1998), shrub height (Wallestad and Pyrah 1974), or other vegetation characteristics (Wakkinen 1990). However, others found sage-grouse nest success rates to be greater under sagebrush (Connelly et al. 1991) and shrubs of medium heights (40-80 cm) (Gregg et al. 1994). Increased grass height (Gregg et al. 1994, Holloran et al. 2005) and shrub density (Wallestad and Pyrah 1974) were positively correlated to nest success, while others,

using artificial nests, reported higher predation rates in areas of increased herbaceous cover and shrub height (Ritchie et al. 1994).

Knowledge about the predator community in relation to nest habitat and sage-grouse behavior may help clarify these inconsistencies. For example, some habitat characteristics that are needed for nest concealment may increase nest success by reducing predation by visually-cued predators (Martin 1993), such as predatory birds, but may not be as important as scent barriers in reducing predation of predators that rely on olfaction, such as mammalian mesopredators (Crabtree and Wolfe 1988, Sargeant et al. 1993, Fleskes and Klaas 1991).

Changes in predator communities, i.e., species composition and abundance, have been known to affect nest success of ground nesting birds in other ecosystems (Sovada et al. 1995, Greenwood and Sovada 1996, Evans 2004). Generalist predators have the greatest effect on ground nesting birds (Harris and Saunders 1993) because predator numbers are independent of prey density and can cause prey population suppression, decline, or extinction (Evans 2004). Identifying and measuring abundances of generalist predators in landscapes would be important and helpful for formulating management actions meant to enhance sage-grouse populations.

Human-altered environments typically affect predator communities by promoting survival and reproduction of generalist predators (Boarman 1993, Boarman 2003). In particular, predators often are subsidized by non-natural food, shelter, and nest substrate which results in increased predator abundance (Knight and Kawashima 1993, Boarman 2003, Kristan and Boarman 2003). Elevated predator abundance as a consequence of human resource subsidies appears to cause hyperpredation on prey (Crooks and Soule

1999, Courchamp et al. 2000). Hyperpredation occurs when predator populations are unnaturally high causing increased predation rates (Kristan and Boarman 2003). Even when prey populations are low, abundant generalists may suppress prey population growth (Newsome et al. 1989). Increased corvid abundances have been reported to cause higher nest predation rates of many bird species (Angelstam 1986, Andrén 1992, Luginbuhl et al. 2001), including prairie grouse (Manzer and Hannon 2005) and were shown to reduce annual productivity of Old World birds (Andrén 1992).

Ravens are subsidized, generalist predators that consume eggs and young of many ground nesting birds (Boarman 1993, 2003, Boarman and Heinrich 1999) including sage-grouse (Schroeder et al. 1999, Schroeder and Baydack 2001). Raven abundance has increased as much as 1500% in some areas of western North America since the 1960s (Boarman 1993) and there has been an average of >200% increase throughout the United States (Sauer et al. 2004). Where ravens and sage-grouse distributions overlap, abundant ravens have been hypothesized to suppress or reduce sage-grouse populations due to increased nest predation (Batterson and Morse 1948, Autenrieth 1981). However, the relative importance of raven as sage-grouse nest predators and the effects of raven predation in relation to their abundance have not been adequately studied. Nevertheless, wildlife managers use egg baits treated with 3-chloro-p-toluidine hydrochloride (CPTH) to reduce raven numbers in sage-grouse habitat (Spencer 2002) with the intention of increasing sage-grouse productivity. Although some authors have indicated that nest success increases when ravens are removed (Batterson and Morse 1948), estimation of parameters and precision in quantifying effect size is needed to evaluate management strategies for protecting sage-grouse populations.

Fine-scale information of sage-grouse incubation rhythms and behavior in relation to predator community, nest microhabitat, age class, and timing of incubation would also substantially improve our understanding of factors underlying sage-grouse nest success. Few studies have addressed incubation rhythms of galliform birds in the wild and reports of incubation behavior of sage-grouse are largely anecdotal (Schroeder et al. 1999). Sage-grouse are large-bodied, uniparental incubators that are energetically constrained during incubation and must trade-off self-maintenance activities (e.g., foraging) for meeting metabolic demands in order to incubate eggs and conceal eggs from predation (Conway and Martin 2000, Deeming 2002).

Nest predation represents an important source of natural selection in birds (Ricklefs 1969, Martin 1995) and may influence the expression of successful parental incubation behavior (Ghalambor and Martin 2001, 2002). For example, in large-bodied, uniparental incubators like sage-grouse, greater risk of predation may favor increased incubation constancy (% of time on nests in a 24-h period) because of multiple potential benefits of constancy, including egg concealment (Martin 1993), parental nest defense (Montgomerie and Weatherhead 1988), and decreased incubation periods reducing opportunities for predators to locate nests (Deeming and Ferguson 1991) despite costs of constancy in the form of negative energy balance. Nest predation increases with parental movements to and from nests in several bird species (Martin et al. 2000) and species with higher predation risks exhibit behavioral plasticity in parental activity near nest (Conway and Martin 2000). If this is true for sage-grouse, predator composition and abundance may influence sage-grouse incubation rhythms.

Variation in nest habitat quality may also influence rhythms. For example, variation in recess duration may be explained by availability of food and water for meeting energetic demands during incubation (Afton and Paulus 1992, Deeming 2002), especially for yearling grouse that have relatively low lipid reserves (Erikstad 1986). Nest microhabitat may also influence incubation behavior by influencing microclimate at nests, which influences parental energy loss (Ar and Sidis 2002). Information regarding sage-grouse incubation rhythms in relation to microhabitat and predators is unknown and would be worth consideration when trying to understand the roles of habitat characteristics and predation in sage-grouse population dynamics.

The primary objectives of my dissertation were to measure greater sage-grouse incubation rhythms and nest success in relation to predators, microhabitat, age of grouse, and timing of incubation in northeastern Nevada within the Great Basin sagebrush ecosystem. Also, I measured the efficacy of reducing local raven numbers on local sage-grouse nest success. To achieve these objectives I developed 4 studies. Each study is presented as a separate chapter and will be or has been submitted for publication in peer-reviewed journals. All chapters were written in style and usage to meet journal publication guidelines, but formatting was changed only when necessary for this dissertation. In chapter 1, I describe unambiguous identification of sage-grouse nest predators using continuously-recording videography. Additionally, I compared post-depredation sign among nests based on confirmed nest predator and compared nest-predation sign and behavior among known predators. I also used video-monitoring to make precise measurements of sage-grouse incubation constancy and recess duration and present these data in chapter 2. I describe fine-scale incubation patterns of female sage-

grouse and model incubation constancy and recess duration in relation to timing, grouse age, nest predator abundance, and microhabitat features using an information theoretic approach. In chapter 3, I describe a technique to remove common ravens using chicken egg baits treated with CPTH (3-chloro-p-toluidine hydrochloride) and measure the efficacy of this technique at reducing a local population of ravens. Furthermore, I used videography of experimentally-placed egg baits to estimate a ratio of egg bait loss to raven consumption of egg baits. Also, I estimate actual raven take and describe egg bait consumption by non-target species. In chapter 4, I measured the effects of reducing raven numbers at a local scale (the management action was described in Chapter 3) on sage-grouse nest success. Using measurements over a 4-year period, I modeled sage-grouse nest success in relation to factors that characterize predators, grouse age, nest microhabitat, and timing of incubation using an information theoretic approach. I challenged the best model developed through modeling procedures with additional measurements of nest microhabitat variables collected during the last 2 years of my study. Also, I described the probability of nest depredation by each predator species that was described in chapter 1 using videography in relation to predator indices and microhabitat characteristics at nest sites.

In summary, this 4-part study was designed to address four fundamental questions (1) What predator species depredate sage-grouse nests in my study area? (2) Does local removal of a confirmed predator influence nest success? (3) What incubation rhythms do sage-grouse employ and what factors explain variation in incubation behavior? (4) Does predator community and nest microhabitat influence grouse incubation behavior and probability of depredation? These studies were designed to advance our knowledge of

interactions between sage-grouse incubation behavior, microhabitat characteristics, and the predator community and ultimately guide management and restoration actions that promote productivity, especially in areas where predation rates are found to be unnaturally high. Specific recommendations for managers are provided within each chapter. Information on these interactions is informative for studies that measure the effect of human developments (e.g., powerlines and roads) and human-altered landscapes (e.g., sagebrush removal) on sage-grouse productivity and predator communities.

PREFACE LITERATURE CITED

- Afton, A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 *in* D. J. Batt, A. D. Afton, M. D. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis.
- Aldridge, C. L. 1998. Status of the sage-grouse (*Centrocercus urophasianus* *urophasianus*) in Alberta. Alberta Environmental Protection, Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 13, Edmonton. 23 pp.
- Aldridge, C. L., and R. M. Brigham. 2003. Distribution, status, and abundance of Greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field Naturalist 117:25-34.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794-804.
- Andrén, H., and P. Angelstam. 1988. Elevated predation rates on as an edge effect in habitat islands: experimental evidence. Ecology 69:544-547.
- Andrén, H., P. Angelstam, E. Lindstrom, and P. Widen. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos 45:273-277.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47:365-373.
- Ar, A., and Y. Sidis. 2002. Nest microclimate during incubation. Pages 143-160 *in* D. C. Deeming, editor. Avian incubation: behavior, environment, and evolution. Oxford University Press Inc. New York.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game, Federal Aid in Wildlife Restoration Project W-125-R and W-160-R, Wildlife Bulletin No. 9. Boise, Idaho.

- Back, G. N., M. R. Barrington, and J. K. McAdoo. 1987. Sage grouse use of snow burrows in northeastern Nevada. *Wilson Bulletin* 99:488-490.
- Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission, Oregon Fauna Service 1. Portland, Oregon. 29 pp.
- Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage-grouse habitat. *Wildlife Society Bulletin* 28:993-1002.
- Bergerud, A. T. 1988. Population ecology of North American grouse. Pages 578-648 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis.
- Berry, J. D., and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. *Journal of Wildlife Management* 49:237-240.
- Benedict N., S. J. Oyler-McCance, S. E. Tayler, C. E. Braun, and T. W. Quinn. 2003. Evaluation of the eastern (*Centrocercus urophasianus urophasianus*) and western (*Centrocercus urophasianus phaios*) subspecies of sage-grouse using mitochondrial control-region sequence data. *Conservation Genetics* 4:301-310.
- 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. Miller, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. Conservation and resource management. Pennsylvania Academy of Science, Philadelphia.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing Common Raven predation on desert tortoises. *Environmental Management* 32:205-217.
- Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). *In* A. Poole and F. Gill, editors. The Birds of North America, No. 476. The Academy of Natural Sciences, Philadelphia and The 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.

- Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. *Wildlife Society Bulletin* 5:99-106.
- Bro, E., B. Arroyo, and P. Miggot. 2006. Conflict between grey partridge *Perdix perdix* hunting and hen harrier *Circus cyaneus* protection in France: a review. *Wildlife Biology* 12:233-247.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. *Journal of Wildlife Management* 55:521-524.
- Conway, C. J., and T. E. Martin. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* 54:670-685.
- Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modeling the hyperpredation process. *Journal of Animal Ecology* 69:154-164.
- Crabtree, R. L., and M. L. Wolfe. 1988. Effects of alternate prey on skunk predation of waterfowl nests. *Wildlife Society Bulletin* 16:163-169.
- Crooks, K. R., and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563-566.
- Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* 27:811-841.
- Deeming, D. C. 2002. Behavior patterns during incubation. Pages 63-87 in D. C. Deeming, editor. *Avian incubation: behavior, environment, and evolution*. Oxford University Press Inc. New York. USA.
- Deeming, D. C., and M. W. J. Ferguson. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. Pages 147-171 in D. C. Deeming and M. W. J. Ferguson, editors. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge University Press, New York.

- Erikstad, K. E. 1986. Relationship between weather, body condition, and incubation rhythm in willow grouse. *Cinclus* 9:7-12.
- 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.
- Fleskes, J. P., and E. E. Klaas. 1991. Dabbling duck recruitment in relation to habitat and predators at Union Slough National Wildlife Refuge, Iowa. U. S. Fish and Wildlife Service Technical Report 32, Washington, D.C. 19 pp.
- Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* 292:494-497.
- Ghalambor, C. K., and T. E. Martin. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology* 13:101-108.
- Greenwood, R. J., and M. A. Sovada. 1996. Prairie duck population management. *Transactions of the North American Wildlife and Natural Resources Conference* 61:31-42.
- 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.
- Harris, S., and G. Saunders. 1993. The control of canid populations. *Symposium of the Zoological Society of London* 65:441-464.
- 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.
- Holloran, M. J., B. J. Heath, A. J. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal Wildlife Management* 69:638-649.

- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.
- Knight, L. R., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management* 57:266-271.
- Kristan, W. B., and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84:2432-2443.
- Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements, and habitats of sage grouse *Centrocercus urophasianus* on the Upper Snake River Plain of Idaho: changes from the 1950s to the 1990s. *Wildlife Biology* 6:265-270.
- Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael, and D. E. Varland. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. *Journal of Field Ornithology* 72:556-572.
- 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. 1993. Nest predation and nest sites: New perspectives on old patterns. *BioScience* 43:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65:101-127.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society. Series B, Biological Sciences* 267:2287-2293.
- Montgomerie, R. D., and P. J. Weatherhead. 1988. Risks and rewards of nest defense by parent birds. *The Quarterly Review of Biology* 63:167-187.
- 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. Schmidtman, 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 sage grouse. *Ecological Letters* 7:704-713.
- Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effects of fire on sage grouse habitat. *Journal of Range Management* 53:586-591.
- Newsome, A. E., I. Parer, and P. C. Catling. 1989. Prolonged prey suppression by carnivores — predator-removal experiments. *Oecologia* 78:458-467.
- Patterson, R. L. 1952. *The sage grouse of Wyoming*. Sage Books, Denver, Colorado.
- Popham, G. P., and R. J. Gutierrez. 2003. Greater sage-grouse *Centrocercus urophasianus* nesting success and habitat use in northeastern California. *Wildlife Biology* 9: 327-334.
- Ricklefs, R. E. 1969. An analysis of nesting morality in birds. *Smithsonian Contributions in Zoology* 9:1-48.
- Ritchie, M. E., M. L. Wolfe, and R. Danvir. 1994. Predation of artificial sage grouse nests in treated and untreated sagebrush. *Great Basin Naturalist* 54:122-129.
- Sargeant, A. B., R. J. Greenwood, M. A. Sovada, and T. L. Shaffer. 1993. Distribution and abundance of predators in the Prairie Pothole Region that affect duck production. U.S. Fish and Wildlife Service Resource Publication 194. 96pp.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2004. *The North American Breeding Bird Survey, Results and Analysis 1966-2003. Version 2004.1*. United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
- Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. *Wildlife Society Bulletin* 29:24-32.
- Schroeder, M. A., D. W. Hayes, M. L. Livingston, L. E. Stream, J. E. Jacobson, D. J. Pierce, and T. McCall. 2000. Changes in the distribution and interior Columbia Basin, U. S. A. *Conservation Biology* 16:1232-1242.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. B. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deirbert, S. C. Gardner, M. A. Hilliard, G. D. Kobridger, 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., J. A. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In A. Poole and F. Gill, editors. *The Birds of North America*. No. 425. Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C.
- Sovada, M. A., A. B. Sargeant, and J. W. Grier. 1995. Differential effects of coyotes and red foxes on duck nest success. *Journal of Wildlife Management* 59:1-9.
- Spencer, J. O., Jr. 2002. DRC-1339 use and control of common ravens. *Proceedings of the Vertebrate Pest Conference* 20:110-113.
- Stephens, S. E., D. N. Koons, J. L. Rotella, and D. W. Willey. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biological Conservation* 115:101-110.
- Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage grouse in south-central Washington. *Journal of Range Management* 51:265-269.
- Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse after ploughing of sagebrush steppe. *Biological Conservation* 41:125-132.
- Wakkinen, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. Thesis, University of Idaho, Moscow. 57 pp.
- Wallestad, R., and D.P. Pyrah. 1974. Movement and nesting of sage grouse hens in Central Montana. *Journal of Wildlife Management* 38:630-633.
- 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 1:

IDENTIFICATION OF GREATER SAGE-GROUSE NEST PREDATORS AND DEPREDATION SIGN USING CONTINUOUS VIDEO-MONITORING

ABSTRACT

I used videographic monitoring of greater sage-grouse (*Centrocercus urophasianus*) nests to provide unambiguous identification of nest predators, document nest fate, and compare post-depredation sign among nests based on actual nest predators. Continuous, time-lapsed video recordings using infrared micro-cameras also allowed me to measure timing of predation events and behaviors of nest predators and incubating sage-grouse. Common ravens (*Corvus corax*) and American badgers (*Taxidea taxus*) commonly depredated nests and left similar sign and remains at nest sites. Both species also exhibited individual variation in predatory behavior and resulting nest remains. Wyoming ground squirrels (*Spermophilus elegans nevadensis*) and Piute ground squirrels (*Spermophilus mollis*) encountered intact sage-grouse eggs in active nests during female incubation recesses and sometimes attempted to open eggs but were always unsuccessful as were all rodent encounters with intact eggs. Most depredations were initiated during active incubation by females. Raven depredations were most frequent during morning and evening hours following grouse incubation recesses. Badger depredations occurred during day and night. Active nest defense by grouse was rare and always unsuccessful.

Key Words: American badger, *Centrocercus urophasianus*, common raven, greater sage-grouse, predator identification, nest depredation, nest defense, videography

INTRODUCTION

Nest predation is an important ecological factor that affects population viability (Martin 1993, 1995) and shapes life history traits and reproductive strategies (Martin 1993, 1995, Fontaine and Martin 2006). Increased predator abundance can result in increased nest depredation in many birds (Angelstam 1986, Andrén 1992). Additionally, predator composition (i. e., bird, mammal, etc.) plays an important role in nest success (Martin 1987, Miller and Knight 1993). Human-altered landscapes can influence predator communities by providing generalists predators with food, shelter, and nest site subsidies (Boarman 1993, 2003).

Greater sage-grouse range is substantially smaller than it was prior to European settlement (Schroeder et al. 2004) and populations are declining in most portions of the remaining species range (Connelly and Braun 1997). Nest failure may limit game bird populations (Bro et al. 2006) and has been suggested as the most important aspect of prairie grouse population dynamics (Bergerud 1988). The primary source of prairie grouse nest failure is loss of eggs to predators, accounting for an average of 79% of nest failures (Bergerud 1988). Nest predation is thought to be an important constraint on sage-grouse population increase (Schroeder and Baydack 2001).

Reported descriptions of sage-grouse nest predators are limited (Holloran and Anderson 2003) and their associated behaviors at nests are unknown. This information is needed and would benefit grouse management. For example, unambiguous identification of predators would lead to recognizing the biologically relevant community, which would aid decisions to mitigate predation by managing predators (Schroeder and Baydack 2001) and nesting habitat (Connelly et al. 1991, Riley et al. 1992, Holloran et al. 2005).

Additionally, unambiguous predator identification is critical to understanding habitat selection behavior by incubating female grouse and its effects on sage-grouse life history.

Conventional methods used to identify predators (Rearden 1951), such as examining nest and egg remains following depredations, can be very misleading (Marini and Melo 1998, Lariviere 1999). Biases include ambiguous remains at nests due to visits by multiple predators, different species of predators leaving similar sign, and individuals of the same species of predators leaving different sign (Lariviere 1999). Management decisions based on erroneous identification of nest predators may have negative repercussions. For example, Use of conventional methods to identify predators may explain reported inconsistencies in the role of ground squirrels (*Spermophilus* spp.) as sage-grouse egg predators (Patterson 1952, Watters et al. 2002).

Video-monitoring through day and night is a reliable and accurate method to determine predator identity and does not bias depredation rates (King et al. 2001). Continuous videography of nests can unambiguously identify nest predators and simultaneously document predator prey interactions at the nest (Pietz and Granfors 2000). Recent developments in miniature cameras for the field and time-lapsed VCRs present an excellent opportunity to identify sage-grouse nest predators and document behaviors of predators and incubating grouse (Cutler and Swann 1999). Monitoring natural instead of artificial nests is critical to the identification of predators and to understanding dynamics of nest predation (Pietz and Granfors 2000) because variation in nests and eggs between species influences predation rate and predation behavior (Willebrand and Marcstrom 1988, Major and Kendal 1996, Wilson et al. 1998).

The principle objectives of my study were to document unambiguously (1) identity of sage-grouse nest predators, (2) timing of predation events, (3) behaviors of predators at nests, and (4) any defensive behaviors of incubating sage-grouse. To validate my methods I also tested the hypothesis that camouflaged video cameras at natural nests do not influence depredation rates by comparing nests with and without cameras and report the results here. I also compared post-depredation remains among nests relative to predator identity to evaluate the hypothesis that the use of nest remains is not reliable in identifying predators.

STUDY AREA

I video-monitored sage-grouse nests in northeastern Elko County, Nevada (N0670859, E 4599749, zone 11, NAD 83) during March-July of 2002-2005. I chose four areas to monitor sage-grouse nests based on information provided by Nevada Department of Wildlife (Figure 1.1). Study areas were separated by ≥ 20 km. A public landfill and private disposal site were located approximately 7 and 3 km northeast of the northernmost study area and > 20 km from other study sites (Figure 1.1).

Lower elevations were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and basin big sagebrush (*A. t. tridentata*) with an understory of grasses, primarily crested wheatgrass (*Agropyron cristatum*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). Higher elevations were characterized by mountain big sagebrush (*A. t. vaseyana*), serviceberry (*Amelanchier alnifolia*) and native bunchgrasses. Utah Juniper (*Juniperus osteosperma*) occurred in the peripheral regions of 2 sites but was absent from the others. Topography of the study sites consisted primarily of rolling hills and creek drainages that held surface water throughout the year.

Some of the variation in common raven (*Corvus corax*) numbers among study areas was a result of wildlife damage management by United States Department of Agriculture/Animal Health Inspection Service/Wildlife Services (WS) in cooperation Nevada Department of Wildlife (NDOW) for the purpose of protecting a recently reestablished population of Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) (Coates and Delehanty 2006). Approximately 10,500 chicken egg baits were treated with an avicide (3-chloro-p-toluidine hydrochloride) and placed systematically at the southernmost area by WS personnel to remove ravens during 2002-2005 (Coates et al., In press). Consumption of egg baits by ravens caused an estimated removal of 69, 130, 66, and 157 ravens from the site during 2002, 2003, 2004, and 2005.

Most of the study area was on land administered by the U.S. Bureau of Land Management (BLM) while much of the surrounding land was privately owned. Within the study area, I observed many species of potential egg predators (reported in Schroeder et al. 1999), including coyotes (*Canus latrans*), weasels (*Mustela* spp.), elk (*Cervus elaphus*), American badgers (*Taxidea taxus*), ground squirrels, American magpies (*Pica hudsonia*), common crows (*Corvus brachyrhynchos*), and common ravens. Cattle grazed most of the study site annually.

METHODS

I captured female sage-grouse by spotlighting (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003) near lek sites between 15 March and 1 May of 2002-2005. I equipped grouse with necklace style, battery-powered radio transmitters equipped with 22 cm antennae. To minimize transmitter-caused mortality (Carroll 1990), radio collars were <3% of grouse body mass, based on average mass of female sage-grouse (1.0-1.8

kg, Schroeder et al. 1999). Antennae were bent near their bases and rested along the backs of grouse to minimize interference with flight (Marks and Marks 1987). I classified all grouse by age based on plumage (Ammann 1944).

I located radio-marked grouse every 2-3 days using 3-element hand-held Yagi antennae and receivers (Advanced Telemetry Systems, Isanti, Minnesota). I reduced location error (Hupp and Ratti 1983, Garrott et al. 1986) and avoided flushing grouse by circling each grouse at a distance of approximately 30-50 m using the “loudest signal method” (Springer 1979). Aircraft were also used to locate missing grouse, followed by ground surveys to verify grouse location. I recorded Universal Transverse Mercator (UTM) coordinates for each grouse location using hand-held GPS units (Garmin International Inc., Olathe, Kansas).

When a grouse occupied the same site on 2 consecutive occasions, I then located the grouse every 1-2 days and after 3 consecutive locations of the bird in the same area I visually confirmed the presence of a nest. I normally located grouse nests during the laying period or the initial days of incubation. I recorded UTM coordinates 5 m north of nests and described characteristics associated with nest location allowing me to relocate nests when grouse were not present.

I monitored nesting females every 2-3 days to record female status (present or absent) and nest fate (successful or unsuccessful). I considered nests to be successful if ≥ 1 egg hatched (Rearden 1951) and unsuccessful if the nest was depredated or abandoned (female was >300 m from nest for 3 consecutive relocations). Depredations were classified as partial (≥ 1 intact egg remained in the nest bowl) or complete (all eggs destroyed or missing from nest bowl). Also, depredations were classified as multiple (>1

animal consumed eggs, eggshells, eggshell membranes, or embryonic membranes within 24 hours of the first egg depredation) or single (one animal depredated nest within 24 hours). I recorded predator sign at depredated nests including animal tracks, feces, hair and feathers. Descriptions of depredated nest remains were also recorded including nest bowl condition (i.e., disturbed or destroyed), disturbed surrounding vegetation, missing eggs, eggshell fragments, punctured eggs, and condition of eggshell membranes that inside of eggshells (e.g., missing, fragmented, intact).

Video-Monitoring

I identified nest predators and recorded predator and grouse behaviors using continuously recording video-monitoring systems. Nests were randomly chosen for video-surveillance ≥ 7 days (range 7-25) following the onset of incubation to avoid researcher-induced nest abandonment (Renfrew and Ribic 2003). Following the termination of a nesting effort, I moved cameras to other randomly chosen nests.

I used miniature, camouflaged cameras ($40 \times 40 \times 60$ mm) (Fuhrman Diversified Inc., Seabrook, Texas; Supercircuits, Austin, Texas) equipped with 12 infrared-emitting diodes (850-950 nm wavelength), which allowed night video-recording using light that was not detectable by vertebrates (Pietz and Granfors 2000). I deployed cameras 0.5-1.0 m from the nest bowl and 10-20 cm above ground. I mounted cameras directly to the nearest shrub trunk (usually sagebrush) and occasionally to a camouflaged stake using rebar tie wire. Stakes were also covered with grasses and shrub branches. I connected a cable that extended 15-20 m to a VCR system and power source. Connection cables were buried 3-5 cm into the ground to reduce chance of damage or of attracting or deterring predators. I scattered small rocks and litter over buried cord and used sagebrush leaves to

remove human tracks. I used time-lapsed VCR systems operating at 2-3 frames/sec, which allowed accurate identification of species and individual behavior. Video-cassette recorders were housed in camouflaged cases and placed under the canopy of a large shrub. I powered cameras and recorders with two deep-cycle, 12-volt marine batteries. Burlap and vegetation were used to cover the VCR cases and batteries. I replaced batteries and tapes every 2-3 days and used hand-held LCD monitors in the field to determine the status of nests and examine previously recorded images.

I camouflaged all cameras and other equipment to avoid predation biases (Herranz et al. 2002) by covering cameras completely with camouflaged vinyl photography tape and paint using colors that matched the shrubsteppe microhabitat. Grasses and small sagebrush branches and leaves were secured to camera casings with painted wire. I applied camouflaged, adhesive cloth tape across LEDs, which still allowed night video-recording. I used rubber boots and gloves during video system deployment and maintenance to minimize human scent at nests.

I attempted to install cameras and VCRs during morning hours while grouse were away from nests (Schroeder et al. 1999). However, most installations (82%) took place while grouse were incubating, typically resulting in flushing grouse from nests. On two occasions, grouse remained on their nests throughout the duration of video-system deployment. I did not install cameras during times of snow, rain, and relatively high wind speed and ambient temperatures to prevent researcher-induced egg mortality. I continued video-recording nests for 24 hours following termination of nesting attempts to identify any subsequent animal encounters and record post-nest-fate behaviors of predators at hatched and depredated nests. Cameras were removed when I determined the nest was

abandoned. Video systems were then removed and installed at other randomly selected nests. Video systems also were left recording for an additional 24 h if a nest was partially depredated.

I used natural nests without video systems as controls to measure camera effects during all years of study. During 2004 and 2005, I further measured camera effects by placing pheasant eggs in 18 (9 per year) sage-grouse nest bowls randomly chosen from 36 nest bowls following termination of use by sage-grouse. I placed 6 pheasant eggs in each nest and monitored nests with and without video-systems every 2 days for a 10-day exposure period. Monitoring of pheasant eggs was initiated and terminated on the same dates at all nest bowls each year.

Statistical Analyses

I used binary logistic regression analyses (SAS Institute Inc., Cary, North Carolina) to measure camera effects on predation rates of natural sage-grouse nests. Because video systems were not deployed on each nest throughout the entire incubation period, I calculated the percent of the total incubation period that each nest was exposed to a video camera and used three regression models to test for effects of video exposure time on nest fate. First, I tested the influence of video exposure time on nest fate using all nests. Second, to reduce biases associated with timing of camera deployment, I chose a 10-day period of incubation (days 13-23) to test the influence of video exposure on nest fate. Although I did not deploy cameras on nests until ≥ 7 days following initial day of incubation, nests often were depredated naturally during this time. The 10-day model avoided bias due to early depredation. Third, I tested the effects of video exposure time on nest fate of only those nests that were exposed to cameras throughout the incubation

period. In addition to this assessment of natural nests, I used Fisher's Exact Test to measure the difference in depredation frequencies of nests with and without cameras of 18 former sage-grouse nest bowls containing experimentally placed pheasant eggs.

RESULTS

I monitored 87 sage-grouse nests (camera exposure, $n = 55$; no camera, $n = 32$; Table 1.1). I confirmed 17 depredations (video-monitoring, $n = 16$; direct observation, $n = 1$). Of the nests with cameras, 4 depredations were not video-recorded due to camera failure. Of the nests with no-camera, 1 depredation was directly observed in the field. I recorded approximately 15,500 h of incubation averaging 12.0 ± 0.83 days of incubation per nest. Thirty-six (41%) nests were partially or completely depredated, six (7%) were abandoned, and 45 (52%) hatched. Sage-grouse abandoned all nests that were partially destroyed.

Video-monitoring exposure time did not influence nest fate of grouse considering all nests ($G > 0.001$, $P = 0.993$), nests during a 10-day period midway through incubation ($G = 0.614$, $P = 0.433$), and nests of camera deployment only ($G = 0.811$, $P = 0.368$). Also, of the 18 randomly selected sage-grouse nest bowls into which I placed pheasant eggs and monitored for 10-days during 2004 and 2005, four and two depredation events occurred at nests with cameras and without cameras, respectively. I did not detect a difference in depredation rates among nests with and without cameras (*Exact* $P = 0.658$).

Raven Encounters

I documented 10 nest depredations by ravens, 9 of which were recorded using continuous video-monitoring (Figure 1.2) and 1 was directly observed. All raven depredations were diurnal (Figure 1.3) and mean of a depredation was 70.8 ± 24.8 minutes. Mean duration

of time interval between eggs taken from nests was 11.1 ± 4.0 minutes. Three raven depredations were partial and seven were complete (Table 1.2). Grouse were incubating at the onset of the depredation event for 8 of the 10 events. When the female grouse was present, one or more ravens flushed the grouse from the nest before depredating eggs. No adult grouse was present when ravens located the eggs of one nest and the status of the female grouse was unknown prior to the direct observation. I observed variation in nest and egg sign at the nest sites among individual ravens (Table 1.2).

On 3 separate nest depredations, the grouse stood over the eggs between ravens taking individual eggs. I observed one grouse actively, but unsuccessfully, defend her nest from ≥ 2 ravens (Figure 1.4). In this case, the grouse lunged across the nest with wings extended on 3 occasions attacking a raven. The grouse defense momentarily prevented depredation from ravens, but as the grouse was attacking one raven, another raven would take an egg from the opposite side of the nest. In all 3 cases of nest defense, the grouse were unsuccessful and the nests were depredated.

Badger Encounters

I recorded 7 depredations by badgers of sage-grouse nests, all of which resulted in complete nest destruction (Table 1.2). Immediately prior to badgers appearing in video images, grouse flushed from nests. Badgers did not appear to attempt to capture fleeing grouse. I did not observe any nest-defense during badger depredations. Badger encounters occurred during various times of the day ($n = 4$) or night ($n = 3$) (Figure 1.3). Mean duration of badger encounters at nests was 19.53 ± 3.37 minutes. All badgers opened all eggs and consumed them at the nest sites. Eggs were consumed one at a time and mean duration of time of consumption of individual eggs was 2.22 ± 0.42 minutes.

Badger sign varied among depredations (Table 1.2). Also, at multiple nests I found ≥ 1 type of egg depredation pattern left by the same badger (e.g., badger crushed shells and broke holes in eggs). At 4 nests, badgers left holes in the sides or tops of eggs, leaving the rest of the eggshell intact (Figure 1.1). During these depredations, badgers sucked and licked the contents of the eggs through the hole in the egg. At 5 nests, badgers broke eggshells into fragments while consuming egg contents (Figure 1.1). During 2 depredations, badgers consumed the entire egg and shell leaving no intact eggs or eggshells at the nest. During all depredations, most eggs were consumed by badgers outside the nest bowl. However, I observed 3 depredations when badgers ate eggs in the nest bowl and left fragments or largely intact eggshells with holes. Nest material was removed from bowls at 5 nests destroyed by badgers, while at 3 nests I did not observe any disturbances to nesting material nor did I find badger tracks or sign. One nest was completely destroyed by a badger and removed from underneath a shrub.

Cow Encounters

One of 6 encounters by cows resulted in a partial nest depredation. A cow flushed an incubating grouse, causing an egg to be displaced from the nest bowl and the egg subsequently was eaten by the cow. After consuming one egg, the cow sniffed and moved other eggs within the nest bowl but I did not observe any further depredation. The final image was lost, however, because the cow moved the camera out of position. Five other encounters by cows were observed. In each case, grouse were flushed away from their nests by the cow. During these encounters cows sniffed eggs and occasionally moved them but did not consume them.

Rodent Encounters

Rodents frequently encountered sage-grouse nests ($n = 167$, Table 1.3) but no rodents consumed sage-grouse eggs. However, rodents often consumed remnant eggshells and membranes following normal hatch or following clutch depredation by ravens or badgers ($n = 42$) often leaving the appearance that the nests had been depredated by rodents. I identified least chipmunk (*Tamius minimus*), Wyoming ground squirrel (*Spermophilus elegans*), Piute ground squirrel (*S. mollis*), northern pocket gopher (*Thomomys talpoides*), Great Basin pocket mouse (*Perognathus parvus*), North American deer mouse (*Peromyscus maniculatus*), and sagebrush vole (*Lemmiscus curtatus*) as rodents that encountered sage-grouse nests. The species of many small rodents visiting nests at night were unidentifiable.

No ground squirrel encounters ($n = 23$) resulted in depredation. Ground squirrel visitations were generally brief (i.e., 1-3 sec). I was unable to identify the species of ground squirrel during 3 encounters. All ground squirrel visitations were diurnal and took place during incubation recesses or at abandoned nests. I did not observe grouse actively defend eggs from ground squirrels and squirrels did not displace grouse from nests. During most visitations ($n = 16$), ground squirrels did not make contact with any eggs and squirrel behavior did not indicate an interest in eggs as food (Table 1.3). However, I observed Wyoming ground squirrels bite intact eggs during 4 visitations but were unsuccessful at opening them (Figure 1.5). One squirrel repeatedly attempted to bite a single egg for 98 seconds (Figure 1.5). Ground squirrels occasionally moved eggs using their teeth and rostrum ($n = 4$). Wyoming and Piute ground squirrels did not lift any eggs or brace eggs against their bodies or the nest bowl, behaviors described for other ground

squirrel species depredating eggs (Sowls 1948, Sargeant et al 1987). One ground squirrel dug up nest material and litter near the eggs in the nest but did not make direct contact with any eggs.

Least chipmunks were the most frequent rodent to visit nests ($n = 41$) following depredation or hatch and regularly consumed or picked up eggshells, eggshell membranes, embryonic membranes, feathers, and nest material. Also, least chipmunks attempted to perforate eggs twice but were unsuccessful. I observed a deer mouse consume a portion of a previously cracked egg.

Snake Encounters

On 2 occasions, a Great Basin gopher snake (*Pituophis catenifer deserticola*) visited sage-grouse nests during an incubation recess. Based on images, each snake was >1 m in length and approximately 4.0 cm at maximum body width. One encounter lasted 72 seconds and the other 55. Eggs were inspected by both snakes for 52 and 28 seconds, respectively. Snakes lightly touched eggs with their mouths but did not attempt to consume them. One snake inspected each egg several times.

DISCUSSION

Continuous video-monitoring was highly successful in revealing the identity of sage-grouse nest predators and yielding new insight into sage-grouse behavior in response to nest predation. My data indicate that depredation sign at nests cannot reliably identify sage-grouse nest predators. The data also show that that ravens and badgers are effective predators of sage-grouse eggs insofar as all encounters with ravens and badgers resulted in egg loss and nest failure. Rodents also regularly encountered sage-grouse nests, but never consumed intact eggs, while regularly consuming egg debris following depredation

events. I also provide the first published evidence of a domestic cow damaging a sage-grouse nest and provide direct evidence that cattle encounter and interact with sage-grouse nests.

Ravens and badgers often left indistinguishable sign following sage-grouse nest depredation supporting the concept of interspecific similarities in nest and egg remains (Lariviere 1999). For example, ≥ 1 egg or eggshell was missing from the nest bowl of 12 nests. Ravens and badgers depredated ten and two of these nests, respectively. Although authors report that duck eggs missing without a trace may be evidence that badgers did not destroy nests, I observed a badger consume an entire clutch of sage-grouse eggs without leaving eggshell fragments and caused no disturbance to the nest bowl. Similarly, red fox (*Vulpes vulpes*), raccoons (*Procyon lotor*), weasels (*Mustela* spp.), and crows have been reported to remove eggs from nests leaving no remains (Montevecchi 1976, Major 1991). My data support the conclusion that documenting eggs that have been removed from nests does not permit accurate identification of predators even to higher taxonomic levels (i.e., class) (Lariviere 1999). Moreover, several eggs with holes on the sides were observed following a raven depredation that were similar to that of badger depredations, and as with badgers, egg shells were scattered in and around the nest bowl. Similar descriptions of holes in eggs caused by rodents and skunks, respectively, have been reported (Lariviere 1999).

I also found intraspecific differences in patterns of egg breakage and nest remains as have others (Lariviere 1999). Not all badgers disturbed the nest bowl or surrounding area or left other characteristic sign (i.e., crushed egg shells, nest disturbance) to identify badgers as the nest predators. My findings are consistent with those of waterfowl. For

example, in the prairie pothole region 40% and 57% of 265 eggs assumed to be destroyed by badgers were observed with holes and were severely crushed, respectively, (Sargeant et al. 1998). Striped skunks (*Mephitis mephitis*) have been reported to crush eggshells, leaving only fragments (Darrow 1938), and also have been described as characteristically opening ends of eggshells (Davis 1959). Nests depredated by ravens often were missing all or most of the eggs, as has been reported for ravens and other corvids elsewhere (Johnson et al. 2005, Montevicchi 1976), but I also observed ravens consuming eggs at the nest in and near a nest bowl following a raven depredation. Although all duck nests were reported to be associated with dug areas in prairie pothole region (Sargeant et al. 1998), I found 2 of 7 nests with no dug areas. Badgers are known to dig around nests for egg caching (Sargeant et al. 1998). However, I did not observe any cached sage-grouse eggs by badgers.

Manner of consumption may be a function of the stage of embryonic development of grouse eggs (Lariviere 1999) and how egg contents can be consumed. In this study, eggs with holes from ravens and badgers were in early phases of embryonic development. Depredation of eggs that were well developed resulted in nests containing small shell fragments or missing eggs, an observation others have also made (Darrow 1938). Furthermore, variation in raven predatory behavior may be a function of stage of raven reproduction. For example, ravens without young to feed may consume eggs at sage-grouse nests rather than carry eggs to their nestlings.

Ravens were the most common nest predator at my study area. Raven numbers have increased >200% in the past 40 years throughout North America (Sauer et al. 2004) and substantial increases have been observed in the western United States (Boarman and

Heinrich 1999) including the intermountain west. In Alberta, Canada, sharp-tailed grouse habitat overlaps with corvid distribution and grouse nest success is significantly higher in areas of low corvid densities (Manzer and Hannon 2005). Furthermore, sage-grouse habitat has become highly fragmented (Knick et al. 2003) and fragmentation may increase nest vulnerability to ravens. In forested landscapes, nest predation by corvids (e.g., ravens, crows, magpies) is well documented to be higher in areas of increased edge (Andr n 1992, Donovan et al. 1997, Hartley and Hunter 1998). Also, nest depredation was reported to be greater for birds than mammals in fragmented landscapes (Chalfoun et al. 2002). In shrubsteppe, magpies were identified depredating sage-grouse nests in Wyoming (Holloran and Anderson 2003) and ravens were identified depredating artificial nests in fragmented areas of eastern Washington (Vander Haegen et al. 2002).

Ravens appeared to locate grouse nests during morning and evening hours, which are the times of day that grouse have been observed at recesses from incubation (Schroeder et al. 1999). I observed greater self-maintenance and nesting movement by females at nests following recesses, such as preening, egg-turning, nest maintenance. Because nearly all raven depredations occurred while grouse were incubating, ravens may have visually cued on movement back to the nest or movement at the nest following incubation recesses to locate and depredate nests.

Badgers previously have been suspected as important predators of natural and artificial sage-grouse nests (Petersen 1980, Ritchie et al. 1994) and on one occasion a badger was identified using still photography depredating a sage-grouse nest in Wyoming (Holloran and Anderson 2003). If badgers find sage-grouse nests opportunistically while foraging for their principle prey of rodents, then rodent abundance may affect rates of

badger predation on sage-grouse nests. In this scenario, areas with high rodent abundance, and thus more badgers, may be risky sites for nesting sage-grouse. Alternative prey availability was thought to influence predation by badgers on artificial sage-grouse nests in northern Utah (Ritchie et al. 1994). Change in availability of alternative prey was proposed for annual variation in mesomammal predation of bobwhite quail (*Colinus virginianus*) (Klimstra and Roseberry 1975, Staller et al. 2005). At Walters' lek site I observed 70% (16 of 23) of ground squirrel nest encounters by video and observed many more ground squirrels during my field activities and badgers were responsible for all video-recorded depredations ($n = 6$). Alternatively, because Walters' lek was an area of WS raven removal, perhaps raven removal provided an opportunity for badgers to depredate sage-grouse nests.

After nest predators discovered grouse nests, females were always unsuccessful at defending their eggs. Active nest-defense was rare and occurred only during raven encounters. Although one grouse briefly delayed predation of eggs during nest defense, multiple ravens appeared to work together and, ultimately, depredated the entire clutch. Although physical attacks by sage-grouse have not been reported previously, aggressive behaviors to protect eggs has been documented for other grouse (Zwickel 1992, Rusch et al. 2000).

In my study, Wyoming and Piute ground squirrels at natural sage-grouse nests appeared to be limited by the width of their gapes and did not depredate grouse eggs. These data are consistent with reports of thirteen-lined and Richardson's ground squirrels not depredating artificial and real sage-grouse nests in Wyoming using remote sensing cameras (Holloran and Anderson 2005). Using videography, I did not observe ground

squirrels employ egg-handling techniques such as lifting or bracing (Sowls 1948, Sargeant et al. 1987) which might have allowed them to overcome gape-size limitations as has been observed for other rodents (Blight et al. 1999, Craig 1998), including Franklin's ground squirrels (Sowls 1948, Sargeant et al. 1987). My field observations of squirrel behavior at sage-grouse nests are consistent with reported behavior of Richardson's ground squirrels when exposed experimentally to eggs of ground nesting birds (*Spermophilus richardsonii*) (Michener 2005). Although functional gape-width of Wyoming and Piute ground squirrels has not been reported, Richardson's ground squirrels, a closely related species of similar size, have an average functional gape-width of ≤ 21 mm (Michener 2005) while an average sage-grouse egg width is 38-39 mm (Schroeder et al. 1999). Ground squirrels in my study may not have been capable of opening sage-grouse eggs because the egg-width is considerably larger than their functional gape-width (Michener 2005). The average body mass of Franklin's ground squirrels (Choromanski-Norris and Fritzell 1986) is greater than that of Wyoming (Fagerstone 1982) and Richardson's ground squirrels (Michener 1984) and perhaps body mass contributes to squirrels ability to handle and open large eggs.

Past studies using nest and egg remains as evidence of ground squirrel predation on sage-grouse eggs have been inconsistent. Ground squirrels have been named as important sage-grouse nest predators (Patterson 1952) and Richardson's ground squirrels were reported to destroy sage-grouse nests in Alberta (Watters et al. 2002). Ground squirrels were reported as responsible for 8-42.6% of depredations of sage-grouse nests elsewhere (Patterson 1952, Gill 1965, Petersen 1980, Niemuth and Boyce 1995). Particularly, Wyoming ground squirrels were considered to be important predators in

North Park, Colorado (Petersen 1980). Conversely, others have not found ground squirrels to be efficient egg predators (Errington 1938, Stanton 1944).

Inconsistencies regarding rodent depredation may result from the difficulty in identifying predators using nest and egg remains (Lariviere 1999). In particular, rodent scavenging of post-depredation debris may result in incorrectly attributing depredation to squirrels. My results support this concept in that I observed 42 occasions of rodents opportunistically scavenging remains at nests which already had been depredated or hatched. Rodents often ate eggshells and membranes within 24 hours of actual nest fate and left various forms of sign at nests and on eggshells. Using videography at bobwhite quail nests, others have found squirrels were not responsible for depredation but visited nests after completion and removed eggshells frequently (Lusk et al. 2006).

I recognize potential shortcomings to using videography to identify sage-grouse predators (Cutler and Swann 1999). Coyotes have been documented as nest predators (Schroeder et al. 1999) and were frequently observed at my study sites but I recorded no encounters at sage-grouse nests, similar to others that used remote sensing cameras (Holloran and Anderson 2003). Coyotes may opportunistically consume sage-grouse eggs but so infrequently that they were not video recorded and, therefore, not common sage-grouse nest predators. Alternatively, human scent and activity at nest sites may have deterred coyotes despite my efforts to minimize scent with rubber boots and gloves. My presence did not deter other olfactory-cued species from encountering nests (i.e., rodents and badgers) and other mammals were video-recorded elsewhere using similar techniques (Hernandez et al. 1997, Sanders and Maloney 2002).

A non-significant, numerical trend of increased survival rates on nests with cameras was most likely caused by timing in camera deployment and not by camera effects on predation rates. For instance, exclusion of nest failures during the laying period and initial seven days of incubation, a time when no nests had cameras may have caused small negative biases in depredation rates. I often observed depredation during initial stages and nests that survived into later stages were often successful, consistent with the observations of others (Thompson et al. 1999, Staller et al. 2005). As nesting season progressed, cameras were moved from hatched, abandoned, or depredated nests to random nests that had already proceeded to advanced incubation. Furthermore, when controlling for timing effects by placing pheasant eggs in sage-grouse nest bowls and monitoring nests for 10 days, I found cameras did not influence nest predation supporting the explanation that trends of slight increases in success at natural nests with cameras was most likely random or caused by timing of camera deployment (Thompson et al. 1999, Staller et al. 2005) and not the presence of a camera per se.

MANAGEMENT IMPLICATIONS

My study refined an important tool to observe sage-grouse predators and their behavior and assess predation evidence in field studies. This technique does not appear to influence sage-grouse nest success. In efforts to restore and manage grouse populations, it is important to properly identify predators in communities to mitigate depredation by appropriate predator or habitat management, especially in areas with unusually high depredation rates. Managers should avoid using egg and nest remains to identify predators because it is not reliable due to intraspecific differences and interspecific similarities following depredation. Furthermore, sign at nests left by scavenging rodents

(i.e., consumption of egg shells, hair, feces) appears to contribute to substantial identification biases. When identification of predators is needed, I encourage the use of devices that document images at nests, as described here and elsewhere (Pietz and Granfors 2000, Herranz et al. 2002, Holloran and Anderson 2003), to prevent biases associated with using nest and egg remains, especially where managers believe there is an unusual predator scenario. Further documentation using videography will be beneficial to understanding the role of other rodents and snakes as sage-grouse egg predators and revealing the identity and relative importance of predators among different conditions of nesting habitat.

Videography confirmed ravens and badgers as predators of sage-grouse nests as suspected previously (Connelly et al. 1991, Schroeder et al. 1999, Vander Haegen et al. 2002) and both egg predators did not cause adult mortality based on subsequent radio-telemetry monitoring. Because I had no video-recorded encounters by coyotes their importance as nest predators remains unsubstantiated, albeit it is possible coyotes were deterred from video-monitored nests. Also, videography provided further support for the contention that ground squirrels are not an effective predator of sage-grouse nests (Holloran and Anderson 2003, Michener 2005). Here the objective was to identify nest predators, and not to measure effect size on sage-grouse population dynamics. However, badger depredation appeared incidental and local, whereas ravens appeared to depredate nests across larger landscapes and tended to be associated with anthropogenic-altered areas (i.e., powerlines, roads).

Managers should be aware that raven numbers are increasing in environments with anthropogenic resource subsidies (Boarman 1993, Boarman and Heinrich 1999,

Boarman 2003) and relatively high raven numbers within sage-grouse habitat increases the probability of depredation (Chapter 2). Ravens caused high predation pressure to sage-grouse when numbers of observed ravens exceeded 7.3 per 10 km of survey transect (Chapter 2). However, this number may be an overestimation within areas of reduced herbaceous cover. Areas where ravens have an unnatural, negative effect on sage-grouse nesting may require a combination of management strategies aimed to reduce predation including increasing herbaceous cover, directly removing ravens, and modifying anthropogenic resource subsidies.

Table 1.1. Number of sage-grouse nests by fate and camera exposure across years in northeastern Nevada during 2002-2005. Percentages of nest fates of camera and no-camera nests by year are in parentheses.

| Year | Camera ^a | | | No-camera | | | Total |
|-------|-------------------------|----------------------|------------------------|-------------------------|----------------------|------------------------|-------|
| | Depredated ^b | Hatched ^c | Abandoned ^d | Depredated ^b | Hatched ^c | Abandoned ^d | |
| 2002 | | 2(100) | | 1(25) | 3(75) | | 6 |
| 2003 | 1(11) | 7(78) | 1(11) | 1(33) | 2(67) | | 12 |
| 2004 | 6(33) | 9(50) | 3(17) | 7(64) | 4(36) | | 29 |
| 2005 | 13(48) | 12(48) | 1(4) | 8(57) | 5(36) | 1(7) | 40 |
| Total | 20(36) | 30(55) | 5(9) | 17(53) | 14(44) | 1(3) | 87 |

^a Cameras were deployed on nest at ≥ 7 days following the initial day of incubation. Days of camera exposure varied among nests.

^b Depredation was classified as partial or complete. I considered nest depredations to be complete if every egg was destroyed or missing from the nest bowl. Partial depredations were scored if ≥ 1 intact egg remained in the nest bowl. Of the nests with cameras, 4 depredations were not video-recorded due to camera failure. Of the nests with no-camera, 1 depredation was directly observed in the field.

^c Nests that produced ≥ 1 chick were classified as hatched.

^d Females located >300 m from nest for 3 consecutive relocations were classified as abandoned.

Table 1.2. Nest and egg remains at depredated greater sage-grouse nests that were video-recorded using infrared, miniaturized cameras and video recorders to identify nest predators and depredation sign in northeastern Nevada, 2002-2005.

| Species | No. encountered | Fragmented eggshell(s) | Hole in eggshell(s) | Missing egg(s) | Disturbed nest bowls ^b | Destroyed nest bowls ^c | Partial depredation ^d | Complete depredation ^e |
|-----------------|-----------------|------------------------|---------------------|----------------|-----------------------------------|-----------------------------------|----------------------------------|-----------------------------------|
| American Badger | 7 | 5(71) | 4(57) | 2(29) | 1(14) | 4(57) | | 7(100) |
| Common Raven | 10 | 2(20) | 2(20) | 10(100) | 1(10) | | 3(30) | 7(70) |
| Domestic Cow | 6 | 1(17) | | 1(17) | 1(17) | | 1(17) | |

^a Disturbed nest was defined by having a hole or scrape in nest in nest.

^b Destroyed nest was defined as nest material removed from nest bowl and/or ground dug up where nest was placed.

^c Partial depredation was defined as ≥ 1 egg not taken or eaten from nest bowl following depredation.

^d Complete depredation was defined as all eggs in clutch were destroyed during predation event.

Table 1.3. Number of encounters and behavior of rodents at sage-grouse nests monitored using infrared miniaturized cameras to identify nest predators and behavior in northeastern Nevada, 2002-2005.

| Species | No. of encounters | Moved intact egg(s) | Attempted to perforate intact egg(s) | Consumed remains ^a |
|----------------------------|-------------------|---------------------|--------------------------------------|-------------------------------|
| Wyoming ground squirrels | 16 | 4 | 4 | 5 |
| Piute ground squirrel | 7 | | | |
| Northern pocket gopher | 3 | | | |
| Least chipmunk | 73 | 2 | 2 | 33 |
| Other small rodent species | 84 | | | 9 |
| Total | 167 | 2 | 2 | 42 |

^a Remains were of previously hatched eggs or eggs depredated by other (larger) predators.

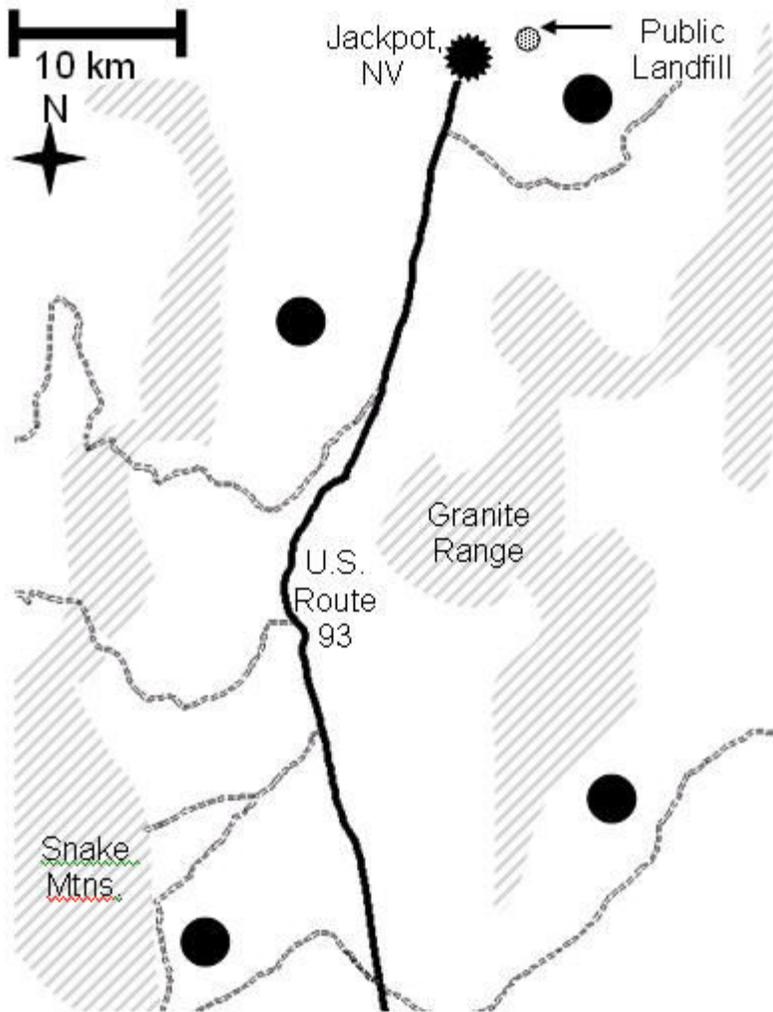


Figure 1.1. Greater sage-grouse study area in northeastern Nevada during 2002-2005. Filled circles represent lek routes where nests were monitored using videography. A public landfill was located approximately 7 km from the northernmost site.



Figure 1.2. Video images of sage-grouse nests in northeastern Nevada. (a) Image of incubating grouse. (b) Raven depredation that resulted in no diagnostic egg remains. (c) Badger perforating egg shell and sucking out egg contents. (d) Eggshells following badger depredation (from c) left in nest bowl, which resulted in holes on the side of eggs (arrow), (e) Badger removing eggs from nest bowl. (f) Eggshell fragments of badger depredation (from e) which were fragmented and the nest destroyed. Image taken with a 35-mm camera following badger depredation to show eggshells that were outside nest bowl. Arrow indicates where nest bowl was located.

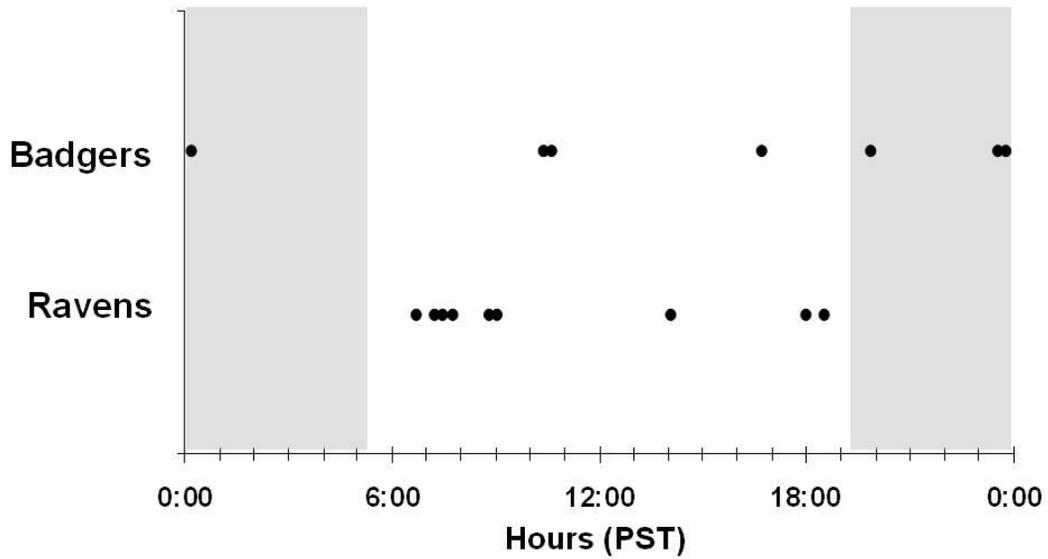


Figure 1.3. Time of predation by badgers ($n = 7$) and ravens ($n = 9$) at natural, video-recorded sage-grouse nests in northeastern Nevada during 2002-2005. An additional raven encounter was reported in the text but the time was not recorded. Time of 0:00 indicates midnight. Dots represent time of first appearance of predators during predation events. Shaded areas indicate approximate nocturnal hours based on average sunrise and sunset times during dates of predation events.

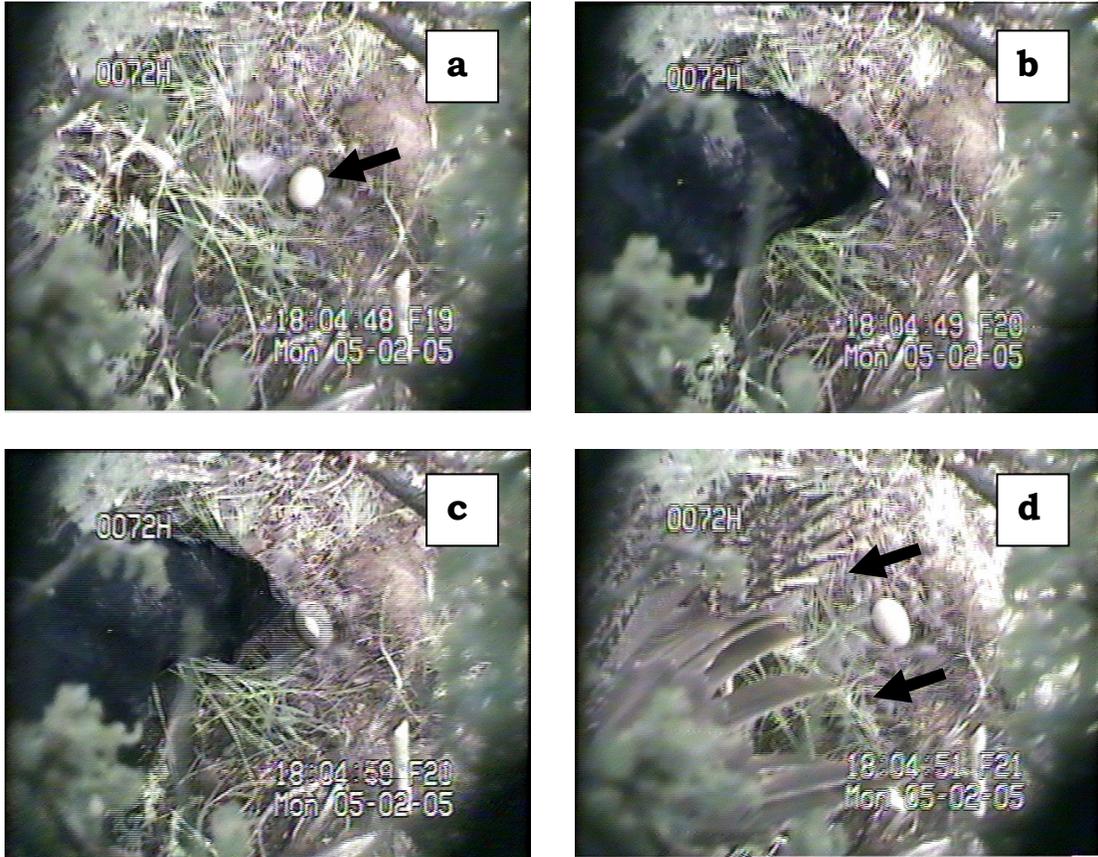


Figure 1.4. Video images of sage-grouse unsuccessfully defending nest against ravens in northeastern Nevada. Seven eggs were depredated within the first egg was taken 9.4 minutes before image (a). All consecutive video images are approximately one second apart. (a) Grouse moves away from nest bowl exposing the last egg (arrow). (b) Raven attempts to pick up the egg from nest bowl. (c) Raven withdraws without taking the egg. (d) Grouse attacks raven with feathers extended from across the nest bowl (arrows). Clutch size was seven and ravens took all eggs. The grouse appeared to attack on several occasions but another raven, opposite of attack, removed eggs from nest.

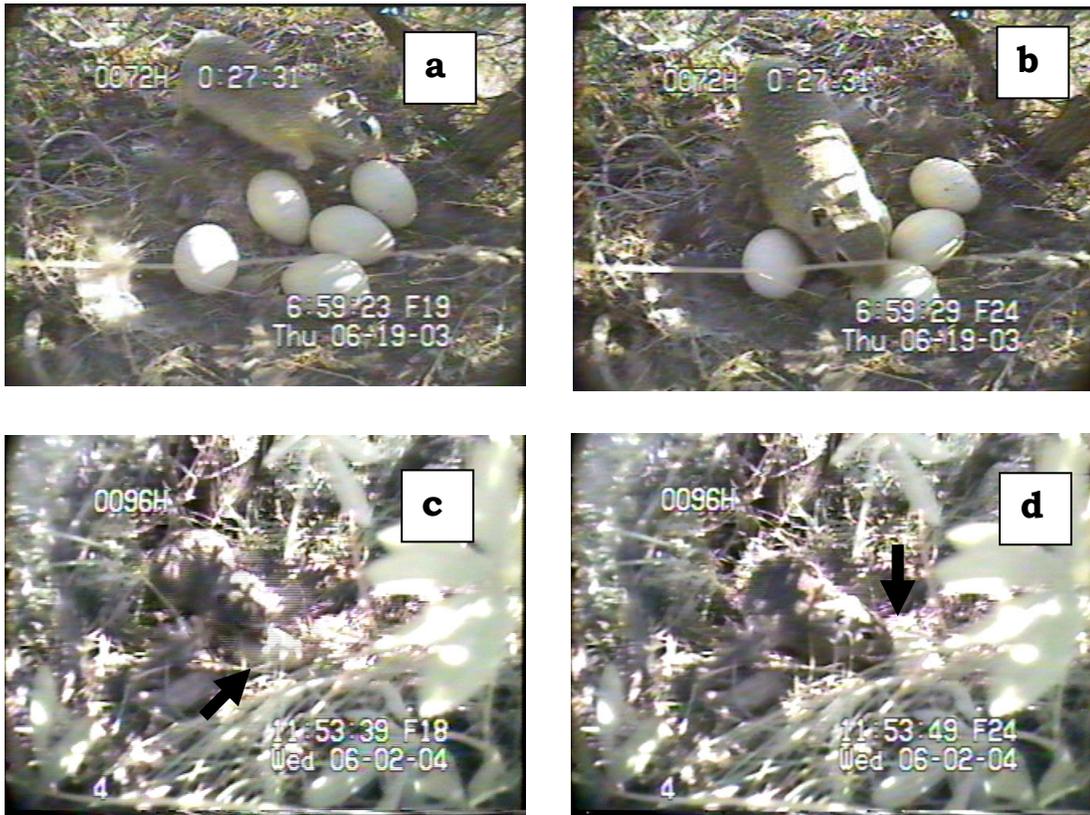


Figure 1.5. Video images of Wyoming ground squirrels attempting to perforate intact sage-grouse eggs at two natural nests in northeastern Nevada. (a-b) Ground squirrel inspected each egg and appeared to use incisors to attempt to perforate eggshell of three eggs. (c-d) Ground squirrel repeatedly biting at an intact egg (arrows) for 98 seconds. This nest was previously partially depredated by a raven. Ground squirrel was not successful at perforating sage-grouse egg and the grouse abandoned single remaining egg following raven depredation. No ground squirrels ($n = 23$) successfully opened eggs.

LITERATURE CITED

- Ammann, G. A. 1944. Determining the age of pinnated and sharp-tailed grouse. *Journal of Wildlife Management* 8:170-171.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794-804.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365-373.
- Bergerud, A. T. 1988. Population ecology of North American grouse. Pages 578-648 in A. T. Bergerud and M. W. Gratson, editors. *Adaptive strategies and population ecology of northern grouse*. University of Minnesota Press, Minneapolis.
- Blight L. K., J. L. Ryder, and D. F. Bertram. 1999. Predation on rhinoceros auklet eggs by a native population of *Peromyscus*. *Condor* 101:871-876.
- Bro, E., B. Arroyo, and P. Miggot. 2006. Conflict between grey partridge *Perdix perdix* hunting and hen harrier *Circus cyaneus* protection in France: a review. *Wildlife Biology* 12:233-247.
- 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. Miller, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. *Conservation and resource management*. Pennsylvania Academy of Science, Philadelphia, Pennsylvania.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing common raven predation on desert tortoises. *Environmental Management* 32:205-217.
- Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). In A. Poole and F. Gill, editors. *The Birds of North America*, No. 476. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, D.C.
- Carroll, J. P. 1990. Winter and spring survival of radio-tagged gray partridge in North Dakota. *Journal of Wildlife Management* 54:657-662.

- Chalfoun A. D., F. R. Thompson III, and M. J. Ratnaswamy. 2002. Nest Predators and Fragmentation: a review and meta-analysis. *Conservation Biology* 16:306-318.
- Choromanski-Norris, J., and E. K. Fritzell. 1986. Seasonal activity cycle and weight changes of the Franklin's ground squirrel. *American Midland Naturalist* 116:101-107.
- Coates, P. S., and D. J. Delehanty. 2006. Effect of capture date on nest-attempt rate of translocated sharp-tailed grouse *Tympanuchus phasianellus*. *Wildlife Biology* 12:277-283.
- Coates, P. S., J. O. Spencer, Jr., and D. J. Delehanty. In press. Efficacy of CPTH-treated egg baits for removing ravens. *Human-wildlife Conflicts Management*.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. Station Bulletin 80. College of Natural Resources Experiment Station, Moscow, Idaho.
- Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. *Journal of Wildlife Management* 52:116-122.
- Craig, D. P. 1998. Chipmunks use leverage to eat oversized eggs: support for the use of quail eggs in artificial nest studies. *Auk* 115:486-489.
- Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin* 27:571-581.
- Darrow, R. 1938. Possibilities of recognizing the evidence of predation and the species involved in the remains of grouse and grouse nests found destroyed. *Transactions of the North American Wildlife Conference* 3:834-838.
- Davis, J. R. 1959. A preliminary progress report on nest predation as a limiting factor in wild turkey populations. *Proceedings of the National Wild Turkey Symposium* 1:138-145.

- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064-2075.
- Errington, P. L. 1938. Experimental evidence of the eating of bobwhite eggs by small Sciuridae. *Journal of Mammalogy* 19:107-108.
- Fagerstone, K. A. 1982. Ethology and taxonomy of Richardson's ground squirrel (*Spermophilus richardsonii*). Dissertation, University of Colorado, Boulder, Colorado.
- Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428-434.
- Garrott, R.A., G. C. White, R. M. Bartmann, and D. L. Weybright. 1986. Treatment of reflected signals in biotelemetry triangulation systems. *Journal of Wildlife Management* 50:747-752.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- Gill R. B. 1965. Distribution and abundance of a population of sage grouse in North Park, Colorado. Thesis, Colorado State University, Fort Collins, Colorado.
- Hartley, M. J., and M. L. Hunter Jr. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. *Conservation Biology* 12:465-469.
- Hernandez, F., D. Rollins, and R. Cantu. 1997. Evaluating evidence to identify ground-nest predators in west Texas. *Wildlife Society Bulletin* 25:826-831.
- Herranz, J., M. Yanes, and F. Suárez. 2002. Does photo-monitoring affect nest predation? *Journal Field Ornithology* 73:97-101.
- 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., B. J. Heath, A. J. 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.
- Hupp, J. W., and J. T. Ratti. 1983. A test of radio telemetry triangulation accuracy in heterogeneous environments. *Proceedings of the International Wildlife Biotelemetry Conference* 4:31-46.
- Johnson, M. D., T. L. Adams, T. M. Branston, R. D. Clark, W. B. Crombie, D. L. Germann, A. D. M. Ives Ringstad, H. Langendorf, and J. L. Moore. 2005. Variables influencing predation of artificial duck nests in northwest coastal California. *Transactions Western Section of the Wildlife Society* 41:11-20.
- King, D. I., R. M. DeGraaf, P. J. Champlin, and T. B. Champlin. 2001. A new method for wireless video monitoring of bird nests. *Wildlife Society Bulletin* 29:349-353.
- Klimstra, W. D., and J. L. Roseberry. 1975. Nesting ecology of the bobwhite in southern Illinois. *Wildlife Monographs* No. 41. 37 pp.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.
- Lariviere, S. 1999. Reasons why predators cannot be inferred from nest remains. *Condor* 101:718-721.
- Lusk, J. J., S. G. Smith, S. D. Fuhlendorf, and F. S. Guthery. 2006. Factors influencing northern bobwhite nest-site selection and fate. *Journal of Wildlife Management* 70:564-571.
- Major, R. E. 1991. Identification of nest predators by photography, dummy eggs, and adhesive tape. *Auk* 108:190-195.
- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138:298-307.

- 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.
- Marks, J. S., and V. S. Marks. 1987. Influence of radio collars on survival of sharp-tailed grouse. *Journal of Wildlife Management* 51:468-471.
- Marini, M. A., and C. Melo. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. *Condor* 100:395-399.
- Martin, T. E. 1987. Artificial nest experiments: Effects of nest appearance and type of predator. *Condor* 89:925-928.
- Martin, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. *BioScience* 43:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65:101-127.
- Michener, G. R. 1984. Sexual differences in body weight patterns of Richardson's ground squirrels during the breeding season. *Journal of Mammalogy* 65:59-66.
- Michener, G. R. 2005. Limitation on egg predation by Richardson's ground squirrels. *Canadian Journal of Zoology* 83:1030-1037.
- Miller, C. K., and R. L. Knight. 1993. Does predator assemblage affect nest success in songbirds? *Condor* 95:712-715.
- Montevecchi, W. A. 1976. Egg size and the egg predatory behavior of crows. *Behaviour* 57:304-320.
- Niemuth, N. D., and M. S. Boyce. 1995. Spatial and temporal patterns of predation of simulated sage grouse nests at high and low densities: an experimental study. *Canadian Journal of Zoology* 73:819-825.
- Patterson, R. L. 1952. *The sage grouse of Wyoming*. Sage Books, Denver, Colorado.
- Petersen, B. E. 1980. Breeding and nesting ecology of female Sage Grouse in North Park, Colorado. Thesis. Colorado State University, Fort Collins.

- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71-87.
- Rearden, J. D. 1951. Identification of waterfowl nest predators. *Journal of Wildlife Management* 36:87-98.
- Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *Auk* 120: 371-383.
- Riley, T. Z., C. A. Davis, M. Ortiz, and M. J. Wisdom. 1992. Vegetative characteristics of successful and unsuccessful nests of lesser prairie chickens. *Journal Wildlife Management* 56:383-387.
- Ritchie, M. E., M. L. Wolfe, and R. Danvir. 1994. Predation of artificial sage grouse nests in treated and untreated sagebrush. *Great Basin Naturalist* 54:122-129.
- Rusch, D. H., S. Destefano, M. C. Reynolds, and D. Lauten. 2000. Ruffed grouse (*Bonasa umbellus*). In A. Poole and F. Gill, editors. *The Birds of North America*, No. 515. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, D.C.
- Sanders, M. D., and R. F. Maloney. 2002. Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. *Biological Conservation* 106:255-236.
- Sargeant, A. B., M. A. Sovada, and R. J. Greenwood. 1987. Responses of three prairie ground squirrel species, *Spermophilus franklinii*, *S. richardsonii*, and *S. tridecemlineatus*, to duck eggs. *Canadian Field-Naturalist* 101:95-97.
- Sargeant, A. B., M. A. Sovada, and R. J. Greenwood. 1998. Interpreting evidence of depredation of duck nests in the prairie pothole region. U. S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota and Ducks Unlimited, Inc., Memphis, Tennessee. USA. 72 pp.

- Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American Breeding Bird Survey, Results and Analysis 1966 - 2003. Version 2004.1. United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
- 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. A. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In A. Poole and F. Gill, editors. *The Birds of North America*. No. 425. Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. B. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deirbert, S. C. Gardner, M. A. Hilliard, G. D. Kobridger, 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.
- Sowls, L. K. 1948. The Franklin's Ground Squirrel *Citellus franklinii* (Sabine) and its relationship to nesting ducks. *Journal of Mammalogy* 29:113-137.
- Springer, J. T. 1979. Some sources of bias and sampling error in radio triangulation. *Journal of Wildlife Management* 43:926-935.
- Staller, E. L., W. E. Palmer, J. P. Carroll, R. P. Thornton, and D. C. Sisson. 2005. Identifying predators at northern bobwhite nests. *Journal of Wildlife Management* 69:124-132.
- Stanton, F. W. 1944. Douglas ground squirrel as a predator on nests of upland game birds in Oregon. *Journal of Wildlife Management* 8:153-161.
- Thompson, F. R., III, W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. *Auk* 116:259-264.
- 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.
- Watters, M. E., T. L. McLash, C. L. Aldridge, and R. M. Brigham. 2002. The effect of vegetation structure on predation of artificial greater sage-grouse nests. *Ecoscience* 9:314-319.
- Willebrand, T., and V. Marcstrom. 1988. On the danger of using dummy nests to study predation. *Auk* 105:378-379.
- Wilson, G. R., M. C. Brittingham, and L. J. Goodrich. 1998. How well do artificial nests estimate success of real nests? *Condor* 100:357-364.
- Zwikel, F. C. 1992. Blue grouse (*Dendragapus obscurus*). In A. Poole and F. Gill, editors. *The Birds of North America*, No. 15. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, D.C.

CHAPTER 2:

GREATER SAGE-GROUSE INCUBATION RHYTHMS AND THE EFFECTS OF AGE, TIMING OF INCUBATION, PREDATORS, HABITAT, AND CLIMATE

ABSTRACT

I used continuous videography to make precise measurements of greater sage-grouse (*Centrocercus urophasianus*) incubation constancy (% of time spent at nest in 24-hour period) and recess duration. I used an information-theoretic modeling approach to evaluate incubation rhythms in relation to age, timing of incubation, predator abundance, microhabitat, and food availability. Females exhibited a relatively high degree of incubation constancy (96%) and employed a distinctive bimodal distribution of brief incubation recess that peaked at sunset and 30 min prior to sunrise. Grouse typically returned to their nests during low light conditions. Incubation constancy of yearlings was lower than adults, particularly in the later stages of incubation. Daily recesses of yearlings were also more frequent than adults and yearlings recessed more often than adults later in mornings and earlier in evenings. Video images revealed that nearly all depredations by ravens (*Corvus corax*), the most frequent predator recorded at grouse nests, took place during mornings and evenings after sunrise and before sunset, respectively. Ravens rely on visual cues and typically depredated nests following incubation recesses. Also, indices of raven abundance were positively related to recess duration. I found evidence that incubation constancy increases with greater nest understory. Nest understory may have multiple effects on incubation rhythms, including parental energy-savings due to influences on nest microclimate and water and food

availability. Knowledge of incubation rhythms in relation to environmental factors will aid managers in conserving nest habitats and ecological communities that promote reproduction through successful incubation.

Key Words: *centrocercus urophasianus*, forbs, incubation constancy, nest attentiveness, predation, recess duration, sage-grouse, temperature, video

INTRODUCTION

Our understanding of greater sage-grouse (*Centrocercus urophasianus*) incubation rhythms is largely anecdotal (Schroeder et al. 1999), despite incubation behavior being central to reproductive success in birds (Deeming 2002). One reason for this is the difficulty of making fine-scale measurements of sage-grouse incubation processes in the wild. Sage-grouse abundance and distribution is of great conservation concern because sage-grouse range has declined substantially since European settlement (Schroeder et al. 2004) and population sizes have been substantially reduced within their current range (Connelly and Braun 1997). Knowledge of sage-grouse incubation behavior would be useful to research, management, and restoration efforts. For example, sage-grouse incubation behavior in relation to factors, such as experience, body condition, predator abundance, microclimate, and nesting habitat, is largely unknown but would be valuable when formulating management actions for sage-grouse intended to promote breeding in the wild.

Sage-grouse are large-bodied birds in which only females provide incubation and do so without assistance from mates or other helpers. Incubating birds are constrained energetically and must balance their own needs to forage and the risk of egg loss caused by environmental factors (e.g., unfavorable microclimate) and predation (Conway and

Martin 2000, Deeming 2002) while foraging away from the nest. Uniparental birds, like sage-grouse, are faced with a direct conflict between the mutually exclusive activities of foraging for self-maintenance and incubation. Parents which take fewer but longer recesses to forage reduce total energy spent in clutch rewarming (Drent 1975) and lessen risk of predation by moving to and from the nest less often (Conway and Martin 2000) but may trade-off slowing or impairing embryonic development due to substantial egg cooling during long recesses, especially when egg temperature falls below physiological zero temperatures (the temperature at which embryonic development ceases) (Clark and Wilson 1985, Gill 2006). In balancing self-maintenance activities and risk of predators finding eggs, parents may take crepuscular recesses (Erikstad 1986) but may limit recess duration because of increased egg cooling rates (Naylor et al. 1988). The relative importance of objects surrounding nests in aiding thermoregulation of eggs (Hansell and Deeming 2002) and visually obstructing eggs from predators (Martin 1995) while parents are away is unclear.

Large-bodied birds, like sage-grouse, tend to demonstrate substantially greater incubation constancy than small bodied birds (Deeming 2002). Smaller birds normally store less endogenous reserves for incubation and need more time to forage (Carter and Montgomerie 1985). Therefore, incubation rhythms of small birds may be influenced more by environmental factors than large birds. However, considerable variation exists in incubation constancy of large-bodied waterfowl in relation to ambient temperature and precipitation (Caldwell and Cornell 1975, Yerkes 1998). Furthermore, the ages of large-bodied birds influences their incubation rhythms (Aldrich and Raveling 1983, Yerkes 1998), probably because younger birds tend to store less lipid reserves for incubation and

need to spend more time foraging than older birds (Erikstad 1986). Incubation constancy of large-bodied birds can also decrease as the incubation period advances (Yerkes 1998).

The principle objective of my study was to measure fine-scale, around-the-clock incubation constancy and recess patterns of greater sage-grouse. Using videography, I observed diel patterns in incubation throughout the incubation period for both yearling females and older females. First, I tested 3 *a priori* hypotheses related to age: (1) Daily recesses of yearling grouse are more frequent than adults. (2) Adults take more crepuscular recesses than yearlings. (3) Yearlings have greater variation in recess duration than adults. These hypotheses were based on observations of other large-bodied, uniparental birds reported in the literature. Second, I examined timing of incubation recesses in relation to nest depredation events by visually-cued predators. Third, I used an information theoretic approach (Anderson et al. 2000) to assess the relative importance of explanatory variables on sage-grouse incubation constancy and recess duration by developing and comparing multiple, predictive models.

STUDY AREA

My study area encompassed 4 sage-grouse lek routes (an area encompassing 1 or more grouse leks [i.e., traditional display sites]) in an approximately 1,430 km² area of northeastern Elko County, Nevada (N 0670859, E 4599749, zone 11, NAD 83). The most northern and southern lek routes were approximately 10 km and 48 km south of Jackpot, Nevada. At all lek-routes, dominant plant communities consisted of shrub-steppe at lower elevations and mountain shrub at higher elevations. In shrub-steppe, shrub canopy cover predominantly consisted of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and basin big sagebrush (*A. t. tridentata*). Crested wheatgrass (*Agropyron cristatum*) and

bluebunch wheatgrass (*Pseudoroegneria spicata*) characterized the understory. Mountain big sagebrush (*A. t. vaseyana*), serviceberry (*Amelanchier alnifolia*) and native bunchgrasses predominated in mountain shrub. Utah juniper (*Juniperus osteosperma*) occurred in the peripheral regions at 2 of the 4 sites.

Climate at the study area was characterized by cool, dry winters and hot, dry summers with most annual precipitation occurring during the spring. Annual long-term (1952 to 2005) ambient temperatures ranged from -3.17 to 14.83°C. During the sage-grouse nesting season (March to July), temperatures ranged from 0.18 to 18.37°C. Ambient temperatures during sage-grouse nesting season of this study averaged 0.96 to 18.94°C. Long-term precipitation averaged 26 cm per year and 11.7 cm during sage-grouse nesting season (U. S. Climatological Database, Gibbs Ranch, N656486, E 4578188, zone 11). During this study, precipitation averaged 11.0 cm during grouse nesting seasons.

The Nevada Department of Wildlife (NDOW), in cooperation with United States Department of Agriculture, Animal Health Inspection Service, Wildlife Services (WS) carried out raven removal activities (Coates et al., In press) at the southernmost lek-route. The purpose of raven removal was to protect a recently reestablished population of Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) (Coates and Delehanty 2006) for which ravens were suspected to be nest predators (Coates, Idaho State University, unpubl. data) and had established a lek within the sage-grouse lek-route. A variety of potential sage-grouse egg predators reported in Schroeder et al. (1999) were observed within the study areas, including common ravens, coyotes (*Canus latrans*), weasels (*Mustela* spp.), elk (*Cervus elaphus*), American badgers (*Taxidea taxus*), ground

squirrels (*Spermophilus* spp.), American magpies (*Pica hudsonia*), and common crows (*Corvus brachyrhynchos*).

METHODS

I captured sage-grouse by using spotlights and hand-held nets at night (Giesen et al. 1982) and affixed 17 to 21g necklace-style, battery-powered radio transmitters with 22 cm antennae (<4% body mass) and classified grouse by age based on plumage (Ammann 1944). During 2002-2003, grouse were captured only at the southernmost lek route. During 2004-2005, I continued to capture from this lek-route and captured from 3 additional lek routes. I located grouse every 2 to 3 days using radio-telemetry (Advanced Telemetry Systems, Isanti, Minnesota) and used caution not to flush grouse during location by circling around them at a 30 to 50 m distance. I used GPS to record Universal Transverse Mercator (UTM) coordinates during locations. I located nests by approaching female grouse after 3 consecutive relocations at the same coordinate. I sought to locate grouse nests either during the laying period or during the initial days of incubation. I recorded UTM coordinates 5 m north of nests and described characteristics related with nest location allowing me to return and locate nests when grouse were not present.

Videography

I monitored nests with video recording systems (Fuhrman Diversified Inc., Seabrook, Texas; Supercircuits, Austin, Texas). I used miniature, camouflaged cameras equipped with 12 infrared-emitting diodes (850-950 nm wavelength) allowing night recording using light not detectable by vertebrates (Pietz and Granfors 2000). I mounted cameras to nearest shrub trunks or camouflaged stakes using wire. Cameras were 0.5 to 1.0 m from the nest bowl and 10 to 20 cm above ground. Video-recording systems and power sources

(deep-cycle batteries) were approximately 15 to 20 m away from nests and connected to the camera by a cable buried 3 to 5 cm in the ground. I used time-lapsed VCR systems operating at 2-3 frames/sec allowing me to record with accuracy and precision grouse presence on nests and movements of grouse to and from nests and, thus, measure timing and duration of incubation bouts and recesses. All VCR systems were programmed to record date, time, and frame number. I housed VCR systems in camouflaged cases and concealed them with burlap and vegetation under nearby shrub canopy.

I installed video systems ≥ 7 days following the onset of incubation to avoid researcher-induced nest abandonment (Renfrew and Ribic 2003) and video tapes and batteries were changed every 2-3 days. I sought to install cameras and VCRs during morning hours while grouse were thought to be away from nests (Schroeder et al. 1999). I did not install cameras during extreme weather conditions (i.e., snow, rain, or high temperatures) to prevent researcher-induced egg mortality, but once cameras were in place, I was able to record grouse behavior in all weather conditions. I camouflaged all cameras and other equipment to avoid predation biases (Herranz et al. 2002) by covering equipment with vegetation and camouflaged vinyl photography tape that visually matched the nesting sites.

Vegetation Measurements

I measured habitat characteristics 1-3 days following termination of nesting effort at nest bowls and within 50 m diameter areas centered on nests. I estimated total canopy cover (%) by establishing 4 orthogonal ground transects of 25 m beginning in a random direction and intersecting at the nest bowls. I measured all shrubs along each transect (cm) using the line-intercept technique (Canfield 1941) and, also, used this technique to

estimate sagebrush canopy cover (%). I established 20 sample points centered at random directions and distances from nests (range 0-25 m) to estimate understory visual obstruction (%) using a cover board (modified from Jones 1968) and biomass of forbs. The cover board consisted of 3 sides. Each side was 625 cm² consisting of 25 squares (25 cm²) in a checkerboard pattern. I placed the 3-sided board upright at each sample point in a random facing direction. I counted the number of squares at a 2 m distance from the board that were 0 to 50% visually obstructed. Measurements were taken at 0° (10 to 15 cm from ground) and approximately 45° (2 m from ground) for each side of the board. At nest bowls, I placed the board directly over the bowl and measured at 0°, 45° for each side. Then, I laid the board flat and measured at 90° (2-m directly over board). Values from each of the 3-sides of the board were averaged at each measurement height to estimate obstruction (%). To estimate forb biomass in the nesting area, I clipped all forbs within a 25 × 50 cm plot centered at each random sample point. Samples were labeled and stored in paper bags in the field and subsequently dried and weighed (g) in the lab. Plots with no grasses or forbs were noted in the field and calculated into averages for the nest areas.

Index of Raven Abundance

I conducted transect surveys ($n = 124$) to index raven abundance (Garton et al. 2005) (see Chapter 3) between 17 March-25 July during 2002-2005, encompassing the period of sage-grouse nesting. One survey was conducted every 3-7 days at each lek-route. Survey transects were a distance of 27 km during 2002-2003 and 20 km during 2004-2005. I established 25 and 33 survey points along each 20 and 27 km transect, respectively. At each survey point along transects, I used binoculars to count the number of ravens, flying

or perched, during a 3-min period. I avoided recounting individual ravens by separating survey points by an 800 m distance and by keeping track of ravens previously counted as I moved to the next survey point. Because transects differed in lengths, I indexed raven abundance by calculating the number of ravens observed per 10 km. Indices of raven abundance were calculated for each active grouse nest by averaging the local index values from surveys that were performed throughout the incubation period of each grouse. This calculation was performed to avoid pseudoreplication and account for variation in raven abundances through time, incubation initiation dates, and incubation periods.

Statistical Analyses

I calculated incubation constancy (% time attending nest during a 24-hour period) and duration of each incubation recess (min). Incubation constancy and mean recess duration during days of video failure and or camera installation were not included in calculations. Incubation constancy was arcsine-transformed and mean recess duration was log-transformed to meet assumptions of normality. I programmed video recorders to document date, time, and frame number in the field and subsequently observed tapes in the lab. I calculated the ordinal date of incubation (number of days elapsed from 1 January through date of incubation under consideration) and day of incubation (days elapsed between date of nest initiation and incubation date). I compared the mean duration of recesses initiated before noon (am) to recesses after noon (pm) using a 2 sample t-test (Minitab® Release 14). I calculated a coefficient of variation in recess duration of each grouse and used ANOVA (one-way, Minitab® Release 14) to measure differences in within-individual variation between 2 age classes (yearling breeder versus

adult breeder). I reduced the likelihood of pseudoreplication between individual grouse behavior by limiting my sample of nests to 1 per grouse. If grouse nested in >1 year or nested twice in the same year, I randomly selected 1 nest for that grouse. In *post hoc* analyses, I tested differences in nest understory visual obstruction between age classes using ANOVA (Minitab® Release 14).

I obtained sunrise, noon, and sunset data of each day (U. S. Navy Observatory, Astronomical Applications Department) of video recorded recesses and expressed recess times relative to sunrise, noon, and sunset. I calculated the number and duration of recesses and measured differences among age classes using a Pearson's Chi-Square Test (Test of Independence, Minitab® Release 14) as a *post hoc* analysis after observing the recess timing frequency. I defined recesses as crepuscular if they began within a 180 minute interval centered on sunrise or sunset. These intervals encompass twilight periods (defined as starting when the sun is 12° below horizon before sunrise and after sunset, respectively). All recesses 90 minutes after sunrise and 90 minutes prior to sunset were referred to as daylight hour recesses.

I acquired climate data (U. S. National Climate Data Center, Asheville, North Carolina) collected daily at 2 nearby weather stations, Gibbs Ranch (N 656486, E 4578188, zone 11) and Jackpot (N 708375, E 4607274, zone 11). I matched dates of precipitation, and maximum and minimum temperatures with dates of video-recorded incubation for each grouse nest. To investigate climate effects further, I divided daily maximum ambient temperature by precipitation (DMT/PRC).

Modeling incubation constancy and recess duration. I used an information-theoretic approach (Anderson and Burnham 2002) based on information described by

Kullback-Leibler (1951) and maximum likelihood (de Leeuw 1992) to develop predictive models of incubation constancy and recess duration using explanatory variables describing raven density, age of grouse, climate, timing of incubation, and microhabitat vegetation (Table 2.1). Explanatory variables in models were chosen based on effects that were reported in the literature of incubation rhythms of large-bodied, uniparental birds. I included quadratic functions describing influences of timing variables because these effects have been found in other large-bodied ground nesting birds (Yerkes 1998) and age interactions. I measured and compared results of 2 response variables, incubation constancy and recess duration, to understand the ecology of incubation rhythms because limitations in inferences may arise when considering only 1 response variable. However, factors explaining incubation constancy may reflect those of recess duration because daily recesses of sage-grouse are not frequent (Schroeder et al. 1999) and I considered all time spent off nests as recess from incubation. Nevertheless, I evaluated both responses to attempt to distinguish between factors that affect total daily time away from nest versus the duration of recesses.

To avoid multicollinearity, I performed a Pearson's product-moment correlation matrix using 16 variables and excluded 1 variable of any pairwise comparison that co-varied ($r \geq 0.65$). I used biological rationale and increased variance inflation factors to decide subjectively which variables should be excluded. Because all combinations of explanatory variables were biologically feasible, I developed candidate models ($n = 307$) for incubation constancy and recess duration based on all combinations of ≤ 3 variables. I chose no more than 3 variables in each model to allow all possible combinations without

developing more models than my sample size to prevent spurious results (Burnham and Anderson 1998).

I used Akaike's Information Criterion (Akaike 1973) corrected for small sample size (AIC_c) (Anderson et al. 2000) to compare models using Akaike's ranks (ΔAIC) (representing a unit of comparison between 2 models under consideration) and weights (ω_i) (representing the estimated probability that model i was the best among those considered) (Anderson and Burnham 2002) for each model. The importance of each explanatory variable was determined by separately by summing all weights for models in which the variable was present (parameter likelihood; Burnham and Anderson 1998). I reported the deviance statistics ($-2 \text{ Log Likelihood}$) of each model, which is a measure of lack of fit of the model to the data and number of estimated parameters (K).

I carried out model analyses in 2 steps to measure relative effects within groups of explanatory variables (e.g., temperature versus precipitation) and among all variables on incubation constancy and recess duration. In step 1, I compared models within each group. The purpose of these comparisons was to identify the most influential variables of those measured within each group without including effects of other groups of variables. I included a group of variables consisting of timing and age interactions to better understand variation in incubation constancy among ages of grouse as reported in the literature. In step 2, I compared models developed using variables derived from step 1. Variables in models with $\Delta AIC > 2$ were not considered in step 2 because they do not have substantial support from the data (Burnham and Anderson 1998). This procedure allowed me objectively to reduce the number of explanatory variables by choosing the most important variable(s) of each group. I carried out step 2 to understand the best-fit

models consisting of the most influential explanatory variables to better understand their relative importance on affecting incubation rhythms.

I performed data analyses using PROC MIXED procedures (SAS Institute Inc, Cary, N. C.) allowing me to model covariance for repeated-measures and implement random effects (Littell et al. 1998). Because not all models have the same fixed effects, full maximum likelihood (ML) estimation was used to compare information criterion (i.e., AIC) robustly among models. I treated year and study site as random effects for every model under consideration.

RESULTS

Patterns in Incubation Rhythms

Incubation constancy. I video recorded a total of 392 complete 24-hour days (2002, $n = 7$; 2003, $n = 123$; 2004, $n = 98$; 2005, $n = 164$) of incubation by 43 grouse (2002, $n = 2$; 2003, $n = 9$; 2004, $n = 14$; 2005, $n = 18$). Sage-grouse incubation constancy was $96.1\% \pm 0.20$ (mean \pm standard error) (range 93.0-97.7%). Mean adult incubation constancy was $96.2\% \pm 0.19$ and yearling was $94.7\% \pm 0.38$.

Incubation recesses. I recorded 1,042 incubation recesses (2002, $n = 21$; 2003, $n = 332$; 2004, $n = 245$; 2005, $n = 445$) of 46 grouse (2002, $n = 2$; 2003, $n = 9$; 2004, $n = 15$; 2005, $n = 20$). Overall mean recess duration (min) was 26.5 ± 0.92 (range 14.1-43.9). Mean recess duration of adults was 24.9 ± 1.02 ($n = 667$) and yearling was 31.4 ± 1.30 ($n = 370$). The maximum time spent away from the nest during a single recess was 103 min by a yearling grouse. Duration of recesses that were initiated before noon (24.25 ± 0.96 min) were significantly shorter than after noon (28.80 ± 1.20 min) ($t_{81} = -2.89$, $P = 0.005$). I also found yearlings had greater within-individual variation (43.17 ± 7.02 min)

in recess duration than adults (29.61 ± 1.72 min) ($F_{1,42} = 5.61, P = 0.011$) using calculated coefficients of variation of each grouse.

Most incubation recesses (798/1,037, 77%) were crepuscular resulting in a bimodal, 24-hour recess distribution (Figure 2.1). I did not observe any nocturnal recesses in any year of the study. Using *post hoc* analyses, I detected a difference in timing of recess between age classes ($\chi_1^2 = 13.33, P = <0.001$). Adult recesses were more often crepuscular (537/667, 81.0%) than yearling recesses (261/370, 70.5%). Also, adults recessed during twilight before sunrise or after sunset (330/667, 49.5%) more than yearlings (121/370, 32.7%) (Figure 2.1). Yearling recesses occurred primarily after sunrise and throughout the day and into the evening while adults usually recessed before sunrise and nearer to sunset. Grouse took an average of 2.21 ± 0.06 (mean \pm SE) recesses per day. Adults took fewer daily recesses (2.15 ± 0.04) than yearlings throughout the incubation period (3.01 ± 0.07) ($F_{1,40} = 5.33, P = 0.026$) (Figure 2.2).

Incubation Constancy Models

Step 1. —In comparing only models of incubation timing effects, incubation constancy was best described by ordinal date (quadratic) (Model 3, Table 2.2). I found that incubation constancy increased during earlier dates (116 to 126) and decreased during later dates (136 to 176) (Figure 2.3). When I considered interactions between age and timing, the top 2 models included an interaction between age and incubation day (quadratic) (Models 5 and 6, Table 2.2). This interaction and ordinal date (quadratic) were the most likely of any explanatory variable to explain the data (1.0 parameter likelihoods) (Table 2.4). Incubation constancy of yearlings was substantially different than adults throughout the incubation period (Figure 2.4). During the first half of the

incubation period, yearling incubation constancy increased from 93 to 95% (days 1 to 14) and substantially decreased during the second half of the period from 95 to 92% (days 15 to 27), while adult incubation constancy remained at approximately 96% throughout the incubation period.

When considering only microhabitat variables, the best-fit models included parameters of visual obstruction at nest and around nest (Model 9, Table 2.2). However, following parameter likelihood calculations, I found that visual obstruction at nests and in the area had a 61% probability of being the best-fit model. A competitive model was nest visual obstruction only (Model 10, Table 2.2). Model 9 was 1.6 times (ω_i/ω_j) more likely to be best for describing incubation constancy than model 10. Greater nest understory visual obstruction was directly related to an increase in incubation constancy (Figure 2.5). During 2004-2005, I modeled habitat effects on incubation constancy with 2 additional variables (canopy cover and dried forb biomass) and found that these 2 variables did not fit the data better than nest visual obstruction and 50 m visual obstruction (Table 2.5). Therefore, in step 2 I did not carry out separate analyses for data from these 2 years with the addition of these habitat variables because models that included the additional variables were not informative.

Step 2. —The overall best-fit model consisted of an interaction between age and incubation day (quadratic), ordinal date (quadratic), and nest visual obstruction (Model 11, Table 2.2). In ranking models, no others were $\leq 2 \Delta AIC$. The probability that this model was the best among those considered was 63% (ω_i). The second best-fit model consisted of raven abundance instead of nest visual obstruction (Model 12, Table 2.2). I found the mean index of raven abundance was 2.88 ± 0.28 ravens observed per 10 km

along transects. Model 11 was 3.4 times (ω_i/ω_j) more likely to be best for describing incubation constancy than model 12. When considering variables from all groups, the parameter likelihoods (relative importance of variable among those considered) were greatest for the interaction between age and incubation day (quadratic) (estimate, -0.0007 ± 0.0002) and ordinal date (quadratic) (estimate, -0.0008 ± 0.0001). Nest visual obstruction and indices of raven abundance had parameter likelihoods of 0.64 (estimate, 0.0050 ± 0.0019) and 0.18 (estimate, 0.0098 ± 0.005), respectively (Table 2.4). In *post hoc* analyses, I found that the percent of nest visual obstruction at yearling nests (82.81 ± 3.8) was numerically lower than adults (88.9 ± 2.1) but I failed to detect a significant difference ($F_{1,31} = 2.27, P = 0.142$).

Incubation Recess Models

Step 1 —Ordinal date (quadratic) and incubation day explained recess duration best (Model 3, Table 2.3), in comparing models of timing only variables. Ordinal date (quadratic) was in all models with $\leq 2 \Delta AIC_c$. During early ordinal dates (116-126) recesses were shorter and at later dates recess durations were greater (days 136-176). In evaluating age interactions, I found the best model consisted of day of incubation (quadratic) and ordinal date (quadratic) both interacting with age of grouse (Model 6, Table 2.3). Yearling grouse had relatively lengthy recess bouts early in incubation (days 1-15), shorter bouts mid-incubation (15-20), and lengthy bouts during late incubation (days 20-27), whereas adult recess duration did not change notably through incubation.

A model of maximum ambient temperature alone was 70% (ω_i) likely to be the best model and 2.5 times (ω_i/ω_j) more likely (Model 7, Table 2.3) to fit the data than a model with temperature and precipitation (Model 8, Table 2.3). Recess duration was

positively related to maximum temperature (Figure 2.6), meaning grouse spent longer bouts away from nests during days of increased temperature.

When considering only microhabitat variables. The best-fit model consisted of both visual obstruction parameters (model 9, Table 2.3). As with the incubation constancy models, the 2 additional habitat variables (i.e., canopy cover and dry biomass of forbs) measured during 2004-2005 were not informative in my modeling of recess duration (Table 2.5) and, thus, I did not carry out a separate modeling analysis of these 2 years. Nest visual obstruction was the only parameter that was substantiated by the data during 2004-2005. Although 50-m visual obstruction was not supported by the data during 2004-2005 (Table 2.5), I included this variable in step 2 because of importance when using an additional 2 years of data.

Step 2. —The overall best-fit model for recess duration consisted of an interaction between age and incubation day (quadratic), ordinal date (quadratic), and indices of raven abundance (Model 10, Table 2.2). In ranking models, no other models were $\leq 2 \Delta AIC$. The probability that this model was best for describing recess duration was 82% (ω_i). The effects of timing and age were described above. An increase in raven abundance was inversely related to duration of recesses (Figure 2.7). The second best-fit model consisted of maximum ambient temperature (Model 11, Table 2.2). Model 10 was 4.8 times (ω_i/ω_j) more likely than model 11 to explain recess duration. The parameter of an interaction between age and incubation day (quadratic) (estimate, 0.0021 ± 0.0005) and ordinal date (quadratic) (estimate, 0.0015 ± 0.0005) were substantiated the most by the data (parameter likelihood = 1.0). Parameter of raven abundance (estimate, $-0.0449 \pm$

0.0164) also had substantial support from the data in describing recess duration. (parameter likelihood = 0.82) (Table 2.4).

DISCUSSION

Around-the-clock video-monitoring of incubating sage-grouse revealed a strong, unequivocal pattern to sage-grouse incubation. Sage-grouse employed an unusually high level of incubation constancy (96.1%), similar to that of large waterfowl with female-only incubation and precocial young (Deeming 2002). For adult sage-grouse, incubation constancy typically was interrupted by only two, short, crepuscular recesses, 1 at dawn and 1 at dusk. Yearlings augmented this bimodal recess pattern with additional, irregular daytime recesses and taking slightly longer recesses than adults, on average. Yearlings may have less endogenous reserves than adults and thus may need more time to obtain supplemental nutrients, especially later in the incubation period. Both age classes exhibit 100% incubation constancy at night. My modeling of factors associated with variation in sage-grouse incubation behavior was an effort to explain time away from the nest in a system characterized by very high nest attendance.

Sage-grouse incubation constancy of 96% was greater than the reported average of 76.8% for 319 species in which incubation is performed exclusively by females (Deeming 2002), and also was greater than the average of 89.4% for 61 uniparental females of precocial species (i.e., Anseriformes, Galliformes, and Charadriiformes) (Deeming 2002). Because sage-grouse are a large-bodied species (1.2-3.2 kg, Schroeder et al. 1999), they may store more endogenous reserves than small-bodied species allowing more time for incubation than self-maintenance activities (Carter and Montgomerie 1985, Deeming 2002). Increasing incubation constancy may increase the

probability of nest success by thwarting predator detection through prolonged camouflaging of eggs (Erikstad 1986) as well by providing for the thermal requirements of eggs.

The decrease in incubation constancy and increase in recess duration at later dates of the nesting period likely results from constraints that sage-grouse encounter during incubation. Incubating female birds face energetic trade-offs between regulating egg temperature at the nest and negative energy balance due to reduced foraging (Deeming 2002). Energy requirements for incubation are partly satisfied by lipid and protein reserves stored during a pre-laying period. As incubation advances, sage-grouse may experience depleted nutrient reserves and are forced to rely more on foraging. Information is needed on forage activity during recess for sage-grouse, but white-tailed ptarmigan (*Lagopus leucura*) forage vigorously during incubation recess (Wiebe and Martin 1997).

If this energetic hypothesis is correct, then adults appear to be less constrained energetically than yearlings based on strong effects of age and timing interactions on incubation constancy and recess duration through the incubation period. In particular, yearling incubation constancy decreased and recess duration increased during late incubation (days 20-30). Adult sage-grouse likely store more reserves for incubation than yearlings, as has been shown for willow grouse (*L. lagopus*) (Erikstad 1986). Yearlings may leave nests to forage for supplementary nutrition, thereby decreasing incubation constancy and increasing recess duration. Similarly, young female Canada geese (*Branta canadensis*) lose body mass toward the later stages of incubation, and increase foraging and reduce nest attentiveness compared to older geese (Murphy and Boag 1989).

Many studies have reported incubation constancy of birds progressively decreasing as the incubation period progresses (Afton 1980, Brown and Fredrickson 1987, Yerks 1998). This pattern has been attributed variously to increased embryonic heat production (Drent 1970), decrease of parent endogenous nutrient reserves (Afton and Paulus 1992), increased ambient temperatures (Mallory and Weatherhead 1993), and increased recess frequency with decreased recess duration due to increased cooling rates of eggs in advanced stages of development (Turner 2002). If embryonic heat production, heat loss, or increases in ambient temperature were most important in explaining declines in constancy through the incubation period of sage-grouse, then yearlings and adults should have behaved similarly during later stages. However, the distinct difference between ages suggests that nutrient reserves limit incubation constancy and yearling grouse were leaving nests to forage.

Alternatively, nesting experience might have contributed to the differences I detected in incubation constancy and recess duration between ages. Average nest success at my site over 4 years was 51% (Coates unpubl. data), consistent with averages range-wide (Schroeder et al. 1999). It is likely that adult grouse that had nested previously had experienced depredation because approximately 79% of nest failure in prairie grouse is a result of depredation (Bergerud 1988). Birds with relatively greater predation rates show more behavioral plasticity in anti-predator strategies than birds with low rates leading to a reduction in predation (Conway and Martin 2000, Ghalambor and Martin 2000, Martin 2002). Perhaps, adult sage-grouse exhibited greater incubation constancy and longer recess durations to help conceal eggs from predators while naïve yearlings employed a more risky incubation strategy.

Incubation constancy is inversely related to the length of the incubation period (Deeming and Ferguson 1991). Therefore, the high incubation constancy that I observed, especially in adults, may have multiple anti-predator advantages. For example, this behavior results in shorter incubation periods which almost certainly decrease the chance of predators finding nests while simultaneously lengthening periods of egg camouflaging, which were suggested elsewhere for other birds (Marzluff 1985, Thompson and Raveling 1987, Wiebe and Martin 1997). In this sense, adults likely can speed embryonic growth to avoid predation by increasing contact incubation because they are more capable of meeting metabolic requirements (Wiebe and Martin 1997). These scenarios would indicate that some portion of incubation behavior is learned and perhaps grouse with failed nests had associated reduced nest attentiveness with depredation. Selection should favor high incubation constancy related to parental energetics and favor the learned portion of incubation constancy. Both processes favor the expression of greater incubation constancy in adults relative to yearlings.

Influences of grouse experience and body condition are not mutually exclusive. Although incubation constancy was different between age classes during the early stage of incubation, recess duration was similar during this stage, which resulted in adults recessing less frequently than yearlings (Figure 2.2). Because nest predators cue on movements of birds to and from nests (Deeming 2002), then perhaps the differences in recess frequency that I observed in the early stages represent differences in incubation experience between grouse rather than differences in body condition with adults presumably having more experience than yearlings. During later stages of incubation, yearling incubation constancy decreased and yearling recesses were longer than adults,

which most likely is a function of nutrient needs. Thus, differences in incubation experience and energetic constraints placed on yearlings may account for differences between ages during early and later stages of incubation, respectively.

A likely explanation for the bimodal pattern of daily recess timing by grouse is to prevent nest detection and depredation by visually-cued predators, an observation reported by others regarding timing of grouse incubation recesses (Angelstam 1984, Erikstad 1986). Average recess duration was 26.5 minutes and most recess initiation occurred at sunset or 30 min before sunrise. Videographic images (Chapter 1) revealed that ravens preyed on sage-grouse nests primarily in morning hours immediately following sunrise (0630 to 0930) and immediately preceding sunset (1800 to 1900) (Figure 2.1). Ravens are diurnal egg predators that rely primarily on visual cues (Boarman and Heinrich 1999) and were the most frequent sage-grouse nest predator in this study (Chapter 1). Predation by ravens has been suggested as a factor limiting sage-grouse production (Batterson and Morse 1948, Autenrieth 1981).

If grouse use light levels to cue recess timing as a behavior to avoid predators, then I might expect to observe the peak frequencies of recesses at low light levels. Indeed, the greatest parental absence from nests occurred between approximately 0-30 min before sunrise and 0-45 min after sunset (i.e., twilight period) resulting in similar illumination among recess times (Figure 2.1). Through morning twilight, females exhibited a sharp increase in recess initiation until approximately 30 min before sunrise when frequency of recess initiation declined. Females taking an average recess were returning to nests just prior to sunrise. During evening, I observed a sharp reduction in

recess initiation 30 min after sunset resulting in most females returning to nests just prior to dark.

Most females recessed at times that allowed them to return to nests at low light. This behavior may help females avoid being detected by visually-cued predators in light and also avoided nocturnal predators in dark that may be difficult to evade. Perhaps crepuscular recesses, so characteristic of the female grouse in my study, allowed grouse sufficient light to carry out off-nest self-maintenance activities while reducing probability of detection by predators. Furthermore, nearly all raven depredations occurred shortly after sunrise and before sunset during relatively high light conditions (Figure 2.1), supporting a predator avoidance hypothesis for twilight recesses. Observations of grouse returning to nests under low light conditions and timing of raven depredations suggests that the process of a female returning to and settling on a nest makes the nest vulnerable to detection, especially by visually-cued nest predators like ravens.

Although it is possible that ravens can cue on human movements to and from nests during video maintenance activities and depredate nests, this was not a concern here because I did not approach nests within approximately 200 m if ravens were seen in areas. Furthermore, images of video-recorded depredations revealed >4 hour time elapsed from my visitations to VCRs and most depredations occurred 1-2 days following my visitations at nests.

Indices of raven abundance were important in explaining recess duration. Recess duration declined with increased raven abundance (see figure 2.7). Longer recess bouts may increase the chance of nests located by visually-cued predators because extended recesses result in off-nest parental activities extending into high light conditions. Female

sage-grouse are cryptically colored (Schroeder et al. 1999) and demonstrate passive behavior (i.e., motionlessness) to protect eggs (Coates, unpubl. data). During daylight, if predators cue on exposed eggs or foraging female grouse and follow females back to their nests, then greater time away from nests may increase the likelihood of detection and subsequent depredation. Parental activity near nests in daylight has been reported to be positively related to nest predation in passerines, which was attributed to detection by visually-cued predators (Martin and Menge 2000). Here, it appeared that females traded time to forage for time to remain on nests as raven abundances increased, which was likely to be an anti-predator strategy.

Alternatively, the bimodal recess pattern I observed might be a function of crop capacity following foraging bouts, something suggested for white-tailed ptarmigan in Colorado (Wiebe and Martin 1997). Specifically, grouse may fast during dark hours. Then, when enough illumination is available, grouse forage due to hunger until their crops are full, which takes approximately 20-30 min. Grouse forage again during evening but may choose the latest possible time to allow enough food to sustain them for the night. This hypothesis, however, does not adequately explain the differences I saw in daylight recesses between adults and yearlings.

Differences in incubation recess patterns between ages are more complicated. Egg cooling rate is negatively correlated to ambient temperature and cooling rates are highest before sunrise during morning meaning that high cooling rate may limit recess duration in grouse (Naylor et al. 1988). Recess duration, in turn, can be viewed as a trade-off between embryonic development and parental self-maintenance (Hainsworth and Voss 2002). Egg cooling slows embryonic development leading to longer incubation periods

(Deeming and Ferguson 1991) and temperatures below physiological zero stop embryonic development (Gill 2006). Therefore, females usually incubate when egg cooling rates are high to prevent extended incubation periods and avoid embryo stress (Hainsworth and Voss 2002). Also, reducing recesses when egg cooling rates are high may minimize energy loss by avoiding the need for egg rewarming (Hainsworth and Voss 2002).

If yearlings are energetically constrained and need more recess time to meet metabolic requirements, then I would expect to observe yearlings recessing during times when egg cooling rates are reduced to allow more time to forage in a single bout. Indeed, yearlings recessed during twilight periods less often than adults and more often during daylight periods when eggs cool at slower rates, which is consistent with observations reported of other grouse (Erikstad 1986). It may be difficult for yearlings to acquire enough food during times of high cooling rates to meet their metabolic needs (Naylor et al. 1988). The additional yearling recesses, at times when the nest microclimate was more favorable for recess (e.g., daylight) explains differences in recess frequency between age classes. The effect of prevailing conditions on egg cooling rates can make adjusting duration of recess rather than recess frequency advantageous because of the high energetic cost associated with rewarming cool eggs (Hainsworth and Voss 2002).

One explanation for the positive relationship between nest visual obstruction and incubation constancy is that increased understory provides thermal insulation to incubating grouse reducing evaporative and convective heat loss saving energy and resulting in less time needed to obtain food and water. Nest sites often are selected by birds to control the thermal environment (Ar and Sidis 2002). Birds experience

substantial energetic savings with insulated nests compared to exposed nests (Calder 1973, White and Kinney 1974). Because incubating grouse trade time of incubation with time to acquire nutrients and water to meet energetic demands, nest microhabitat that provides energy savings would allow grouse more time to incubate. Conversely, when parents are at recess, insulation would tend to favor increased recess duration by decreasing egg cooling rates. For example, insulation may influence egg-cooling rates by disrupting airflow across the nest and decreasing heat exchange through convection, as well as by reducing conduction and radiation (Hansell and Deeming 2002). Increased insulation when ambient temperature is lower than egg temperature leads to decreased incubation constancy, which has been reported for small birds (Ricklefs 1974). However, considering sage-grouse spend over 96% of the day incubating and effects of nest insulation is less important to eggs when birds are present (Ar and Sidis 2002), nest understory visual obstruction appears to have stronger effects on microclimate of parents than the microclimate of eggs resulting in parental energy-savings and decreased time foraging.

Maximum ambient temperature may partially influence egg microclimate when the female is absent, which would explain the effect on duration of recess bouts. In that, nest microclimate affects cooling rates when females are not incubating eggs (Ar and Sidis 2002) and is influenced by multiple factors, including insulation around nest bowls, precipitation, exposure to ambient air, and ambient temperature (Carey 2002), that collectively influence heat transfer from egg to the environment. The importance of ambient temperature on incubation constancy has been equivocal. Some have found ambient temperature to be a key factor (Carey 1980). My study and others (Erikstad

1986, Wiebe and Martin 1997) did not detect it as important. The effects of ambient temperature on recess duration may more accurately reflect the effects of egg cooling rates on incubation rhythms (Naylor et al. 1988).

Importantly, vegetation at nest may contribute to water availability for incubating grouse. Incubation is an active, not passive, process and in the exchange of heat from parent to eggs, birds with relatively long incubation sessions have high respiratory water loss and skin evaporation (Ar and Sidis 2002). Respiration and evaporation unavoidably result in a need for water intake for self-maintenance and for egg thermoregulation, especially in cold deserts (Carey 2002) like the Great Basin. As with other birds (Carey 2002), grouse may reduce dehydration through obtaining water in foods such as invertebrates and forbs, as well as from surface water (Carey 2002). Additionally, incubating grouse may ingest water that accumulates on vegetation, such as frost, dew and precipitation. Video images often showed female sage-grouse sporadically pecking at vegetation around the nest without consuming the vegetation (Coates, unpubl.). My impression was that they were gathering water droplets and frost. The need to obtain water may force birds away from nests to maintain water balance (Dawson and O'Conner 1996). If true, vegetation at nests may provide grouse with water without leaving nests. In this way, nest understory could increase constancy through water availability.

Other metabolic explanations related to nest visual obstruction are also possible. In particular, nest understory visual obstruction may be a proxy for food availability. Much of the understory vegetation is comprised of forbs and these have been shown to be important sources of calcium, phosphorous, and crude protein during the pre-laying period for sage-grouse (Barnett and Crawford 1994). Because food and water is needed to

maintain embryonic development through contact incubation, recess duration appears to be a function of hunger and thirst (Deeming 2002). If sage-grouse spend most of their recess foraging as shown in white-tailed ptarmigan (Wiebe and Martin 1997), and food is plentiful and readily consumed near nest, then minimum time to forage is required to maintain body reserves as suggested in passerines (Drent et al. 1985). Perhaps, grouse that rely on exogenous nutrients throughout incubation increase recess frequency rather than recess duration. My findings support this in that yearlings, which took more recesses than adults, may need more time off the nest to obtain supplemental forage but are limited in recess length by egg cooling rates (Naylor et al. 1988) and compensate through additional recess when ambient temperatures are more favorable.

When evaluating the hypothesis of food availability during 2004-2005, I found that the evidence for forb biomass influencing incubation constancy was not as strong as evidence supporting overall nest understory visual obstruction as a factor influencing incubation constancy. However, forb biomass may not have represented the total food availability that may be represented by understory vegetation. Unfortunately, complete information on diet and dietary selection during the incubation period of sage-grouse is lacking and females also are known to feed on insects (Schroeder et al. 1999), which may be more abundant in grass dominated environments, and sagebrush (Rosentreter 2004).

In a *post hoc* analysis, I found suggestive evidence that adult sage-grouse chose nest sites that were comprised of greater nest visual obstruction than yearlings. Although stored nutrients prior to nesting substantiates differences in incubation constancy between ages (Erikstad 1986), perhaps more experienced sage-grouse selected sites with better nest visual obstruction to provide a more favorable nest microclimate and increased water

availability resulting in parental energy-savings and less time away from nests. Also, more experienced grouse may choose greater visual obstruction to obstruct visual and olfactory cues used by predators to detect nests and movements of grouse. Although I did not find the difference in nest visual obstruction selection between age classes to be statistically significant, this merits further study for 3 reasons: (1) Age classes may not indicate fully grouse nesting experience in that some adults may not have nested previously. (2) Here, sample size for yearling nests was much lower than sample size for adults, increasing a probability of statistical error (Type II) (Gotelli and Ellison 2004). (3) I found higher variation in yearling nest visual obstruction possibly due to differences in habitat availability at larger scales. For example, yearlings may select better quality habitat by chance in large breeding areas where more high quality habitat is available. Therefore, detecting differences in habitat selection between age classes may be more likely when relatively few high quality nest sites are available. Indeed, reported differences in nest habitat between yearlings and adult sage-grouse were reported in a study area with relatively less high habitat quality (Lowe 2006).

Populations of sage-grouse are declining severely within their range partially as a result of loss, degradation, and fragmentation of nesting habitat (Connelly and Braun 1997). The positive relationship between nesting visual obstruction and nest success of sage-grouse reported in literature (Connelly et al. 1991, Gregg et al. 1994, Holloran et al. 2005) may be explained by successful incubation behavior as a result of greater incubation constancy and recessing during twilight periods. Because I found sage-grouse incubation constancy to be high, relative to other species (Deeming 2002), and grouse appeared to rely primarily on passive nest defense (Coates, unpubl. data), loss of visual

obstruction appears to have detrimental impacts on successful nesting behavior by reducing attentiveness and possibly increasing exposure. This may be particularly important for yearlings which are constrained energetically (Erikstad 1986), inexperienced in incubation, and may select poorer nesting habitat in terms of microclimates and food and water availability.

Reduced incubation constancy because of nest visual obstruction loss may have a compounding effect. For example, more off-nest time would extend recesses into high light conditions, when grouse appear more vulnerable to visually-cued predators like ravens. Without visual obstruction at nests, which understory provides, visually-cued predators may have less difficulty in locating exposed grouse nests and cueing on movement by parents to and from nest sites.

Also, overabundance of visually-cued, generalist predators may lead to substantial energetic constraints placed on incubating grouse, especially in areas of reduced nesting understory because incubation constancy increases with increased predator abundance. For example, human-altered landscapes provide resource subsidies to generalist predators, like ravens, that frequently lead to increased reproduction and survival (Boarman 1993, 2003, Webb et al. 2004). Ravens may have hyperpredation effects (Courchamp et al. 2000) on sage-grouse as thought for other prey, such as desert tortoise (Kristan and Boarman 2003). In this case, hyperpredation process may occur when sage-grouse experiences an increase in predation pressure caused by a predator species like ravens that is sustained by abundant, alternative resource subsidies. Because increased raven abundance in this study resulted in decreased recess duration, ravens may significantly disrupt successful incubation by forcing female sage-grouse to their

energetic limits, especially in areas with poor understory and unnaturally high raven numbers. Studies that examine this relationship in relation to nest predation and nest abandonment may prove to be informative.

Table 2.1. Explanatory variables used in mixed model analyses of incubation constancy and recess duration of greater sage-grouse in northeastern Nevada during 2002-2005.

| Variable | Description | <i>n</i> ^a | mean | ±SE |
|--|--|-----------------------|------|------|
| Predator variable | | | | |
| RVN | Index of raven abundance (10 km ²) calculated for each active sage-grouse nest | 37 | 2.88 | 0.28 |
| Age variable | | | | |
| AGE | Age of grouse (< or >1 year of age) | 43 ^b | | |
| Timing variables | | | | |
| INC | Day of incubation (date of year minus incubation initiation date) | 43 | | |
| INC ² | Quadratic function of INC | | | |
| ORD | Ordinal date (days elapsed between 01 Jan and incubation date) | 43 | | |
| ORD ² | Quadratic function of ORD | | | |
| Climate variables | | | | |
| PRC | Daily precipitation (cm) | 43 | 7.2 | 1.04 |
| DMT | Daily maximum temperature (C°) | 43 | 19.9 | 0.32 |
| DMT/PRC | Climate effect (daily maximum temperature divided by daily precipitation) | 43 | 16.4 | 0.52 |
| Nesting habitat variables ^c | | | | |
| NVO | Nest visual understory obstruction (% obstructive cover using checkered board at zero and 45° angle) | 37 | 76.1 | 0.82 |
| 50VO | 50 m visual understory obstruction (% cover checkered board at zero and 45° angle of 16 plots within 25-m of nest bowls) | 37 | 56.5 | 0.81 |
| MFB | Mean forb biomass (average dry weight in grams of 16 micro-plots within 50 m of each other at nest areas) | 22 | 1.9 | 0.09 |
| CC | Shrub canopy cover (% cover along four, 25-m line transects from nest bowls) | 22 | 40.5 | 1.08 |

^a Number of grouse for each variable used in repeated-measures analyses.

^b Number of yearlings (*n* = 11) and adults (*n* = 32) used in analyses.

^c The variables MFB and CC were added in 2004-2005 and analyzed separately against most important variables from 2002-2005 data.

Table 2.2. Mixed models explaining incubation constancy of greater sage-grouse in relation to predators, age of grouse, timing of incubation, climate, and microhabitat variables in northeastern Nevada, during 2002-2005.

| Model | Explanatory variables ^a | K ^b | -2LL ^c | L R ² ^d | Δ AIC _c ^e | ω_i ^f |
|--|---|----------------|-------------------|-------------------------------|--|-------------------------|
| Step 1 ^g | | | | | | |
| Predator effect (1 model) | | | | | | |
| 1 | RVN | 4 | 234.7 | 0.25 | | |
| Age effect (1 model) | | | | | | |
| 2 | AGE | 4 | 202.5 | 0.33 | | |
| Timing effect (8 models) | | | | | | |
| 3 | ORD ² | 5 | 210.3 | 0.31 | 0.0 | 0.53 |
| 4 | ORD ² , INC | 6 | 209.1 | 0.31 | 0.9 | 0.34 |
| Age and timing interactions (6 models) | | | | | | |
| 5 | AGE*INC ² , ORD ² | 9 | 136.1 | 0.47 | 0.0 | 0.71 |
| 6 | AGE*INC ² , AGE*ORD ² | 10 | 135.7 | 0.47 | 1.8 | 0.29 |
| Climate effects (3 models) | | | | | | |
| 7 | DMT | 4 | 235.1 | 0.25 | 0.0 | 0.69 |
| 8 | PRC | 4 | 236.6 | 0.24 | 1.6 | 0.31 |
| Vegetation effects (3 models) | | | | | | |
| 9 | NVO, 50VO | 5 | 228.1 | 0.27 | 0.0 | 0.61 |
| 10 | NVO | 4 | 230.8 | 0.25 | 1.0 | 0.37 |
| Step 2 ^h | | | | | | |
| Three best-fit models (45 models) | | | | | | |
| 11 | AGE*INC ² , ORD ² , NVO | 10 | 130.3 | 0.48 | 0.0 | 0.63 |
| 12 | AGE*INC ² , ORD ² , RVN | 10 | 132.8 | 0.47 | 2.5 | 0.18 |
| 13 | AGE*INC ² , ORD ² | 9 | 136.1 | 0.47 | 3.6 | 0.10 |

^a Main effects were included in models with polynomial terms and higher-order interactions.

^b Number of parameters estimated in model (Anderson and Burnham 2002).

^c -2 Log-likelihood

^d R² based on likelihood-ratio test, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where LogL_m and LogL_o are log-likelihood of models of interest and intercept, respectively, and *n* is number of observations (Magee 1990).

^e Δ AIC represents difference between model of interest and best-fit model of all others considered.

^f Akaike's ω_i represents the probability that model is best among those considered (Anderson et al. 2000).

^g Step 1 compares only models within groups of related variables (e. g., timing effects compares models 3 and 4). Models with Δ AIC >2 are not shown.

^h Step 2 evaluates the best overall model using the best-fit variables from all groups (step 1). Best-fit variables were chosen based on variables in models with Δ AIC \leq 2 because these models had substantial support from the data (Anderson and Burnham 1998).

Table 2.3. Mixed models explaining duration of recess of greater sage-grouse in relation to predators, age of grouse, timing of incubation, climate, and microhabitat variables in northeastern Nevada, during 2002-2005.

| Model | Explanatory variables ^a | K ^b | -2LL ^c | L R ² ^d | Δ AIC _c ^e | ω_i ^f |
|---|---|----------------|-------------------|-------------------------------|--|-------------------------|
| Step 1 ^g | | | | | | |
| Predator effect (1 model) | | | | | | |
| 1 | RVN | 4 | 695.6 | 0.30 | | |
| Age effect (1 model) | | | | | | |
| 2 | AGE | 4 | 701.2 | 0.28 | | |
| Timing effect (8 models evaluated) | | | | | | |
| 3 | ORD ² , INC | 6 | 684.1 | 0.33 | 0.0 | 0.55 |
| 4 | ORD ² , INC ² | 7 | 683.7 | 0.33 | 1.7 | 0.23 |
| 5 | ORD ² | 5 | 688.1 | 0.32 | 1.9 | 0.21 |
| Age and timing with interactions (6 models) | | | | | | |
| 6 | AGE*INC ² , AGE*ORD ² | 9 | 650.9 | 0.40 | 0.0 | 1.00 |
| Climate effects (3 models) | | | | | | |
| 7 | DMT | 4 | 700.1 | 0.29 | 0.0 | 0.70 |
| 8 | DMT, PRC | 4 | 699.8 | 0.29 | 1.8 | 0.28 |
| Vegetation effects (3 models) | | | | | | |
| 9 | NVO, 50VO | 4 | 687.2 | 0.32 | 0.0 | 0.96 |
| Step 2 ^h | | | | | | |
| Three best-fit models (45 models) | | | | | | |
| 10 | AGE*INC ² , ORD ² , RVN | 10 | 636.9 | 0.43 | 0.0 | 0.82 |
| 11 | AGE*INC ² , ORD ² , DMT | 10 | 640.1 | 0.42 | 3.2 | 0.17 |
| 12 | AGE*INC ² , ORD ² , NVO | 10 | 646.5 | 0.42 | 9.5 | 0.01 |

^{a-h} See table 2 footnotes.

Table 2.4. Relative importance of explanatory variables used to model incubation constancy and recess duration of greater sage grouse in northeastern Nevada during 2002-2005.

| Response Variable | Parameter | Estimate ^a | ±SE ^b | L R ² ^c | P L ^d |
|----------------------|----------------------|-----------------------|------------------|-------------------------------|------------------|
| Incubation constancy | AGE*INC ² | -0.0007 | 0.0002 | 0.35 | 1.00 |
| | ORD ² | -0.0008 | 0.0001 | 0.31 | 1.00 |
| | NVO | 0.0050 | 0.0019 | 0.26 | 0.64 |
| | RVN | 0.0098 | 0.0054 | 0.25 | 0.18 |
| Recess duration | AGE*INC ² | 0.0021 | 0.0005 | 0.32 | 1.00 |
| | ORD ² | 0.0015 | 0.0005 | 0.32 | 1.00 |
| | RVN | -0.0449 | 0.0164 | 0.30 | 0.82 |
| | DMT | 0.0291 | 0.0088 | 0.29 | 0.17 |

^a Averaged parameter estimate across all models and corrected using Akaike's weights (ω_i).

^b Averaged standard error across all models and corrected using Akaike's weights (ω_i).

^c Likelihood R²-value is based on likelihood-ratio test of the variable under consideration alone, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where $\text{Log}L_m$ is log-likelihood of the single-variable model, $\text{Log}L_o$ is intercept-only model, and n is number of observations (Magee 1990).

^d Parameter likelihoods were sums of model weights for models in which the tested variable was present (Burnham and Anderson 1998). Parameter likelihood indicates relative importance of the explanatory variable in the presence ≤ 2 other variables. Values < 0.05 were not included in the table.

Table 2.5. Explanatory microhabitat variables used to model incubation constancy and recess duration in northeastern Nevada during 2004-2005.

| Response variable | Parameter variable | -2LL ^a | ΔAIC_c^b | L R ^{2c} | P L ^d |
|----------------------|--------------------|-------------------|------------------|-------------------|------------------|
| Incubation constancy | NVO | 136.8 | 0.0 | 0.21 | 1.00 |
| | 50VO | 153.2 | 18.6 | 0.14 | 0.39 |
| | CC | 154.0 | 19.4 | 0.13 | 0.25 |
| | MFB | 152.4 | 17.8 | 0.14 | 0.23 |
| Recess duration | NVO | 242.3 | 0.0 | 0.28 | 0.99 |
| | 50VO | 256.5 | 16.3 | 0.22 | 0.78 |
| | MFB | 260.0 | 19.8 | 0.21 | 0.48 |
| | CC | 260.9 | 20.7 | 0.20 | 0.16 |

^a -2 Log-likelihood

^b ΔAIC_c represents difference between model of interest and best-fit model of those considered.

^c Likelihood R²-value is based on likelihood-ratio test of the variable under consideration alone, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where $\text{Log}L_m$ is log-likelihood of the single-variable model, $\text{Log}L_o$ is intercept-only model, and n is number of observations (Magee 1990).

^d Parameter likelihoods are AIC_c weights summed across all models that contained that parameter from the pool of all models considered. Parameter likelihood indicates relative importance of the explanatory variable in the presence ≤ 2 other variables.

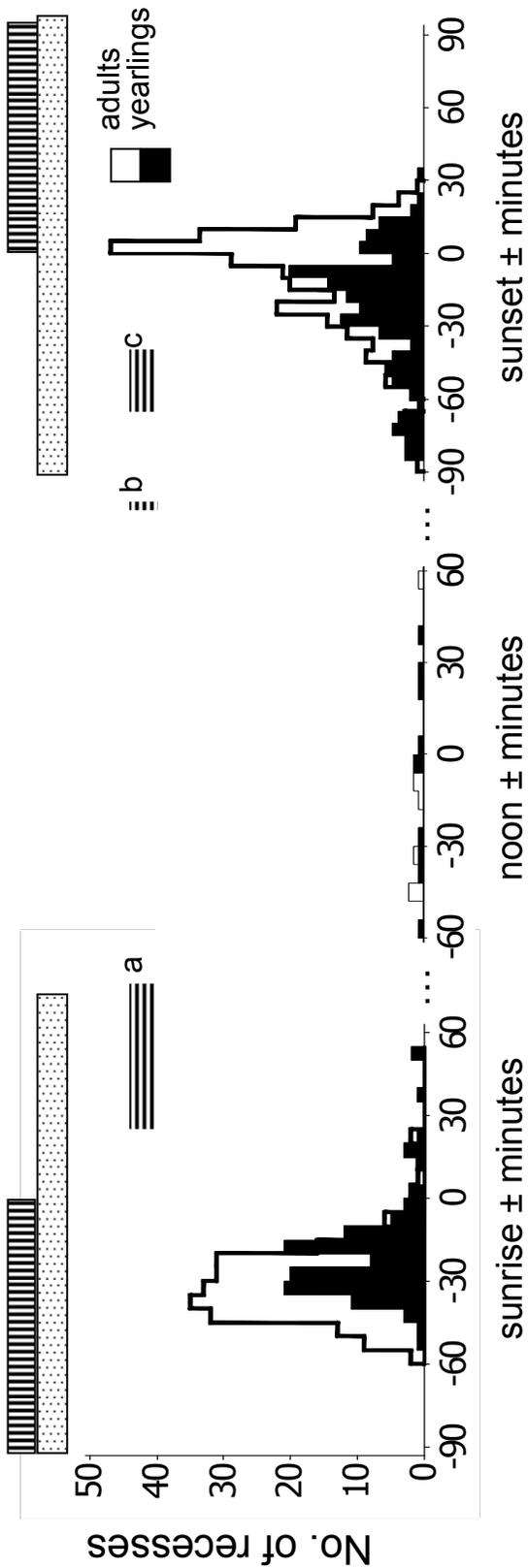


Figure 2.1. Bimodal distribution of incubation recesses ($n = 1,037$) in relation to sunset, noon, and sunrise by greater sage-grouse in northeastern Nevada during 2002-2005. Zero represents sunrise, noon, and sunset. Peak frequency of recesses of age classes pooled occurred 30 min before sunrise and at sunset. Vertical striped pattern (▨) represents civil and nautical twilight periods. Dotted pattern (⋯) represents crepuscular period. Horizontal striped pattern (≡) represent approximate timing of raven depredations, (a) 0622-0842 ($n = 6$), (b) 1359-1404 ($n = 1$), (c) 1754-1831, ($n = 2$), Raven depredations averaged 70.8 ± 24.8 min.

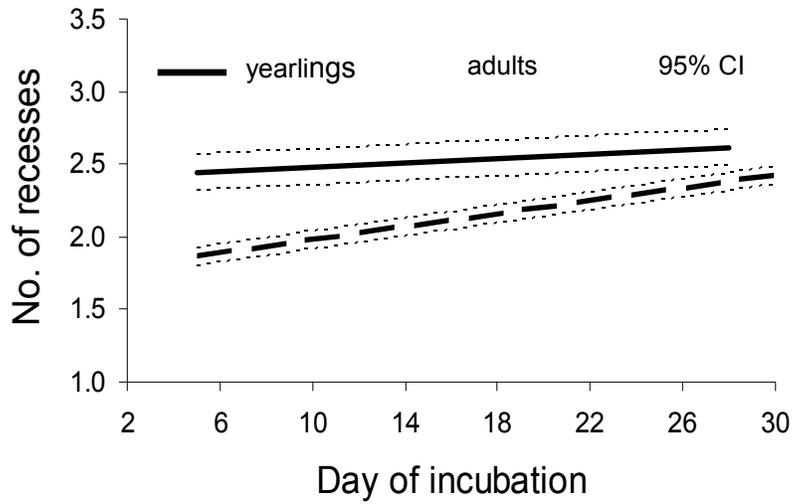


Figure 2.2. Differences in the number of recesses among yearlings ($n = 11$) and adults ($n = 32$) in relation to the day of incubation of greater sage-grouse in northeastern Nevada during 2002-2005. Trend lines were calculated from repeated-measures each day of incubation.

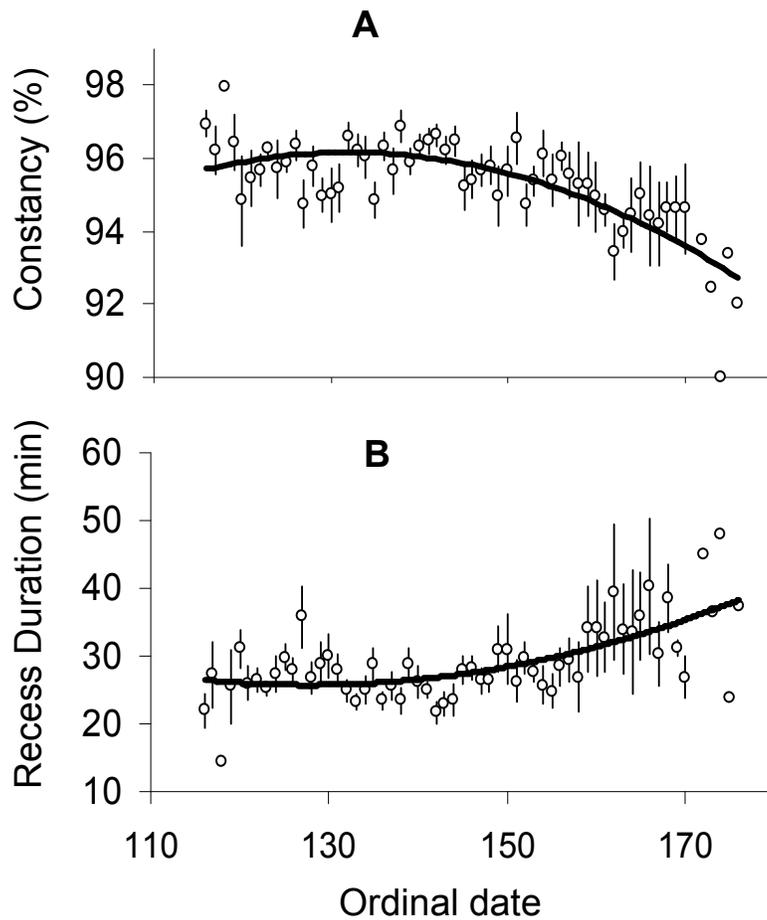


Figure 2.3. Ordinal date (days elapsed between 01 Jan and day of incubation) in relation to incubation constancy (%) and recess duration (min) of greater sage-grouse ($n = 43$) in northeastern Nevada during 2002-2005. Points along x-axis are repeated-measures and represent mean values at each date. Bars indicate standard errors.

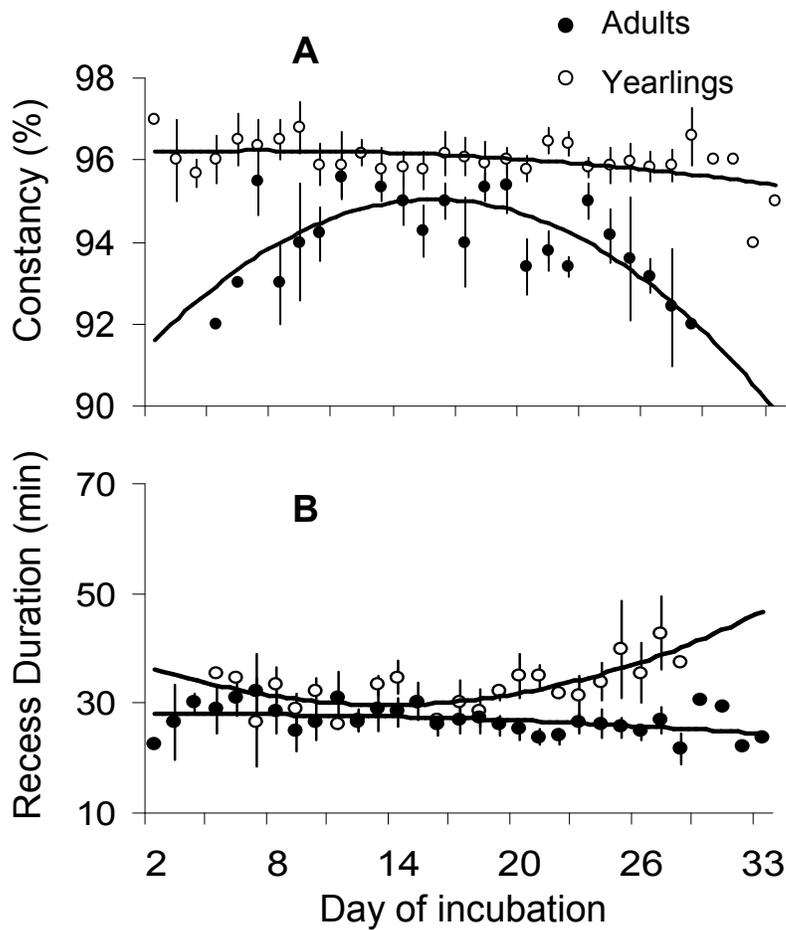


Figure 2.4. Interaction between age (yearling, $n = 11$; adult, $n = 32$) and day of incubation (quadratic) in relation to incubation constancy (%) and recess duration (min) of greater sage-grouse in northeastern Nevada during 2002-2005. Points along x-axis are repeated-measures and represent mean values at each day of incubation. Bars indicate standard errors.

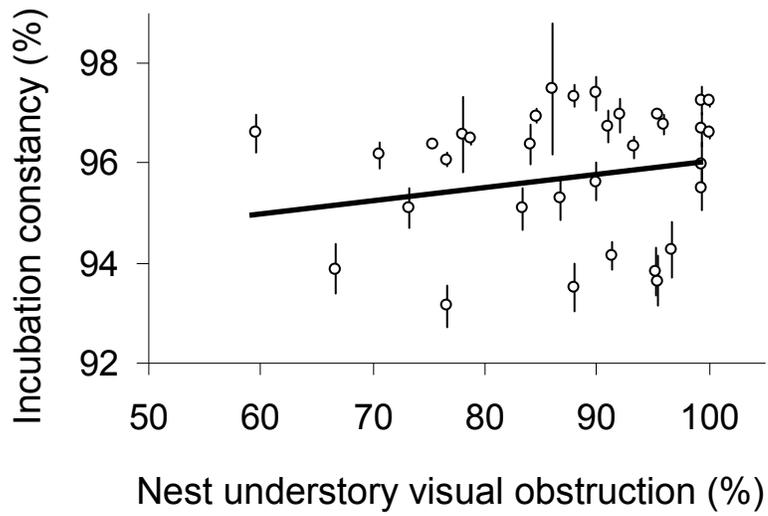


Figure 2.5. Visual obstruction at nest in relation to incubation constancy (%) of greater sage-grouse ($n = 37$) in northeastern Nevada during 2002-2005. Points and bars represent mean and standard error values, respectively.

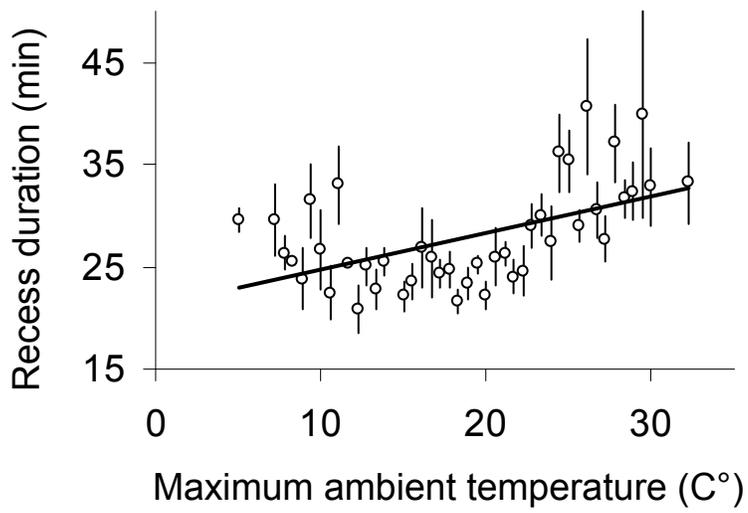


Figure 2.6. Recess duration (min) of greater sage-grouse ($n = 43$) in relation to maximum ambient temperature in northeastern Nevada during 2002-2005. Points and bars represent mean and standard error values, respectively.

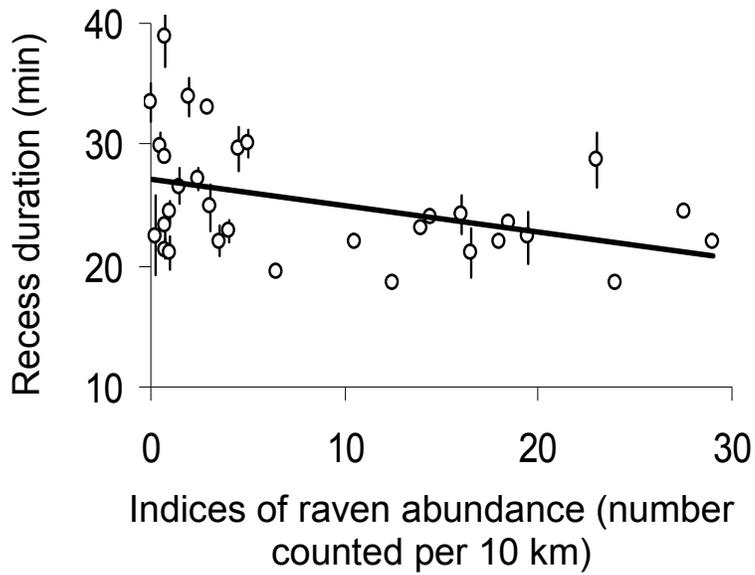


Figure 2.7. Indices of raven abundance (number counted per 10 km) in relation to recess duration (min) of greater sage-grouse ($n = 36$) in northeastern Nevada during 2002-2005. Points and bars represent mean and standard error values, respectively.

LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaksi, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.
- Ammann, G. A. 1944. Determining the age of pinnated and sharp-tailed grouse. *Journal of Wildlife Management* 8:170-171.
- Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66:912-918.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912-923.
- Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.
- Afton, A. D., and S. L. Paulus 1992. Incubation and brood care. Pages 62-108 *in* D. J. Batt, A. D. Afton, M. D. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Aldrich, T. W., and G. D. Raveling. 1983. Effects of experience and body weight on incubation behavior of Canada geese. *Auk* 100:670-679.
- Angelstam, P. 1984. Sexual and seasonal differences in mortality of black grouse *Tetrao tetrix* in boreal Sweden. *Auk* 100:670-679.
- Ar, A., and Y. Sidis. 2002. Nest microclimate during incubation. Pages 143-160 *in* D. C. Deeming, editor. *Avian incubation: behavior, environment, and evolution*. Oxford University Press Inc. New York. USA.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game, Federal Aid in Wildlife Restoration Project W-125-R and W-160-R, Wildlife Bulletin No. 9. Boise, Idaho.

- Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission, Oregon Fauna Service 1. Portland, Oregon. 29 pp.
- Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition on sage grouse hens in Oregon. *Journal of Range Management* 47:114-118.
- Bergerud, A. T. 1988. Population ecology of North American grouse. Pages 578-648 in A. T. Bergerud and M. W. Gratson, editors. *Adaptive strategies and population ecology of northern grouse*. University of Minnesota Press, Minneapolis.
- 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. Miller, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. *Conservation and resource management*. Pennsylvania Academy of Science, Philadelphia.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing Common Raven predation on desert tortoises. *Environmental Management* 32:205-217.
- Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). In A. Poole and F. Gill, editors. *The Birds of North America*, No. 476. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, D.C.
- Brown, P. W. and L. H. Fredrickson. 1987. Time budget and incubation behavior of breeding white-winged scoters. *Wilson Bulletin* 99:50-55.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Calder, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. *Ecology* 54:127-134.
- Caldwell, P. J., and G. W. Cornell. 1975. Incubation behavior and temperature of the mallard duck. *Auk* 92:706-731.
- Canfield, R. H. 1941. Applications of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388-394.
- Carey, C. 1980. The ecology of avian incubation. *Bioscience* 30: 819-824.

- Carey, C. 2002. Incubation in extreme environments. Pages 238-253 *in* D. C. Deeming, editor. Avian incubation: behavior, environment, and evolution. Oxford University Press Inc. New York. USA.
- Carter, R. V., and R. B. Montgomerie. 1985. The influence of weather on incubation scheduling of the white-rumped sandpiper (*Calidris fuscicollis*): a uniparental incubator in cold environment. *Behavior* 95:261-269.
- Clark, A. B., and D. S. Wilson. 1985. The onset of incubation in birds. *American Naturalist* 125:603-611.
- Coates, P. S., and D. J. Delehanty. 2006. Effects of capture date on nest-attempt rate of translocated sharp-tailed grouse *Tympanuchus phasianellus*. *Wildlife Biology* 12:277-283.
- Coates, P. S., J. O. Spencer, Jr., and D. J. Delehanty. In press. Efficacy of CPTH-treated egg baits for removing ravens. *Human Wildlife Conflicts*.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. *Journal of Wildlife Management* 55:521-524.
- Conway, C. J., and T. E. Martin. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* 54: 670-685.
- Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modeling the hyperpredation process. *Journal of Animal Ecology* 69:154-164.
- Dawson, W. R., and T. P. O'Conner. 1996. Energetic features of thermoregulatory responses. Pages 85-124 *in* C. Carey, editor. Avian Energetics and Nutritional Ecology. Chapman Hall, New York.
- Deeming, D. C. 2002. Behavior patterns during incubation. Pages 63-87 *in* D. C. Deeming, editor. Avian incubation: behavior, environment, and evolution. Oxford University Press Inc. New York. USA.

- Deeming, D. C., and M. W. J. Ferguson. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. Pages 147-171 *in* D. C. Deeming and M. W. J. Ferguson, editors. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge University Press, New York.
- de Leeuw, J. 1992. Introduction to Akaike (1973) information theory and an extension of the maximum likelihood principle. Pages 599-609 *in* S. Kotz and N. L. Johnson, editors. *Breakthroughs in statistics*. Volume 1. Springer-Verlag, London. United Kingdom.
- Drent, R. H. 1970. Functional aspects of incubation in the herring gull. *Behaviour Supplement* 17:1-132.
- Drent, R. H. 1975. Incubation. Pages 333-429 *in* D. S. Farner and J. R. King editors. *Avian Biology*, Volume 5. Academic Press, New York. USA.
- Drent, R. H., J. M. Tinbergen, and H. Biebach. 1985. Incubation in the starling: Resolution of the conflict between egg care and foraging. *Netherlands Journal of Zoology* 35:103-123.
- Erikstad, K. E. 1986. Relationship between weather, body condition, and incubation rhythm in willow grouse. *Cinclus* 9:7-12.
- Garton, E. O. J. T. Ratti, and J. H. Giudice. 2005. Research and experimental design. Pages 43-71 *in* C. E. Braun, editor. *Techniques for wildlife investigations and management*. Sixth Edition. The Wildlife Society. Bethesda, Maryland.
- Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Animal Behavior* 60:263-267.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- Gill, F. B. 2006. *Ornithology*. Edition 3. W. H. Freeman and Co., New York. USA. 720 pp.

- Gotelli, N. J., and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Inc., Sunderland. 492 pp.
- 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.
- Hainsworth, F. R., and M. A. Voss. 2002. Intermittent incubation: predictions and tests for time and heat allocations. Pages 223-237 *in* D. C. Deeming, editor. *Avian incubation: behavior, environment, and evolution*. Oxford University Press Inc. New York. USA.
- Hansell, M. H., and D. C. Deeming. 2002. Location, structure and function of incubation sites. Pages 8-87 *in* D. C. Deeming, editor. *Avian incubation: behavior, environment, and evolution*. Oxford University Press Inc. New York. USA.
- Herranz, J., M. Yanes, and F. Suárez. 2002. Does photo monitoring affect nest depredation? *Journal of Field Ornithology* 73:97-101.
- Holloran, M. J., B. J. Heath, A. J. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal Wildlife Management* 69:638-649.
- Jones, R. E. 1968. A board to measure cover used by prairie grouse. *Journal of Wildlife Management* 32:28-31.
- Kristan, W. B., and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84:2432-2443.
- Kullback, S., and R. A. Leibler. 1951. On information and sufficiency. *Annals of Mathematical Statistics* 22:79-86.
- Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. *Journal of Animal Science* 76:1216-1231.
- Lowe, B. S. 2006. Greater sage-grouse use of three-tip sagebrush and seeded sagebrush-steppe. Thesis, Idaho State University, Pocatello.

- Magee, L. 1990. R^2 measures based on Wald and likelihood ratio joint significance tests. *American Statistician* 44:250-253.
- Mallory, M. L., and P. J. Weatherhead. 1993. Incubation rhythms and mass loss of common goldeneyes. *Condor* 95:849-859.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65:101-127.
- Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London Series B* 269:309-316.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society. Series B, Biological Sciences* 267:2287-2293.
- Marzluff, J. M. 1985. Behavior at a pinyon jay nest in response to predation. *Condor* 87:559-561.
- Murphy, A. J., and D. A. Boag. 1989. Body reserve and food use by incubating Canada geese. *Auk* 106:439-446.
- Naylor, B. J., K. J. Szuba, and J. F. Bendell. 1988. Nest cooling and recess duration of incubating spruce grouse. *Condor* 90:489-492.
- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71-87.
- Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *Auk* 120:371-383.
- Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152-297 *in* R. A. Paynter, Jr., editor. *Avian Energetics*. Nuttall Ornithological Club No. 15., Cambridge.
- Rosentreter, R. 2004. Sagebrush identification, ecology, and palatability, relative to sage-grouse. *USDA Forest Service Proceedings RMRS-P-000:1-14*.

- Schroeder, M. A., J. A. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In A. Poole and F. Gill, editors. The Birds of North America. No. 425. Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. B. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deirbert, S. C. Gardner, M. A. Hilliard, G. D. Kobridger, 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.
- Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707-716.
- Turner, J. S. 2002. Maintenance of egg temperature. Pages 119-142 in D. C. Deeming, editor. Avian incubation: behavior, environment, and evolution. Oxford University Press Inc. New York. USA.
- Webb, C. W., W. I. Boarman, and J. T. Rotenberry. 2004. Common raven juvenile survival in a human-augmented landscape. *Condor* 106:517-528.
- White, F. N. and J. L. Kinney. 1974. Interactions among behavior, environment, nest and eggs result in regulation of egg temperature. *Science* 189:107-115.
- Wiebe, K. L., and K. Martin. 1997. Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan *Lagopus leucurus*. *Wildlife Biology* 3:219-227.
- Yerkes, T. 1998. The influence of female age, body mass and ambient conditions on redhead incubation constancy. *Condor* 100:62-68.

CHAPTER 3:

EFFICACY OF CPTH-TREATED EGG BAITS FOR REMOVING COMMON RAVENS

ABSTRACT

Human-altered landscapes have provided resource subsidies for common ravens (*Corvus corax*) resulting in a substantial increase in raven abundance and distribution throughout the United States and Canada in the past 25 years. Ravens are effective predators of eggs and young of ground nesting birds. I tested the effectiveness of using chicken egg baits treated with CPTH (3-chloro-p-toluidine hydrochloride) to reduce raven numbers in an area where raven depredation appeared to be impacting sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) and greater sage-grouse (*Centrocercus urophasianus*) populations in Nevada during 2002-2005. I performed multiple raven surveys at a treatment site (raven removal) and 3 control sites (no raven removal) and used videography to identify predators and estimate egg bait consumption. I detected reductions in raven abundances over time at the treatment site during all years of this study and did not detect declines in raven abundances at control sites. Videographic observations of egg consumption indicated that the standard 1:2 ratio (1 raven removed per 2 eggs consumed) substantially overestimated raven take because non-target species (rodents) consumed some egg baits. The technique described here likely will be effective where lethal removal of ravens is the intended management action.

INTRODUCTION

Human-altered landscapes provide resource subsidies to common ravens (*Corvus corax*) that frequently lead to increased reproduction and survival (Boarman 1993, Boarman 2003, Webb et al. 2004). Ravens often use electrical transmission towers, highway overpasses and railroad trestles as nesting substrate (Boarman and Heinrich 1999), aiding reproduction in areas that lack natural nest sites. Ravens forage efficiently in agricultural fields (Engel and Young 1992a), sanitary landfills (Webb et al. 2004), lambing ranges (Larsen and Dietrich 1970), rangelands (Knight 1984), and linear rights-of-way (e.g., electric power transmission lines) (Knight and Kawashima 1993, Steenhof et al. 1993). Raven abundance has increased >200% in the past 40 years throughout North America (Sauer et al. 2004), and increased as much as 1500% since the 1960s in portions of the western United States (Boarman 1993, Sauer et al. 2004).

In the Great Basin, ravens feed opportunistically on eggs and young of many animals (Boarman and Heinrich 1999), including prairie grouse (Apa 1998, Schroeder et al. 1999, Schroeder and Baydack 2001, Coates, unpubl. data), and unnaturally high raven populations as a consequence of anthropogenic resource subsidies may cause “spillover predation” (Schneider 2001). Spillover predations occur when raven abundance increases due to resource subsidies and ravens move to and hunt for prey in adjacent landscapes causing unnaturally high predation rates (Kristan and Boarman 2003). Concern that subsidized increases in raven abundances are adversely affecting sensitive species is growing because ravens are effective predators of many threatened and endangered species (Boarman and Heinrich 1999).

Managers often rely on multiple methods to reduce raven predation including shooting, trapping, and poisoning ravens, as well as manipulating habitat (Boarman and Heinrich 1999). Even where long-term management programs (e.g., natural habitat restoration) are carried out, managers often include short-term lethal programs to reduce raven numbers. Toxic compounds are often a method of choice for lethal control because of advantages of reduced labor (Conover 2002) and applications designed to target specific species. The compound CPTH (3-chloro-p-toluidine hydrochloride), or DRC-1339, is the only legal toxicant currently registered by the U. S. Environmental Protection Agency (EPA) for raven population control (Larsen and Dietrich 1970, Spencer 2002). A lethal dose of CPTH causes irreversible kidney necrosis (DeCino et al. 1966) resulting in a period of listlessness followed by death within 24-72 hours of ingestion (Cunningham et al. 1979). Lethal dosages vary substantially among avian species and corvids are highly sensitive to CPTH effects ($LD_{50} = 5.6$ mg/kg; Larsen and Dietrich 1970). Other avian species found in shrubsteppe communities are also highly sensitive to CPTH, including red-winged blackbirds (*Agelaius phoeniceus*; $LD_{50} = 1.8$ to 3.2 mg/kg) and mourning doves (*Zenaidura macroura*; $LD_{50} = 5.6$ to 10.0 mg/kg) (DeCino et al. 1966).

To target ravens and other corvids, managers inject CPTH into chicken egg baits and place baits where they are likely to be encountered by ravens but not by non-target species that are also sensitive to CPTH effects from ingesting the compound (Spencer 2002). No cases of secondary poisoning by CPTH of raptors or mammals have been observed (Cunningham et al. 1979), most likely because of rapid degradation following ingestion coupled with relatively low CPTH sensitivity of species that would typically scavenge raven carcasses. CPTH has been used to reduce abundance of other birds where they are

judged to be pests including red-winged blackbirds (Blackwell et al. 2003), American magpies (*Pica hudsonia*) (Guarino and Schafer 1967), European starlings (*Sturnus vulgaris*) (Besser et al. 1967, Royall et al. 1967), American crows (*Corvus brachyrhynchos*) (Boyd and Hall 1987) and herring gulls (*Larus argentatus*) (Seamans and Belant 1999).

Many managers have had limited success in using CPTH in the field to remove ravens and other corvids (Spencer, pers. comm., USDA/Wildlife Service, Reno, NV), perhaps because published descriptions of application techniques and their efficacy are lacking or have not been previously developed. Managers typically estimate the number of ravens removed by interpolating from number of egg baits that disappear from bait stations, under the assumption that missing egg baits have been consumed by ravens (Spencer 2002). A common estimate is that 1 raven is removed from the population for every 2 missing egg baits at a station (i.e., 1:2 ratio) (Spencer 2002).

My objectives were to measure the efficacy of using systematically placed chicken eggs treated with CPTH to remove ravens. Raven removal was used to reduce predation during the breeding season of a small, reintroduced population of sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) and a natural population of greater sage-grouse (*Centrocercus urophasianus*) in northeastern Nevada during 2002-2005. Here, I describe the CPTH application technique and its effects on a raven population. I also used video surveillance to identify consumers of egg baits and to estimate the number of ravens removed from the population by quantifying consumed CPTH egg baits.

STUDY AREA

I conducted systematic raven removal and raven surveys on transects that overlap a treatment site of approximately 10,000 ha located on the east side of the Snake Mountains in northeastern Nevada, USA (N 0670859, E 4599749, zone 11, NAD 83) during the springs of 2002-2005. The study area was chosen by Nevada Department of Wildlife (NDOW) based on efforts to establish a reintroduced, nascent population of sharp-tailed grouse (Coates and Delehanty 2006). Nevada Department of Wildlife, in cooperation with United States Department of Agriculture, Animal Health Inspection Service, Wildlife Services (WS) chose to remove ravens because ravens were thought to be a primary predator of sharp-tailed grouse nests based on interpreting nest and egg remains following depredation during 1999-2001 (Coates, unpubl. data). Dominant plant communities were shrub-steppe at lower elevations and mountain shrub at higher elevations. A variety of other potential egg predators were found, including coyote (*Canus latrans*), striped skunk (*Mephitis mephitis*), American badger (*Taxidea taxus*), ground squirrels (*Spermophilus* spp.), American magpie, and American crow.

METHODS

Raven Surveys

I conducted transect surveys ($n = 64$; Table 3.1) (Garton et al. 2005) for ravens every 3-7 days at the treatment site between late-March and late-June during 2002-2005, which coincided with the periods of egg bait treatment and sage-grouse nesting. During 2004 and 2005, I conducted raven surveys ($n = 60$) every 3-7 days at 2 and 3 control sites (no CPTH application), respectively, consisting of the same standard protocol as the treatment site. The first (CS1), second (CS2), and third (CS3) control sites were located

approximately 22, 37, and 53 km from the treatment site, respectively. I chose control sites located at distances >3 times the reported average of foraging distance by ravens (6.9 km, Engel and Young 1992*b*) to prevent transient ravens from traveling from control sites into the area of raven removal and thereby affecting numbers of ravens at control sites. This average raven travel distance was derived from the nearest studied population of ravens (southwestern Idaho), and was located in a similar shrubsteppe community.

I established 25 and 33 survey points along each 20 and 27 km transect, respectively. Points were separated by 800 m. At each survey point, I searched for a 3-min period using binoculars and counted the number of ravens and other corvids, flying or perched. All survey transects were a length of 27 km during 2002-2003 and 20 km during 2004-2005. I avoided recounting individual ravens by keeping track of ravens previously counted as I moved to the next survey point. I indexed raven abundance by calculating the number of ravens per 10 km along transects at each study site. My objective was to compare indices of raven abundance among and within sites through the sage-grouse nesting season and not to estimate raven population density.

Because I used vehicles to move between points, I designated survey transects based on unpaved roads at the treatment and control areas. Vehicle use along roads was approximately the same among sites. Also, I selected transects that intersected one or more sage-grouse leks (sage-grouse breeding grounds) at all sites. The treatment site transect also intersected a newly established sharp-tailed grouse lek. Because roads were used as transects, the treatment site and CS1 consisted of 2 and 1 curves, respectively, of $<80^\circ$ angles. Transects at CS2 and CS3 had no curves $>30^\circ$ degrees.

During 2002 and 2003, WS personnel performed 10 surveys as standard operational protocol. Results of 5 surveys during 2003 were reported previously (Coates and Delehanty 2004). I occasionally observed and recorded crows and magpies at the treatment area during raven surveys. However, observations of these species were rare, perhaps because of the remote location of the treatment site, and were not included in data analyses.

CPTH Application

Raven removal was carried out in conjunction with WS personnel. I followed standard operational procedures for preparation of eggs treated with CPTH (Spencer 2002). I hard-boiled 220 eggs per week using a cooking pot (22.8 L), propane burner ($\geq 140,000$ BTU), and large wire basket by placing 100 raw eggs at a time in an egg basket and boiling them in water for 13-15 minutes. I then removed the eggs and allowed them to cool for several hours. Cooling eggs prior to applying CPTH prevents cracking and toxicant decomposition from heat exposure. Eggs were rubber-stamped with a warning label (i.e., skull and crossbones or “poison”), as instructed in the compound label, during the cooling period. After cooling, I used a 6.3 mm ratchet hex screwdriver to punch an injection hole at the end opposite the air cell. The injection hole must reach the center of the yolk with a diameter large enough to contain 1 ml of solution without spillage.

To prepare the CPTH solution, I complied with all precautionary statements and directions indicated on the labeling. I made a 2% CPTH solution by dissolving 2 g of CPTH concentrate in 100 ml of potable water warmed to 43.3°C. I injected 1 ml of 2% CPTH solution into each egg injection hole using a 5-ml syringe or a 1-ml pipette. Prior to placement of egg baits at the treatment site, I stored the eggs in an upright position

without covering injection holes for 2-4 hours to allow absorption of the compound into the albumen and yolk of each egg and prevent spillage.

Every 7 days at the treatment site from late-March to late June of 2002-2005, I placed 2 egg baits on the ground per bait station every 250 m along a 27.5 km route from late-March to late-June of 2002-2005. I placed a total of approximately 10,560 eggs (2,640 per year) through the duration of the study. The egg bait route intersected the recently established population of sharp-tailed grouse and sage-grouse leks. Eggs were placed side by side to increase their probability of being observed and consumed by ravens. I positioned eggs upright to prevent spillage of any compound that may not have been completely absorbed into the egg. Also, I placed eggs directly on the ground between shrubs with no horizontal vegetation covering them. To facilitate consumption by ravens I did not use unnatural objects (e.g., platforms) because ravens can be neophobic to novel objects during initial encounters (Heinrich 1988). Also, every year the treatment site was pre-baited (i.e., applying non-toxic egg baits) 2-3 times to habituate ravens to egg baits as a food source. Pre-baiting took place for 1-2 weeks. Between 62-72 hours following placement of egg baits (both treated and non-toxic), I recorded the number of eggs depredated, missing, or undisturbed, and collected and disposed of all non- or partially-consumed eggs. No eggs were left in the environment for more than 2-3 days and no eggs were reused at a later date.

Prior to the start of my research in 2002, WS personnel carried out sporadic, nonmethodical applications of CPTH egg baits for approximately 3 years, in response to movement of reintroduced sharp-tailed grouse at the treatment site. Although ravens were the primary target species in this study, crows and magpies were also considered to be

target species because they are considered to be important predators of grouse eggs (Schroeder et al. 1999, Schroeder and Baydack 2001).

To identify egg bait predators, I used 4 miniaturized cameras with video recording systems (Fuhrman Diversified Inc., Seabrook, Texas; Supercircuits, Austin, Texas) to monitor a random sample of egg baits throughout the treatment period ($n = 18$, 2004; $n = 28$, 2005). Also, I used 4 cameras to video-monitor non-toxic egg baits (no CPTH treatment) at random locations throughout the control sites during the same dates as the videoed treatment eggs to compare frequencies of egg bait predator consumption among sites. Videoed eggs at control sites also had injection holes and warning labels. No other non-treated eggs were placed at the control sites to prevent supplementing raven diets with a large quantity of unnatural food and, thereby, influencing raven abundances by attracting ravens into control areas. Cameras ($40 \times 40 \times 60$ mm) were deployed approximately 1 m from egg baits in a nearby shrub and equipped with infrared night illumination (Pietz and Granfors 2000), not detectable by vertebrates (850-950 nm wavelength). A 20-m cable was buried and connected to a time-lapsed, continuous-recording VCR (Pietz and Granfors 2000). I allowed video systems to record for a continuous 72 hours at egg baits. To avoid bias in the encounter frequency of animals that rely on visual cues to locate nests, I used adhesive camouflage tape and vegetation for concealment (Herranz et al. 2002). To avoid olfactory related biases (Harriman and Berger 1986, Whelan et al. 1994), I used rubber boots and gloves to mask human scent during installation.

Statistical Analyses

I used PROC MIXED procedures (SAS Institute Inc., Cary, N. C.) to test if changes in raven abundance indices through time differed among the treatment site and control sites. Year was assigned as a random effect. Raven abundance indices recorded at the treatment site during pre-baiting were not assigned as a treatment variable in the analyses because CPTH eggs were not yet placed at the site. Also, I performed simple linear regressions at each site using abundance indices as the response variable and ordinal date (number of days elapsed from 1 January) as the explanatory variable. Where the slope of a best-fit regression line differed statistically from zero, I determined whether the relationship was positive or negative.

RESULTS

Rate of change of raven abundance through time differed between the treatment site (Figure 3.1) and control sites ($F = 3.77_{3,115}$, $P = 0.012$) (Figure 3.2). In the secondary analysis, raven abundances declined substantially at the treatment site during each year of the study, whereas abundances remained stable or increased at the control sites (Table 3.1). In each of the 4 years, raven abundance indices declined to near zero by mid-June in the treatment area, regardless of inter-year variation in raven abundance indices during March. An increase in abundance through time was detected at CS1 during 2004 ($t_8 = 2.66$, $P = 0.033$) (Figure 3.2).

Of the 2,640 eggs placed at the treatment site per year, I found 756, 1,432, 721, and 1,736 missing during 2002, 2003, 2004, and 2005, respectively. I video-recorded a total of 42 eggs consumed during 2004-2005. At the treatment site, 2 of 22 (9%) consumptions were by ravens, while ravens were responsible for 18 of 20 (90%)

consumptions at control sites. Other consumers were Wyoming ground squirrel (*Spermophilus elegans*) ($n = 14$, treatment site only), Piute ground squirrel (*S. mollis*) ($n = 3$, treatment site only), Great Basin pocket mouse (*Perognathus parvus*) ($n = 1$, treatment site only), American magpie ($n = 2$, treatment site only), and domestic cattle ($n = 2$, control site only). All rodents completely consumed the egg baits. Using videography, I calculated a 1:11 ratio of raven consumption to missing eggs. Wyoming and Piute ground squirrels were responsible for 71% of egg consumptions by species other than ravens.

DISCUSSION

I measured the effects of CPTH application using chicken egg baits on raven numbers in the wild and found substantial short-term reductions in raven population abundances associated with CPTH application. In that, raven numbers were significantly reduced during the year of treatment but not in following years. This is a first test of the efficacy of CPTH at removing ravens using actual field conditions and control sites, and provides information for making informed policy decisions. Removal of nest predators often increases nest success of ground nesting birds (Greenwood 1986, Garrettson and Rohwer 2001, Littlefield 2003), a necessary antecedent to recruitment and population renewal. Ravens have been documented to be common predators of sage-grouse nests at the treatment site (Coates, unpubl. data), and elsewhere (Autenrieth 1981, Schroeder et al. 1999, Schroeder and Baydack 2001), and removal of ravens may increase nest success of grouse (Batterson and Morse 1948).

Videography did not capture any non-target species that are known to be at risk of fatality from CPTH effects consuming egg baits. However, ground squirrels, which are

not known to be vulnerable to the dosage of CPTH injected into egg baits in this study, were commonly observed consuming eggs. Ground squirrel LD₅₀ values have not been described but reported values of other rodents are relatively high. For example, mouse and white rat LD₅₀ values were reported as 2,000 and 1,170-1,770 mg/kg, respectively (Clark 1986). The EPA approved CPTH for use primarily because of rapid degradation and specificity to ravens and other corvids (raven's LD₅₀ = 5.6 mg/kg; Larsen and Dietrich 1970). Therefore, chicken egg baits treated with CPTH to remove ravens from areas of apparent raven damage appear to have low non-target hazards, i.e., threat of affecting non-offending animals (Conover 2002), something my finding supports. I did not observe dead or noticeable impairment of live animals of non-target species due to the effects of CPTH, and secondary poisoning hazards have not been observed in other studies and are thought to be unlikely to occur (Cunningham et al. 1979, Johnston et al. 1999).

Recent evidence suggests that Richardson's ground squirrels (*S. richardsonii*), Wyoming ground squirrels, and Piute ground squirrels are not effective at depredating grouse eggs unless the eggs have been damaged (i.e., hole or cracking) (Coates and Delehanty 2004, Michener 2005). My video observations indicate that ground squirrels used injection holes to open and consume egg baits. Thus, while ground squirrels may not be important predators of grouse eggs (Michener 2005), they are an important predator of egg baits.

Failure to consider ground squirrels as egg bait predators will lead to substantial error when using egg bait disappearance as a proxy for raven take. Egg bait consumption by ground squirrels will lead to overestimation of raven take but the relationship has its

own complexities. Ground squirrels were common at the control sites but none were video-recorded consuming egg baits as all squirrel consumptions took place at the treatment site. Ravens were primarily responsible for consumption (18 of 20 eggs) at control sites. Perhaps, in areas where ravens were abundant, ravens consumed egg baits prior to squirrels encountering and consuming them. Also, nocturnal rodents rarely consumed eggs. Egg baits were set out in morning hours providing ravens (diurnal) first access to bait relative to nocturnal mammals. Also, I did not deploy video systems on baits until mid-April during 2005 due to weather conditions, which was subsequent to CPTH treatment at the treatment site. Perhaps by this date, raven numbers were reduced enough to allow compensatory predation by ground squirrels at the treatment site and maintained throughout the treatment period, while ravens were primarily consuming egg baits at control sites.

Alternatively, it is possible that ravens avoided treated eggs at the treatment site and not control eggs at the control sites explaining the differences in raven consumption among sites. However, this seems unlikely because I found no videographic evidence of raven avoidance and I measured a marked decline in raven abundance of the treatment site consistent with lethal consumption of egg baits. Nevertheless, experimental research that measures raven consumption rates and allows ravens free choice among treatment and control eggs at bait stations would be beneficial to further understanding any egg bait avoidance by ravens.

Ravens and ground squirrels left similar sign following consumption of egg baits. For example, both species partially consumed eggs at the site and then moved eggs to another location, leaving fragmented egg-shells at the bait site. Thus, ground squirrel and

raven consumptions were indistinguishable using diagnostic egg remains. Relying on more precise ratios derived from unambiguous identification techniques may be the most practical method to estimate raven removal. These estimates should be accompanied with weekly raven surveys in the treatment and control areas.

My results suggest that CPTH application may cause short-term reductions in raven numbers without long-lasting effects on raven populations because of reoccupation of territories. In my study, treatment at least once per week during the nesting period of grouse reduced raven numbers. However, territories of ravens do not remain empty following raven removal. Empty territories of predators can be quickly reoccupied (Greenwood 1986) potentially nullifying any population reduction produced by the initial predator removal (Conover 2002). Within raven populations, many non-breeding ravens without territories are transient (Boarman and Heinrich 1999) and have been reported to travel 40-65 km in a day (Engel and Young 1992*b*, Heinrich et al. 1994). Although I did not measure raven movements, I observed ravens absent from the treatment site for a few days following each treatment and then present in small numbers until reapplication. Presumably, transient ravens were reoccupying territories where original, territorial occupants had been lethally removed. Also, each spring raven numbers appeared to have rebounded to previous abundances or higher prior to CPTH application. Therefore, reapplication must be frequent to prevent colonization of transient ravens from negating the removal effects. In addition, it may be beneficial to replace territorial breeding ravens with transient ravens because transients are often juveniles (Boarman and Heinrich 1999) and may be less likely to have experience in finding grouse nests.

Indices of raven abundance at CS3 were substantially greater than the other 2 sites (Figure 3.1). Perhaps, the high abundances at CS3 were associated with greater availability of anthropogenic subsidies. CS3 was located <5 km from a landfill and surrounded by agricultural activity, while the other sites were >30 km from a landfill with less agriculture. Also, I observed more human-made structures, standing water, linear right-of-ways (i.e., roads and transmission power-lines), and livestock at CS3. My findings are consistent with other recent evidence that indicates increases in raven populations are due to anthropogenic alterations in water, food, and nest sites (Boarman 1993, Knight and Kawashima 1993, Boarman and Heinrich 1999).

When applying CPTH chicken egg baits directly on the ground to remove ravens, I recommend avoiding the 1:2 ratio (ravens to missing eggs) that is currently used by managers to estimate raven take throughout the treatment period because it may substantially overestimate raven take, especially if ground squirrels begin consuming egg baits after an initial period of raven removal. In my study, the frequency of egg predators that consumed egg baits differed between sites, where ravens were most responsible at control sites and ground squirrels at the treatment site. The initial week of treatment following pre-baiting may have resulted in high raven take but prolonged treatment did not appear to continue to remove ravens at high rates, even though eggs disappeared at high rates throughout the treatment period. Unfortunately, I was unable to estimate raven take using videography during initial treatment. However, following the first week of application, my estimated raven take was 1:11 ratio rather than the 1:2 ratio that is currently used. A 1:11 ratio would lead to an estimated 69, 130, 66, and 157 ravens removed from the treatment site during 2002, 2003, 2004, and 2005, respectively. Even

using a 1:11 adjustment, these values still appear high. For example, using indices of raven abundance, I found 38-234 eggs may be needed to take a raven. However, because surveys were conducted every 3-7 days, raven counts likely did not account for transient ravens that moved through the area and consumed eggs. Perhaps, continued research using unambiguous identification techniques will improve or confirm estimates.

Also, ratios likely will change over time at treatment sites, perhaps resulting in a continuum of ratios, especially if the rate of raven take is continually decreasing and ground squirrel numbers are unaffected. My sample sizes did not permit calculating multiple ratios through time, but further research regarding changing ratios would greatly improve my understanding of estimating raven take based on egg-bait consumption. Also, videography may lead to minor overestimation in raven take because ravens are known to take eggs and cache them for later consumption (Boarman and Heinrich 1999) and eggs may be consumed when CPTH is no longer viable or eggs are taken but not consumed.

In conclusion, using the technique described here, compound CPTH egg-bait treatment is effective in short-term (i.e., <1 year) reduction of raven abundance in the immediate area of treatment. Lethal removal of predators is often a successful management action for increasing nest success of ground nesting birds (Greenwood 1986, Garrettson and Rohwer 2001, Littlefield 2003). However, reducing anthropogenic resource subsidies of raven populations (Boarman 1993), and other long-term management actions, may be ultimately needed to reverse effects of spillover predation (Smith and Quinn 1996).

Table 3.1. Linear regression analyses of common raven (*Corvus corax*) densities throughout the nesting season of sharp-tailed grouse and sage-grouse at the treatment site, consisting of egg baits treated with CPTH (3-chloro-p-toluidine hydrochloride), and three control sites located 22, 37 and 53 km from the treatment site in northeastern Nevada during 2002-2005. *P* represents probability values from regression analyses. Asterisks (*) represent significant change in raven densities through time ($\alpha = 0.05$).

| YEAR | TREATMENT | | | CONTROL 1 | | | CONTROL 2 | | | CONTROL 3 | | |
|------|-----------|----------------|---------|-----------|----|----------------|-----------|----------|----|----------------|-------|------------------------------|
| | n | R ² | P | Trend | n | R ² | P | Trend | n | R ² | P | Trend |
| 2002 | 12 | 0.381 | 0.033* | decrease | - | - | - | - | - | - | - | - |
| 2003 | 15 | 0.428 | 0.008* | decrease | - | - | - | - | - | - | - | - |
| 2004 | 20 | 0.283 | 0.016* | decrease | 9 | 0.502 | 0.033* | increase | - | - | - | 10 0.192 0.206 stable |
| 2005 | 17 | 0.734 | <0.001* | decrease | 13 | 0.031 | 0.856 | stable | 13 | 0.011 | 0.733 | stable 15 0.038 0.488 stable |

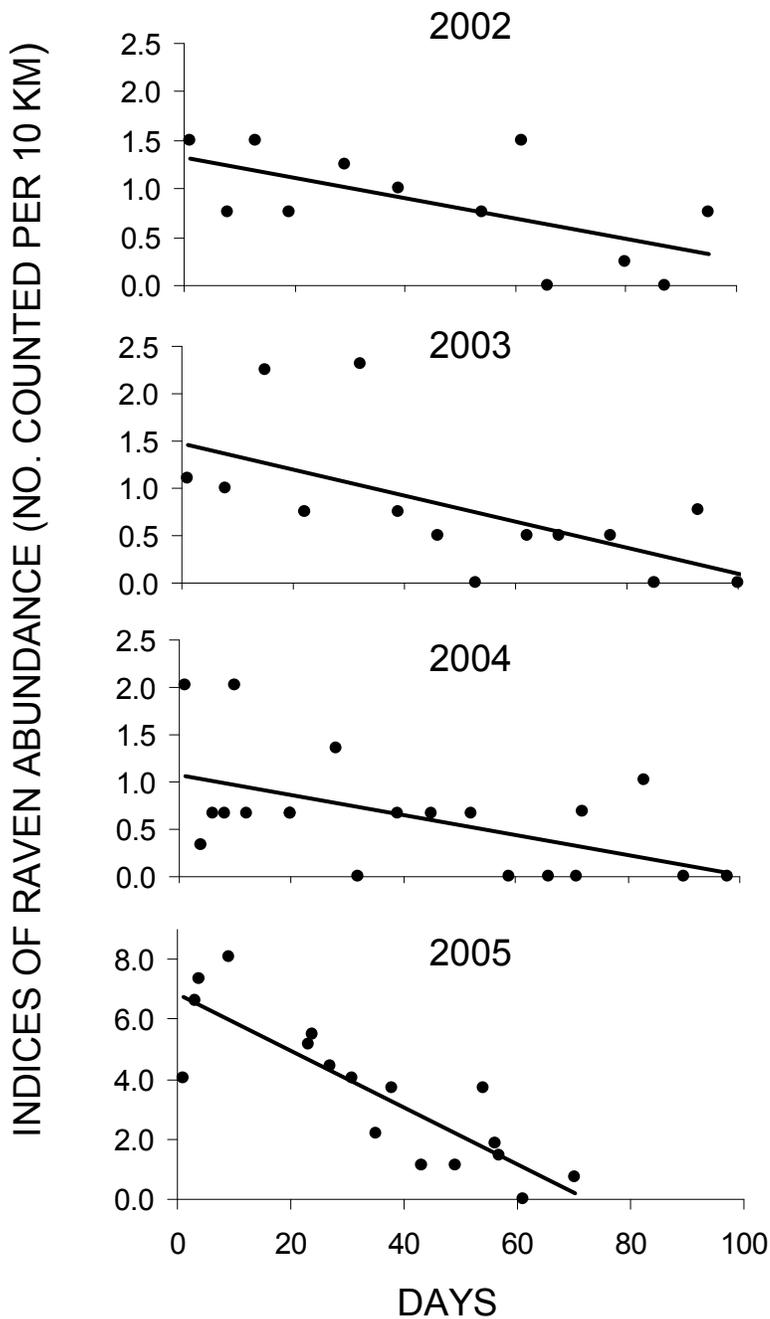


Figure 3.1. Indices of common raven (*Corvus corax*) abundance in relation to days of treatment using CPTH (3-chloro-p-toluidine hydrochloride), which was injected into chicken egg baits and placed in the environment for consumption by ravens every 7 days in northeastern Nevada during 2002-2005. Surveys were conducted between late-March and mid-June, which encompassed the treatment period. Notice change in scale of raven abundances in 2005.

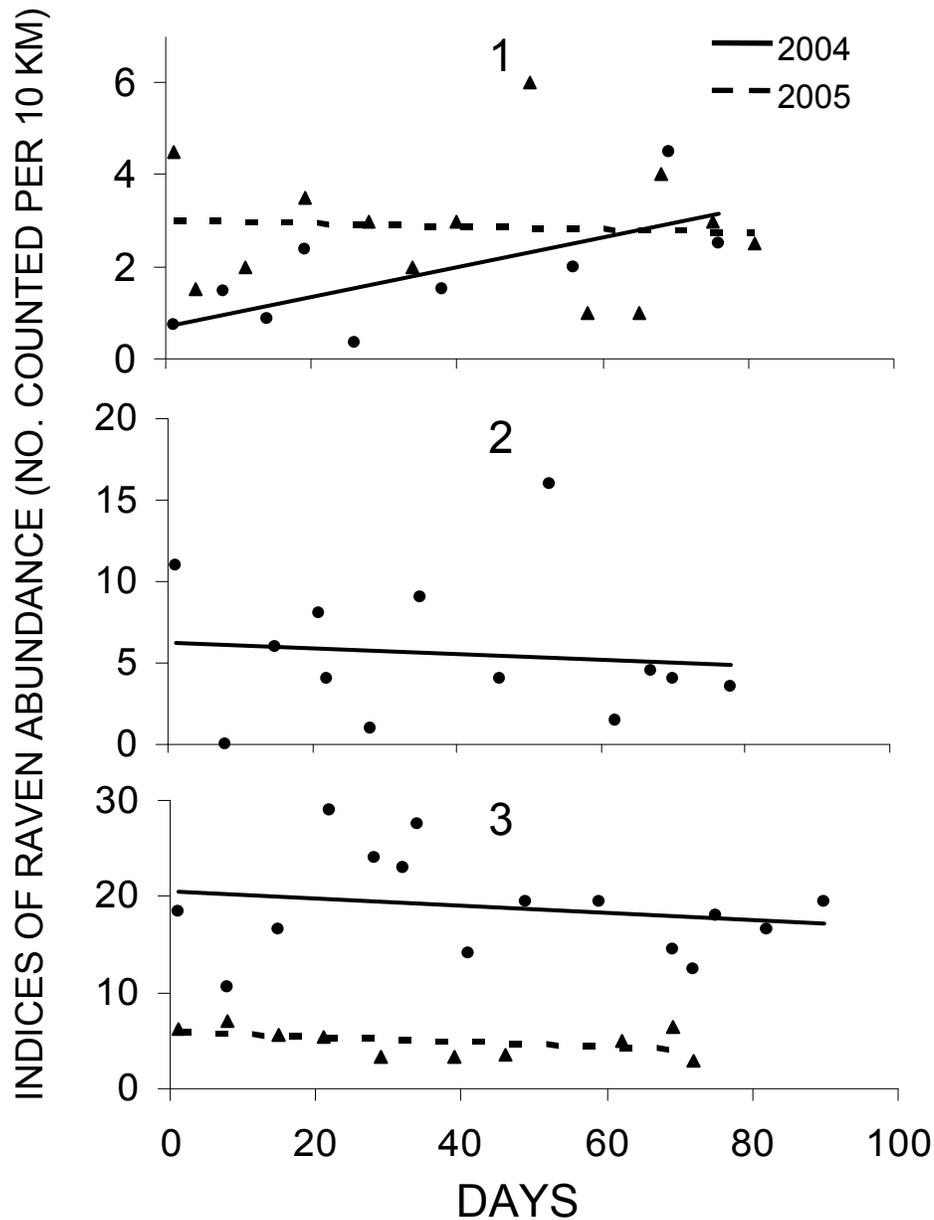


Figure 3.2. Indices of common raven (*Corvus corax*) abundance at 3 control sites (no CPTH, 3-chloro-p-toluidine hydrochloride, treatment) in northeastern Nevada during 2004 (▲) and 2005 (●). Days of surveys were conducted from late-March to mid-June encompassing CPTH treatment that was carried out at the treatment site located 22, 37, and 53 km distance away from control sites 1, 2, and 3, respectively. Notice change in scale of ravens abundances among sites.

LITERATURE CITED

- Apa, A. D. 1998. Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. Dissertation, University of Idaho, Moscow.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game, Federal Aid in Wildlife Restoration Project W-125-R and W-160-R, Wildlife Bulletin No. 9. Boise, Idaho.
- Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission, Oregon Fauna Service 1, Portland, Oregon. 29 pp.
- Besser, J. F., W. C. Royall, and J. W. Degrazio. 1967. Baiting starlings with DRC-1339 at a cattle feedlot. *Journal of Wildlife Management* 31:48-51.
- Blackwell, B. F., E. Huszar, G. M. Linz, and R. A. Dolbeer. 2003. Lethal control of red-winged blackbirds to manage damage to sunflower: An economic evaluation. *Journal of Wildlife Management* 67:818-828.
- 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. Miller, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. *Conservation and resource management*. Pennsylvania Academy of Science, Philadelphia.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing Common Raven predation on desert tortoises. *Environmental Management* 32:205-217.
- Boarman, W. I. and B. Heinrich. 1999. Common raven (*Corvus corax*). In A. Poole and F. Gill, editors. *The Birds of North America*, No. 476. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, D.C.
- Boyd, F. L., and D. I. Hall. 1987. Use of DRC-1339 to control crows in three roosts in Kentucky and Arkansas. *Proceedings of the Eastern Wildlife Damage Control Conference* 3:3-7.
- Clark, J. P. 1986. *Vertebrate pest control handbook*. Division of Plant Industry, California Department of Food and Agriculture, Sacramento. 615 pp.

- Coates, P. S., and D. J. Delehanty. 2004. The effects of raven removal on sage grouse nest success. *Proceedings of the Vertebrate Pest Conference* 21:17-20.
- Coates, P. S., and D. J. Delehanty. 2006. Effect of capture date on nest attempt rate of translocated sharp-tailed grouse *Tympanuchus phasianellus*. *Wildlife Biology* 12:277-283.
- Conover, M. 2002. *Resolving human-wildlife conflicts: the science of wildlife damage management*. CRC Press, New York. 440 pp.
- Cunningham, D. J., E. W. Schafer, Jr., and L. K. McConnell. 1979. DRC-1339 and DRC-2698 residues in starlings: preliminary evaluation of their secondary hazard potential. *Proceedings of the Bird Control Seminar* 8:31-37.
- DeCino, T. J., D. J. Cunningham, and E. W. Schafer. 1966. Toxicity of DRC-1339 to starlings. *Journal of Wildlife Management* 30:249-253.
- Engel K. A., and L. S. Young. 1992*a*. Daily and seasonal activity patterns of common ravens in southwestern Idaho. *Condor* 91:372-378.
- Engel K. A., and L. S. Young. 1992*b*. Movements and habitat use by common ravens from roost sites in southwestern Idaho. *Journal of Wildlife Management* 56:596-602.
- Garrettson, P. R., and F. C. Rohwer. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. *Journal of Wildlife Management* 65:398-405.
- Garton, E. O. J. T. Ratti, and J. H. Giudice. 2005. Research and experimental design. Pages 43-71 in C. E. Braun, editor. *Techniques for wildlife investigations and management*. Sixth Edition. The Wildlife Society, Bethesda.
- Greenwood, R. J., 1986. Influence of striped skunk removal on upland duck nest success in North Dakota. *Wildlife Society Bulletin* 14:6-11.

- Guarino, J. L., and E. W. Schafer. 1967. Magpie reduction in an urban roost. United States Department of Interior, Fish and Wildlife Service Special Scientific Report —Wildlife, No. 104. Washington D. C. 5 pp.
- Harriman, A. E., and R. H. Berger. 1986. Olfactory acuity in the common raven (*Corvus corax*). *Physiology and Behavior* 36:257-262.
- Heinrich, B. 1988. Why do ravens fear their food? *Condor* 90:950-952.
- Heinrich, B., D. Kaye, T. Knight, and K. Schaumburg. 1994. Dispersal and association among common ravens. *Condor* 96:545-551.
- Herranz, J., M. Yanes, and F. Suárez. 2002. Does photo-monitoring affect nest predation? *Journal of Field Ornithology* 73:97-101.
- Johnston, J. J., D. B. Hurlbut, M. L. Avery, and J. C. Rhyan. 1999. Methods for the diagnosis of acute 3-chloro-*p*-toluidine hydrochloride poisoning in birds and the estimation of secondary hazards to wildlife. *Environmental Toxicology and Chemistry* 18:2533-2537.
- Knight, R. L. 1984. Responses of nesting ravens to people in areas of different human densities. *Condor* 86:345-346.
- Knight, L. R. and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management* 57:266-271.
- Kristan, W. B., and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *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.
- Littlefield, C. D. 2003. Sandhill crane nesting success and productivity in relation to predator removal in southeastern Oregon. *Wilson Bulletin* 115:263-269.
- Michener, G. R. 2005. Limitation on egg predation by Richardson's ground squirrels. *Canadian Journal of Zoology* 83:1030-1037.

- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71-87.
- Royall, W. C. Jr., T. J. DeCino, and J. F. Besser. 1967. Reduction of a starling population at a turkey farm. *Poultry Science* 46:1494-1495.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American Breeding Bird Survey, Results and Analysis 1966-2003. Version 2004.1. United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
- Schneider, M. F. 2001. Habitat loss, fragmentation and predator impact: spatial implications for prey conservation. *Journal of Applied Ecology* 38:720-735.
- 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. A. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In A. Poole and F. Gill, editors. *The Birds of North America*. No. 425. Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C.
- Seamans, T. W., and J. L. Belant. 1999. Comparison of DRC-1339 and alpha-chloralose to reduce herring gull populations. *Wildlife Society Bulletin* 27:729-733.
- Smith, A. P., and D. G. Quinn. 1996. Patterns and causes of extinction and decline in conilurine rodents. *Biological Conservation* 77:243-267.
- Spencer, J. O., Jr. 2002. DRC-1339 use and control of common ravens. *Proceedings of the Vertebrate Pest Conference* 20:110-113.
- Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. *Journal of Wildlife Management* 57:271-281.
- Webb, C. W., W. I. Boarman, and J. T. Rotenberry. 2004. Common raven juvenile survival in a human-augmented landscape. *Condor* 106:517-528.

Whelan, C. J., M. L. Dilger, D. Robson, N. Hallyn, and S. Dilger. 1994. Effects of olfactory cues on artificial-nest experiments. *Auk* 111:945-952.

CHAPTER 4:

GREATER SAGE-GROUSE NEST SUCCESS IN RELATION TO AGE, PREDATORS, AND HABITAT, AND EFFECTS OF RAVEN REMOVAL

ABSTRACT

Nest depredation is a natural component of sage-grouse (*Centrocercus urophasianus*) reproduction, but changes in nesting habitat and predator communities may adversely affect grouse populations. I used information criterion to evaluate the relative importance of age class of grouse, indices of predators, and nest microhabitat variables in relation to nest success in northeastern Nevada. I used videography at grouse nests to identify predators and modeled probabilities of depredation caused by each predator species in relation to microhabitat characteristics. Also, I evaluated effects of reducing local raven numbers by measuring nest success in relation to distances (range 0.03-76.73 km) of nests away from a route where ravens consumed egg baits treated with a corvicide. Adult nest success was substantially greater than yearlings and I hypothesize this difference is attributable to differences that have been observed between age classes in incubation rhythms. Indices of raven abundance were strongly associated with nest failure and raven-caused depredations indicating that high raven abundance has substantial, negative effects on sage-grouse reproduction. Lethally reducing raven numbers appeared to increase sage-grouse nest success but badger depredation to partially compensate for raven removal. I found that the probability of nests depredated by ravens increased with decreased shrub canopy cover and there were substantial differences in canopy cover, understory obstruction, and biomass of forbs around nests (within 25 m) between raven-

and badger-caused depredations. Differences in microhabitat between types of predators explain why I did not detect key habitat characteristics when modeling overall nest success and may help explain inconsistencies reported in literature. Ravens are generalist predators and raven presence appears to interact with loss of microhabitat characteristics that provide nest concealment for grouse. Thus, in landscapes with low shrub canopy cover where sage-grouse and raven distributions overlap, ravens could lead to suppression or decline of sage-grouse populations through nest depredation.

Key Words: 3-chloro-p-toluidine hydrochloride, American badger, greater sage-grouse, *Centrocercus urophasianus*, common raven, compensatory predation, habitat, nest predation, wildlife damage management

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) distribution and abundance has declined substantially since Euro-American settlement of western North America (Schroeder et al. 2004) and populations continue to decline in most portions of their current range (Connelly and Braun 1997). Nest success is a natural antecedent to important avian life-stages and, thus, plays a critical role in population viability (Martin 1993, 1995).

Predation is a normal component of game-bird reproduction, but its relative importance to population viability may change with human-caused alterations of habitat and predator communities (Evans 2004). Predation is estimated to account for 79% of the nest failure of prairie grouse (Bergerud 1988) and may be an important factor limiting sage-grouse population dynamics (Nelson 1955, Gregg et al. 1994, Schroeder and Baydack 2001). Habitat features necessary for successful nesting are important proximate

factors in influencing nest success but they affect productivity through indirect pathways. Nest habitat features identified as important to sage-grouse include presence of sagebrush (*Artemisia* spp.) (Connelly et al. 1991), canopy cover (Wallestad and Pyrah 1974, Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005), and understory cover (Gregg et al. 1994, DeLong et al. 1995). When important habitat features are removed, fragmented, or otherwise degraded, populations decline (Braun et al. 1977, Connelly and Braun 1997, Connelly et al. 2000). For example, habitat features conceal bird nests and parents from predators (Evans 2004) while simultaneously providing thermal protection to parents and eggs (Ar and Sidis 2002). Loss of these features can diminish nest success (Connelly et al. 1991, Gregg et al. 1994, Holloran et al. 2005) and possibly lead to population decline (Connelly et al. 1991, Connelly et al. 2000, Holloran et al. 2005).

Generalist predators that thrive in human-altered landscapes are of great conservation concern because they can substantially reduce prey populations (Garrott et al. 1993, Schneider 2001). Subsidized, generalist predators like common ravens (*Corvus corax*) can have substantial predatory impact (Andrén et al. 1985, Boarman 1993, Boarman 2003) because their numbers remain high due to anthropogenic food subsidies despite reductions in prey populations and thus these predators continue depredation even at low prey densities (Polis et al. 1997, Sinclair et al. 1998). Ravens are subsidized generalists and have increased >200% in abundance throughout North America within the past 40 years (Sauer et al. 2004). Increases in raven numbers have been seen as high as 1,500% since the 1960s in some portions of the western United States (Boarman 1993). Greater survival and reproduction of ravens have been associated with increased availability of food and nest substrate in anthropogenic landscapes (Knight and

Kawashima 1993, Webb et al. 2004). Ravens use visual cues to locate eggs and young of many animals (Boarman and Heinrich 1999) including sage-grouse (Schroeder et al. 1999, Schroeder and Baydack 2001).

Habitat change and increased predation can interact at multiple scales and be important causal factors in nest depredation of ground nesting birds (Evans 2004). Many management techniques intended to increase nest success by reducing predation of game birds have been proposed or explored in studies, but these techniques require further development and testing. For example, habitat modification to increase concealment cover (Clark and Nudds 1991), introduction of alternative prey (Crabtree and Wolfe 1988), modification of the predator community (Sargeant and Arnold 1984, Klett et al. 1988), taste aversion (Conover 1989, 1990), predator translocation (Watson and Thirgood 2001), and lethal removal of individual predators (Batterson and Morse 1948, Greenwood 1986, Clark et al. 1995) or several predator species (Duebbert and Lokemoen 1980, Sargeant et al. 1995, Baines et al. 2004) have been suggested or applied in the field to a variety of ground nesting birds.

Lethal removal of predators is a management practice intended to increase prairie grouse nest productivity, but the effects have not been tested adequately (Schroeder and Baydack 2001). Currently, wildlife managers use egg baits treated with 3-chloro-p-toluidine hydrochloride (CPTH) to reduce raven numbers in sage-grouse habitat (Spencer 2002). Due to lack of empirical studies, it is difficult to evaluate effects of raven removal on grouse nest success. One study indicated that nest success was greater with raven removal (Batterson and Morse 1948) but this study provides weak support because estimates of raven abundances among experimental and control sites were not reported

nor were nest predators unambiguously identified. Experimental evidence regarding effects of raven removal on sage-grouse nest success would help in developing management strategies for increasing sage-grouse productivity.

This study had 4 objectives to address these complex issues. First, I sought to measure sage-grouse nest success in relation to lethal removal of ravens. Ravens are sage-grouse nest predators (Schroeder et al. 1999) and based on reported effects of removing ravens (Batterson and Morse 1948), I hypothesized that raven removal might increase sage-grouse nest success. My second objective was to use videography to identify predators at sage-grouse nests. This would allow me to measure unambiguously raven predation rates in relation to raven removal and also to indices of raven abundance. I hypothesized that raven predation would increase with greater raven abundance. My third objective was to measure differences in nest microhabitat characteristics in relation to species of nest predator identified using videography. I hypothesized that avian predators would depredate nests with less herbaceous cover than mammalian predators because avian predators are thought to rely more on visual cues and nests with less herbaceous cover would be more exposed visually (Connelly et al. 1991). My final study objective was to use an information theoretic approach (Anderson et al. 2000) to assess the relative importance of a suite of explanatory variables on sage-grouse nest success by developing and comparing multiple, predictive models. Explanatory variables in models were chosen based on effects that have been reported in the literature in relation to sage-grouse nest success. I included quadratic functions of variables if functions had been found to be important factors in previous studies.

STUDY AREA

I monitored a sample of sage-grouse nests within an area of approximately 1,430 km² located in Elko County, Nevada (N 0670859, E 4599749, zone 11, NAD 83) during 2002-2005. I captured grouse from 4 lek routes. Lek routes were defined as areas of 1-3 breeding grounds (lek) and each of the 4 was separated by ≥ 15 km. Leks and no leks within a route were < 2 km apart. Also, I used videography to monitor 4 additional nesting female grouse that were captured by Idaho Department of Fish and Game from a fifth lek route in southeastern Idaho.

Dominant plant communities consisted of shrub-steppe at lower elevations and mountain shrub at higher elevations across study sites. Predominant overstory of shrub-steppe was basin big sagebrush (*Artemisia tridentata tridentata*), Wyoming big sagebrush (*A. t. wyomingensis*) and low sagebrush (*A. arbuscula*). Crested wheatgrass (*Agropyron cristatum*) and bluebunch wheatgrass (*Pseudoroegneria spicata*) characterized the undercover of shrub-steppe communities. Overstory of mountain shrub communities was characterized by mountain big sagebrush (*A. t. vaseyana*) and serviceberry (*Amelanchier alnifolia*) and understory was primarily native bunchgrasses, such as bluebunch wheatgrass. Utah Juniper (*Juniperus osteosperma*) occurred in the peripheral regions at two of the four sites. A public landfill and private livestock carcass disposal area were located approximately 7 and 3 km northeast of the northernmost lek route in Nevada and approximately 53 and 50 km north of the raven removal area.

The Nevada Department of Wildlife (NDOW), in cooperation with United States Department of Agriculture/Animal Health Inspection Service/Wildlife Services (WS), carried out raven removal at the southernmost lek route (Coates et al., In Press). Wildlife

Services personnel systematically placed 10,500 chicken egg baits treated with CPTH and removed an estimated 69, 130, 66, and 157 ravens during 2002, 2003, 2004, and 2005 (Chapter 3), respectively. These numbers were estimated using an egg ratio (number of eggs removed or depredated in the environment per number of eggs removed or depredated by ravens) developed using video-identification and measurement of consumption by target and nontarget species (Chapter 3). Application of CPTH did not remove all ravens in the treatment area, but it significantly reduced raven numbers (Chapter 3). The U.S. Bureau of Land Management (BLM) administered the majority of the property forming the study areas. Much of the remaining and surrounding land was privately owned. Livestock grazed most private and public land in the study area annually.

Within the study area, I observed species reported to be sage-grouse nest predators (Schroeder et al. 1999) including common ravens, coyotes (*Canus latrans*), weasels (*Mustela* spp.), elk (*Cervus elaphus*), American badgers (*Taxidea taxus*), American magpies (*Pica hudsonia*), and American crows (*C. brachyrhynchus*).

METHODS

I captured female sage-grouse at night by using spotlights, multi-frequency noise, and hand-held nets (Giesen et al. 1982, Wakkinen et al. 1992) and classified grouse by age based on plumage (Ammann 1944). I captured grouse prior to and during the nesting period, 15 March - 15 April. Grouse were equipped with 17-21 g necklace-style, radio-transmitters (Advanced Telemetry Systems, Isanti, Minnesota). I relocated grouse every 2-3 days using hand-held receivers and was careful not to disturb grouse during relocation by circling around them at approximately 50 m. A hand-held Global

Positioning System (GPS) was used to record Universal Transverse Mercator (UTM) coordinates of grouse during relocation. After three consecutive relocations at the same coordinates, I approached grouse to locate their nests and recorded nest location as UTM coordinates. I sought to locate grouse nests either during the laying period or during the initial days of incubation.

Video-Monitoring

I used around-the-clock videography to identify sage-grouse nest predators and measure incubation rhythms at a random sample of nests (Chapters 1 and 2). These nests were monitored with continuously recording video systems and miniaturized, camouflaged cameras equipped with 12 infrared-emitting diodes (850-950 nm wavelength) (Fuhrman Diversified Inc., Seabrook, Texas; Supercircuits, Austin, Texas) allowing video-recording with light not detectable by vertebrates (Pietz and Granfors 2000). Cameras were mounted approximately 1 m from nest bowls and 20 cm above ground by attaching them to shrub trunks or to camouflaged stakes. Actual video-recording systems and deep-cycle batteries powering the recorders were placed approximately 20 m from nests and were connected to cameras by cables buried approximately 5 cm underground. I set video-recorders to record an image every 1.3 seconds and to document date, time, and frame number. Recorders were housed within camouflaged weather proof cases and concealed with burlap and vegetation.

To avoid researcher-induced nest abandonment and egg mortality (Renfrew and Ribic 2003), I deployed cameras at nests ≥ 7 days following the onset of incubation during morning hours provided there were no severe weather conditions (e. g., snow, rain). I attempted to deploy cameras while grouse were at recess from incubation. Video

tapes and charged batteries were installed at video recorders every 2-3 days. To avoid deterring or attracting predators (Herranz et al. 2002), I camouflaged equipment with vegetation and vinyl photography tape that matched the shrub-steppe vegetation.

Vegetation Measurements

I measured nest habitat characteristics at sage-grouse nests and nesting areas (within 25 m of nest) during 2002-2005. Measurements were performed 1-3 days following nest fate. I estimated percent canopy cover (CC) of sagebrush shrubs and of all shrub species within 25 m of nests by using a line-intersect technique (Canfield 1941). This technique consisted of measuring areas of shrub intersections along four, 25 m orthogonal transects in random orientation that intersected at the nest bowl. Also, gaps in foliage that were >5 cm were excluded from the measurement. Maximum heights (50HT) were measured (cm) for of all sagebrush shrubs that intersected each transect. To estimate percent understory visual obstruction (50VO) in nesting areas, I used a 3-sided cover board (modified from Jones 1968) at 16 random subsample points within 25 m of the nest bowl. Each side of the board was 50 cm² and consisted of a checkerboard pattern of 25 squares. Orientation of the board was randomized. I counted the number of squares at a distance of 2 m from each side of the board that were ≤50% visually obstructed. Measurements were conducted at 0° (25 cm from ground) and approximately 45° (2 m from ground) and averaged to estimate cover obstruction across angles and cover board sides. To estimate biomass (g) of non-woody vegetation (VBM) in the nesting area, I clipped all live grasses (GBM) and forbs (FBM) at ground level that were within 16 micro-plots (0.5 m²) placed randomly at ≤25 m from the nest bowl and stored the samples from each micro-plot separately. Samples were subsequently dried and weighed in the lab. Plots with no

grasses or forbs were noted in the field and later considered in averaging subsamples to estimate biomass per nest area. Non-woody biomass samples were collected during 2004 and 2005 only.

To estimate shrub height (cm) at the nest bowls (NHT), I measured the maximum heights of the shrub that visually-obstructed nest bowls when viewed from directly overhead. To estimate percent (%) understory visual obstruction at nest bowls (NVO), I used a 3-sided cover board (see above) and placed the cover board directly on the nest bowl at random orientation. Additionally, I estimated nest overstory obstruction (%) by laying the cover board flat in the nest bowl and viewing one side from a distance of 2 m directly over the board.

Predator Surveys

To create an index of raven abundance, I conducted transect surveys ($n = 64$) (Garton et al. 2005) every 3-7 days at the lek route where ravens were removed between late-March and late-June during 2002-2005. This coincided with egg bait treatment and periods of raven and sage-grouse nesting. During 2004 and 2005, I also conducted raven surveys ($n = 60$) every 3-7 days at the other lek routes. I established 25 and 33 survey points along each 20 and 27 km transect, respectively. Points were separated by 800 m. At each survey point, I searched for a 3-min period using binoculars and counted the number of ravens and other corvids, flying or perched, within approximately 500 m of the transect. All survey transects were a length of 27 km during 2002-2003 and 20 km during 2004-2005. I selected transects centered on the 4 sage-grouse lek routes. I chose a minimum of 20 km transects to encompass breeding areas of grouse because a review of average distances between sage-grouse nests and nearest leks were reported to be 1.1-6.2 km (Schroeder et

al. 1999). I avoided recounting individual ravens by keeping track of ravens previously counted as I moved to the next survey point.

I indexed raven abundance by calculating the number of observed ravens per 10 km. My objective was to compare indices of raven abundances, not to estimate raven population density. Because I used vehicles to move between points, I designated survey transects based on unpaved, low-use roads at the treatment and control areas. I observed rare use of roads by vehicle and it appeared that vehicle use was approximately the same among survey routes. To avoid pseudoreplication, I estimated raven abundance for each nesting grouse. I averaged the indices of raven abundance at each lek route within the dates of each grouse incubation period. Also, this was an appropriate procedure because I found variation in raven abundance through time, as well as variation in grouse nesting initiation dates and length of grouse incubation periods.

To index badger activity, I conducted line transect surveys ($n = 8$) at each lek route on 15 June. Transects were cardinal and intercardinal directions (i.e., N, NW, etc) intersecting at the lek within a given lek route that was attended by the greatest number of males. I established a length of 3.2 km for transects because this value was suggested as the distance from an occupied lek to be most important when protecting nest habitat of nonmigratory sage-grouse populations encompassing the majority of nesting grouse (Connelly et al. 2000). I walked straight lines using GPS receivers for orientation. Within 1 m of each transect, I recorded the number of badger dens and digs. The first 2 transects were surveyed by all field assistants to standardize researcher evaluation of badger activity. I calculated a mean badger sign for each transect. Scat was also found and recorded but not used in analyses due to low number of observations. I estimated badger

activity in relation to each nest by assigning each nest to the local badger activity level as measured by the nearest badger transect. Nests that were located >3.2 km (beyond transect length) from the lek were removed from the analysis to prevent bias. No nests were >300 m from a badger transect. The purpose of this procedure was to index badger activity in relation to nest sites and compare among sites, not to estimate badger densities.

Statistical Analyses

I used a mixed model approach to measure the effect of raven removal on sage-grouse nest success. I calculated shortest distances between nests and the removal route using an animal movement analyses extension (Hooge and Eichenlaub 1997) in a geographical information system (GIS). I performed a generalized, linear, mixed model analysis using PROC GLIMMIX (SAS Institute Inc., Cary, N. C.) allowing me to implement random effects with a binary response (Littell et al. 1998). Distance from the removal route and year were classified as fixed and random effects, respectively. This mixed model approach was appropriate to test the effects of raven removal because it accounted for indirect effects on neighboring raven populations and sage-grouse nest success in those areas. Using this approach, I made inferences as to probabilities of successful nesting at distances between 0 and approximately 80 km from the raven removal route by calculating parameter estimates (i.e., y-intercept and slope).

I also performed mixed model analysis using PROC GLIMMIX to evaluate the effects of raven abundance on sage-grouse nest success. I classified indices of raven abundance as a fixed effect. To account for natural clustering of sage-grouse nests and stochastic, year-to-year variation, lek route and year were assigned as random effects.

I performed an exact logistic regression using LogXact (Cytel Software Corporation, Cambridge, MA) to test if probability of a raven depredation was a function of distance from the raven removal route. Exact logistic regression uses an efficient algorithm for estimating statistical effects within small samples (Hirji et al. 1987). To visualize the relationship, I also calculated parameter estimates using asymptotic logistic regression to fit a response curve to probability of raven depredation as a function of distance from raven removal. A response curve is useful in interpreting findings for field application. The point of inflection on the response curve represented a 0.5 probability of nest failure.

I further evaluated predator effects by using exact logistic regression to measure the probability of each predator species depredating a nest in relation to microhabitat characteristics and indices of predator activity or abundance. Only nest predators that were video-identified were considered in exact regression analyses. I performed Student's t-tests (Minitab® Release 14) to measure differences in microhabitat characteristics between nests that failed by predator species identified using videography. A test was performed for each microhabitat characteristic. I measured the relationship between predator indices (i.e., badger activity and raven abundance) in relation to nest sites and microhabitat variables using Pearson Product Moment Correlation (Minitab® Release 14). Because some indices of badger activity at nests were associated with the same badger transect with no temporal variation, I averaged nest microhabitat at each transect and correlations were conducted at the transect level.

Modeling of sage-grouse nest success. I used an information-theoretic approach (Anderson and Burnham 2002) based on Kullback-Leibler information (Kullback and

Leibler 1951) to develop predictive models of sage-grouse nest success in relation to age class, nest microhabitat characteristics, and indices of raven abundance. To prevent multicollinearity in predictive models, I performed a Pearson's product-moment correlation matrix on all independent variables ($n = 16$). I excluded one of two variables that co-varied ($r \geq 0.65$) based on variance inflation factors ($VIF \geq 10$) and biological rationale. I report variables used in the analyses and associated mean \pm SE (Table 4.1). Because all combinations of explanatory variables were biologically feasible, I developed 63 candidate models of nest success based on all combinations of ≤ 2 variables. I chose no more than 2 variables in each model to prevent the number of models exceeding the samples ($n = 77$), which otherwise may lead to spurious conclusions (Anderson and Burnham 2002). I also used *post hoc* stepwise selection procedures ($\alpha = 0.05$ for removal and entry of covariates) to build predictive regression models to compare to best-fit models formed through the information theoretic approach. All variables were included in the stepwise regression procedures. If grouse nested twice in the same year or nested in >1 year, I randomly selected one nest of each grouse to prevent pseudoreplication. Thus, 75 initial nests and 2 re-nests were included in the models. All parameter estimations were performed using PROC LOGISTIC (SAS Institute Inc, Cary, N. C.). I included year and lek route of grouse as fixed effects to account for potential spatial and temporal correlations. Because I modeled using information criterion, I chose the logistic approach instead of the generalized mixed model analysis (e.g., GLIMMIX, SAS Institute Inc, Cary, N. C.) because logistic approach generates reliable information criteria, whereas GLIMMIX unfortunately needs further research to validate the information criterion.

I used AIC_c (Akaike's Information Criterion, Akaike 1973) corrected for small sample size (Anderson et al. 2000) as the information criterion to compare models. I calculated Akaike's ranks (ΔAIC) (representing a unit of comparison across approximating models) and weights (ω_i) (representing estimated probability that model i was the best among those considered) (Anderson and Burnham 2002) to compare models and evaluate relative importance. Models with ΔAIC values ≤ 2 have substantial support from the data (Burnham and Anderson 1998). Each parameter was evaluated separately by summing all model weights that contained the parameter under consideration (i.e., parameter likelihood) (Burnham and Anderson 1998). I reported the number of estimated parameters (K) and $-2 \log$ -likelihood of each model, which is a measure of lack of fit of the model to the data.

I carried out the analyses in 2 steps. During step 1, I compared 63 models consisting of 12 measured variables during 2002-2005 (Table 4.1). The purpose of this step was to determine the best-fit, predictive models using all 4 years of data. This step allowed me to develop best-fit models using data from variables *a posteriori* to field procedures and collected throughout the duration of the study. During step 2, I challenged variables from the best-fit model in step 1 with 3 additional variables that were collected only during 2004-2005. I compared 15 models in step 2. This step was carried out to determine if other hypothesized microhabitat characteristics were better predictors than those originally chosen. Because measurements of any one variable cannot be missing at nests when comparing models using information criterion (Anderson and Burnham 2002), only data collected during 2004 and 2005 (the second half of the study) was used to evaluate any superiority of the additional variables collected in 2004 and 2005 as

predictors in step 2. Also, 2 nests that I believed to have been abandoned due to researcher effects during deployment of video systems were excluded from analyses.

RESULTS

Raven Removal

Females nesting at greater distances from the raven removal route tended to be less likely to succeed than females located near the raven removal route ($t_{3,30} = 1.92$, $P = 0.060$) (Figure 4.1). The slope parameter estimate was 0.021 ± 0.011 (binary response was coded as success = 0 and failure = 1). Using odds ratios, each kilometer away from the removal site resulted in a 2.1% increase in the odds of nest failure (odds ratio = 1.021, 95% CI = 1.00-1.04). I calculated overall nest success at 51% ($n = 83$) across 4 years. Minimum and maximum distances of nests located from the raven removal route were 0.03 and 76.73 km, respectively. I found that 93.2% (41 of 44) of successful nests were located ≤ 40 km (approximate midpoint of maximum distance) from the raven removal route and 39.0% (15 of 39) of depredated nests were ≥ 40 km from the route. I did not detect a relationship between distance of grouse nests from the raven removal route and age class ($F_{1,70}$, $P = 0.901$).

An increase in raven abundance was related to a decrease in nest success ($t_{3,72} = 2.17$, $P = 0.033$) (Figure 4.1). Slope parameters of this model were 0.139 ± 0.064 (success = 0 and failure = 1). An increase in indices of 1 observed raven (per 10 km) of survey was associated with an approximately 15% increase in the odds of nest failure (odds ratio = 1.149, 95% CI = 1.012-1.306). The inflection point of a logistic response curve was 7.29 ravens observed per 10 km. I found 39% (27 of 69) of nests failed at

raven indices that were less than 7.29 ravens (inflection point) and 77% (10 of 13) of nests failed at indices greater this value.

Distance from the raven removal route was strongly related to the probability of a nest destroyed by ravens (LogXact Test, $P = <0.001$) (Figure 4.2). Slope parameter estimate was 0.121 ± 0.036 . A 1 km increase away from the raven removal route was associated with a 13% increase in probability of raven depredation (odds ratio = 1.13, 95% CI = 1.06-1.23). Therefore, as distance from the raven removal route increased, ravens were more likely to be responsible for nest depredation. The calculated inflection point predicting a 50% probability of nest depredated by ravens was approximately 48.1 km from the raven removal route.

All videoed nest depredations were caused by ravens ($n = 9$) and badgers ($n = 7$) (Chapter 1). An additional raven depredation was directly observed in the field. In considering only those nests depredated by confirmed predators, I found all nests at distances >48.1 km (inflection point of raven depredation curve) from the raven removal route ($n = 9$) were caused by ravens, whereas 1 of 9 (11%) raven-caused predations were within 48.1 km. The minimum distance of a raven depredation was 21.0 km. Also, most badger depredations (86%) were located within 15 km of the raven removal route, and maximum distance of a badger depredation was 21.6 km.

Indices of raven abundance was directly related to the probability of a raven-caused nest depredation (LogXact Test, $P = <0.001$) (Table 4.4 and Figure 4.2). The estimated slope parameter was 0.234 ± 0.078 (successful nests = 0, raven depredation = 1). Every 1 unit increase in ravens observed (per 10 km) was associated with a 26% increase in the odds of a nest being depredated by ravens (odds ratio = 1.26, 95% CI =

1.11-1.51). The inflection point of the logistic response curve was approximately 7.7 ravens (per 10 km).

Sage-grouse Nest Success Models

Step 1. —When comparing 63 competing predictive models of variables that were studied during 2002-2005, I found that nest success was best described by age of grouse and raven abundance (Model 1, Table 4.2). This model was also derived from *post hoc* stepwise selection regression procedures. In ranking models, no other models were ≤ 2 Δ AIC. The probability that the AGE, RVN model was the best for describing nest success was 62% (ω_i). The second best-fit model consisted of age and lek route (Model 2, Table 4.2). However, this model lacked support from the data (Δ AIC ≥ 2) (Burnham and Anderson 1998). Model 1 was 3.4 (ω_i/ω_j) times more likely to be best for describing nest success than model 2 based on strength of evidence ratios (Anderson and Burnham 2002). Raven abundance and age variables were found in 4 and 2 of the top 5 models, respectively, and lek route variable was found in 1 of the 5.

When considering relative variable importance, I calculated a parameter likelihood (sum of weights of models with this variable) of 0.81 (averaged estimate, -0.803 ± 0.29) (Table 4.3) for age of grouse, which was the highest parameter likelihood of all variables considered. Adult grouse had a higher probability of nesting successfully than yearling grouse (Figure 4.3). Sixty-three percent (35 of 56) of adult grouse nested successfully, whereas 35% (8 of 23) of yearlings were successful. Using the averaged parameter estimate, the odds of an adult nesting successfully is 2.23 times greater than a yearling. Also, I calculated a parameter likelihood of 0.77 for raven abundance (averaged estimate, -0.149 ± 0.49), a strong relative effect (Table 4.3).

Step 2. —When challenging the best-fit model derived in Step 1 with microhabitat characteristics that were measured in 2004-2005, I found that the same top variables, age and raven abundance, remained as the best-fit model (Model 6, Table 4.2). However, models 7-9 also showed substantial support from the data ($\Delta AIC \leq 2$). The probability that the model 6 was the best for describing nest success during 2004-2005 was 29% (ω_i). Model 6 was 1.4, 2.3, and 2.6 times (ω_i/ω_j) more likely to describe nest success than models 7, 8, and 9, respectively. The second best-fit model consisted of raven abundance and mean forb biomass (Model 7, Table 4.2). The third best-fit model matched *post hoc* stepwise selection procedure and consisted solely of raven abundance (Model 8, Table 4.2) while the fourth best model consisted of raven abundance and mean biomass of grass (MGR) (Model 9, Table 4.2).

Microhabitat and Predator Relationships

Using a univariate logistic analysis, I found canopy cover had a strong inverse relationship with probability of raven-caused depredation (LogXact Test, $P = 0.004$) (Figure 4.2) and was the most important habitat variable in predicting raven depredation (Table 4.4). The estimated slope-parameter was -0.078 ± 0.031 . I calculated an 8% increase in the odds of raven-caused depredation for every 1% decrease in canopy cover (odds ratio = 1.08, 95% CI = 1.02-1.15). The inflection point (50% probability) on a logistic response curve was at approximately 16.41%. Using videography, I identified ravens as the nest predator at 4 of 5 (80%) nests with $<16.41\%$ canopy cover, whereas ravens depredated 4 of 35 (11%) nests with $>16.41\%$ canopy cover. Sagebrush canopy was approximately 7% less than total shrub canopy. When measuring canopy of

sagebrush only, cover was 18.4 ± 5.1 at raven depredated sites and 34.6 ± 2.46 at successful nests.

Badger-caused depredations were directly related to understory visual obstruction (50 m) (LogXact Test, $P = 0.002$, estimate = 0.103 ± 0.042) and dry biomass of forbs (LogXact Test, $P = 0.010$, estimate = 0.700 ± 0.131) and grasses (LogXact Test, $P = 0.070$, estimate = 0.226 ± 0.126) (Table 4.5). I found badger-caused depredations more often in areas where visual obstruction and vegetation biomass were greatest (Figure 4.2). Furthermore, 70% (16 of 23) of video-recorded ground squirrel encounters at nests were near the southernmost lek route, where badgers were responsible for all video-recorded depredations ($n = 6$). Ground squirrels did not cause egg depredation, despite videographic documentation of frequent encounters with sage-grouse eggs (Chapter 1).

I detected significant differences between means of biomass of grass, 50-m understory visual obstruction, and shrub canopy cover between nests depredated by predator species (Table 4.6). Understory visual obstruction (50-m scale) at nests depredated by ravens ($56.9 \pm 2.8\%$) was less than nests depredated by badgers ($71.2 \pm 4.8\%$). Nests depredated by badgers had greater canopy cover ($46.8 \pm 6.9\%$) than those of ravens (23.8 ± 6.3) and biomass of grass and forbs was greater at badger depredation sites (9.1 ± 1.0) than at ravens (5.8 ± 0.9).

I found a substantial negative correlation between indices of raven abundance and canopy cover ($r = -0.477$, $P = 0.001$) and a positive correlation between raven abundance and biomass of grasses ($r = 0.317$, $P = 0.016$) (Table 4.7). Indices of badger activity were correlated to biomass of forbs ($r = 0.489$, $P = 0.001$) and understory visual obstruction

(50-m, $r = 0.45$, $P = 0.002$; nests, $r = 0.258$, $P = 0.055$). Shrub canopy cover may have been positively correlated to badger activity ($r = 0.261$, $P = 0.092$).

DISCUSSION

This study provides several new findings important to sage-grouse reproduction and management. Index of raven abundance was strongly associated with nest failure and raven-caused depredation indicating that, at high abundances, ravens can strongly influence sage-grouse reproduction. Second, reducing a local raven population appeared to increase local sage-grouse nest success. Third, I identified distinct differences in shrub canopy cover, understory visual cover (50-m), and dry biomass of forbs between raven- and badger-caused depredations. These differences are helpful in understanding patterns of nest failure and also may explain why it can be difficult to detect key microhabitat variables affecting overall nest success.

Grouse that nested at greater distances from the raven removal had a lower probability of nest success. In my study, the confidence interval (95%) of the estimated slope parameter of my model only slightly exceeded zero (0.001). Further studies will be necessary to increase the precision of estimated parameters of raven removal effects. The presence of a public landfill and private livestock carcass waste disposal area at the northernmost study area likely contributed to raven numbers in the north, which, in turn, may have contributed to increased nest depredation at greater distances from the raven removal site. However, at least part of the gradient between low raven numbers in the south and higher raven numbers in the north at my study area was due to decreasing raven numbers at the treatment site (Chapter 3). Furthermore, greater nest success near the removal area is consistent with a previous study, which consisted of a plot design to

compare a raven removal area from a control area and reported nest success at 35% and 3%, respectively (Batterson and Morse 1948).

The effect of local raven abundance in explaining local nest success was substantially stronger than was the distance from raven removal route effect. The difference between these effects has multiple possible explanations. The raven removal method appeared to significantly reduce raven numbers, but caused only short-term (i.e., <1 year) reductions in numbers because of reoccupation of territories by ravens (Chapter 3). Thus, ravens were not consistently absent near the raven removal route throughout sage-grouse nesting period but, rather, were held at low numbers. Many non-breeding ravens without territories are transient (Boarman and Heinrich 1999) and can travel 40-65 km in a day (Engel and Young 1992, Heinrich et al. 1994). Although I did not measure raven movements, I observed ravens absent from the treatment site for a few days following each CPTH treatment and then present in small numbers until reapplication (Chapter 3). Furthermore, I found high variation in raven numbers among sites away from the raven removal area, some of which were naturally lower than the raven removal area. The landfill and private disposal area likely increased raven numbers to the north of the raven removal site, which would be consistent with a landfill that caused high raven numbers in the California (Boarman et al. 2006). Indices of local raven abundance appears to be a more direct and informative measure than distances from a removal area in relation to local nest success.

The reported effectiveness of corvid removal strategies is equivocal. For example, corvid removal did not affect nest success of ducks (Clark et al. 1995), willow ptarmigan (*Lagopus lagopus lagopus*) (Parker 1984), and golden plover (*Pluvialis apricaria*) (Parr

1993), but success increased as a function of removing corvids for willow ptarmigan (Erikstad et al. 1982), and capercaillie (*Tetrao urogallus*) (Summers et al. 2004). Here, badger depredations may have partially compensated for the removal of ravens resulting in the relatively small effect size of distance from raven removal route on nest success. Badgers were responsible for depredating 41% (7 of 17) of video-monitored depredated nests and 4 of 7 of these badger depredations were within 3 km of the raven removal route, where indices of raven abundance were low (Chapter 3). Furthermore, no raven depredations were video-recorded within 20 km of the route. The presence of mammalian compensatory predators may nullify effects of corvid removal on game birds (Parker 1984, Clark et al. 1995). My data are consistent with this interpretation insofar as video evidence showed that badgers were more responsible for depredation near the raven removal site than other areas. In other settings, where mammalian predators were absent from study areas, nest success increased following corvid removal (Erikstad et al. 1982).

If corvid removal is being considered as an option to increase sage-grouse nest success, managers should first identify predators within the community for possible compensatory effects. Studies of multiple species removal strategies have been shown to be effective (Duebbert and Lokemoen 1980, Littlefield 2003), perhaps because compensatory species were targeted. For example, nest success of pheasants (*Phasianus colchicus*) in Minnesota more than doubled when skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and American crows were concurrently removed (Chesness et al. 1968).

Raven removal causes only short-term reductions in raven populations (Chapter 3) and, thus, is a short-term management prescription for increasing nest success close to raven removal areas. A review of 20 studies (Côté and Sutherland 1997) concluded that

predator removal can have positive, significant effects on hatching success and post-breeding populations but had unclear effects on size of breeding populations.

Effectiveness of corvid removal appears to depend on composition of the predator community and may be appropriate only at the local scale in areas where corvids are found to be important predators. Furthermore, removing corvids may aid short-term objectives in sage-grouse management such as enhancing harvestable population but may be less likely to succeed in fulfilling long-term conservation objectives such as restoring and expanding populations (Côté and Sutherland 1997).

Other factors, including other nest predators, undoubtedly are responsible for some nest predation. I video-recorded a domestic cow directly damaging a sage-grouse nest. Also, I suspected that 2 nests were abandoned because of the presence of livestock at nest sites based on video images. In Wyoming, domestic livestock were thought to cause nest abandonment based on images by remote sensing cameras (Holloran and Anderson 2001).

I found a difference in nesting success between age classes and no difference in the proportion of yearlings to adults among study areas. The difference in nest success between age classes appears to be linked to the strong differences in incubation behavior between yearlings and adults (Chapter 2). Because female sage-grouse are cryptically colored (Schroeder et al. 1999) and demonstrate cryptic behavior (i.e., motionlessness) to protect eggs (Chapter 1) differences in daily activity level (i.e., movement) on and near nests may influence predation rates. Three important differences in incubation rhythms between yearlings and adults likely affect vulnerability to predation (Chapter 2). First, both age classes demonstrated a strong bimodal recess pattern. Adult grouse, however,

tended to recess during periods of low light levels. Seemingly, they avoided detection by visually-cued predators (e.g., ravens) at daylight and nocturnal predators (e.g., badgers) at night. Yearlings, on the other hand, often recessed during daylight hours. Adults also took shorter recess bouts than yearlings and had greater incubation constancy. Grouse also decreased recess duration in relation to increased raven abundance, indirectly suggesting that longer recess bouts may increase probability of nest detection by visually-cued predators like ravens because of increased parental movement near nests (Conway and Martin 2000). Visually-cued predators likely detect movements of birds as they move to and from nests (Deeming 2002) and adults exhibited fewer movements than yearlings (Chapter 2). In a separate study, yearling nest success was numerically lower than adult nest success in Idaho (Lowe 2006), which had remarkably similar nest success rates to those reported here but was limited by low sample sizes.

The relationship between reduced canopy cover and increased raven abundance may compound negative effects on sage-grouse reproduction. Greater shrub interspace distance may provide ravens with less visual obstruction to locate nests. Because grouse nest typically under a shrub canopy (Connelly et al. 1991, Schroeder et al. 1999), female grouse may avoid detection with increased shrub cover. The continuing loss of sagebrush has led to substantial fragmentation of sage-grouse habitat (Braun et al. 1976, Swenson et al. 1987, Knick et al. 2003) and corvid densities are reported to be greatest in fragmented landscapes (Luginbuhl et al. 2001). Numerous authors have described clear, positive correlations between corvid abundance and predation of both artificial (Angelstam 1986, Andrén 1992) and real (Johnson et al. 1989) nests of ground nesting birds.

High rates of depredation by corvids are associated with grassland (Winter and Faaborg 1999), fragmented shrubsteppe (Vander Haegen et al. 2002) and forested landscapes (Andrén 1992, Hartley and Hunter 1998), perhaps due to the interaction between increased corvid abundance and loss of vegetation for concealment (Evan 2004). Corvid abundance was reported to be greater in cropland at broad spatial scales, while sharp-tailed grouse nests were significantly more likely to succeed in landscapes of low corvid abundance (Manzer and Hannon 2005). The positive relationship between nest success and herbaceous canopy cover found in other studies (Wallestad and Pyrah 1974, Gregg et al. 1994) may be due to predators in those communities being visually cued as I suggest for ravens in this study.

Human-made structures in the environment (Boarman 1993, Boarman and Heinrich 1999, Boarman 2003) may further increase the effect of raven predation, particularly in low canopy cover areas, by providing ravens with perches from which they can scan the landscape, especially in areas where natural perching substrate is not available for raptors (Ellis 1984, Braun 1998). Sage-grouse may avoid nesting areas near anthropogenic elevated structures to avoid predation (Braun 1998). Moreover, a recent study attributed increased sage-grouse nest depredation to high corvid abundances which, in turn, was caused by anthropogenic food and perching subsidies in areas of natural gas development in western Wyoming (Holloran 2005). Ravens used power-lines for perching and nesting more than their percent of availability and more than natural substrate in the environment (e.g., trees, cliffs) (Knight and Kawashima 1993, Steenhof et al. 1993).

Female sage-grouse employ unusually high incubation constancy (96%) and, like other uniparental incubators balance the requirements of metabolic needs, incubation, and egg concealment (Chapter 2) (Deeming 2002). Incubation recess bouts are shorter in areas of high raven abundance, perhaps to avoid detection by ravens (Chapter 2). However, the probability of depredation substantially increased with raven abundance despite the differences in incubation behavior. The percent of time grouse spend away from the nest is reduced with greater understory cover (Chapter 2). I hypothesize that understory cover contributes to parental energy savings by influencing nest microclimate and water availability (Chapter 2). Therefore, reduced cover (understory and overstory) may have multiple effects on detection of nests by predators including less visual obstruction caused by vegetation (Bowman and Harris 1980, Gregg et al. 1994) and also the increased on- and off-nest movements by grouse, as a function of energetic constraints during incubation. These constraints may be particularly important for yearlings, which appear to rely less on endogenous nutrients during incubation and more on foraging (Chapter 2).

The positive relationship between probability of badger depredation and increased forb biomass and understory visual obstruction at a 50-m scale may be indirect. The principle prey of badgers are burrowing rodents, particularly ground squirrels (Messick and Hornocker 1981, Goodrich and Buskirk 1998). Forbs and bunchgrasses provide important food sources for ground squirrels in shrub-steppe communities (Yensen and Quinney 1992, Yensen et al. 1992) and are positively related to ground squirrel population densities (Parmenter and MacMahon 1983, Dobson and Kjelgaard 1985, Van Horne et al. 1997). In my study, indices of badger activity were correlated to forb

biomass and to understory visual obstruction. Badger activity is strongly, positively correlated to ground squirrel abundance (Yensen et al. 1992). Badger home-ranges often overlap in areas of high squirrel density (Messick and Hornocker 1981, Messick et al. 1981, Minta 1990). In this study, the majority of video-recorded encounters by ground squirrels at sage-grouse nests (70%) were in areas where badgers depredated nests (Chapter 1). If index of badger activity was a proxy for badger abundance, then badgers appeared to find and depredate sage-grouse nests in areas of greater vegetation understory where badger principle prey (e.g., squirrels) abundance was high. The hypothesis of association of vegetation, alternative prey with badger abundance and increased predation was proposed following observations of artificial sage-grouse nests (Ritchie et al. 1994). Alternative prey has also been shown to influence probability of depredation by specific predators in other ground nesting birds (Klimstra and Roseberry 1975, Crabtree and Wolfe 1988, Staller et al. 2005).

In my study, herbaceous cover did not appear to deter badgers identified by videography, perhaps because badgers rely on olfaction for locating prey (Messick 1987). Conversely, a study in Oregon suggested that predation by mammals was possibly reduced with increased vertical cover at artificial nests (DeLong et al. 1995). However, my study was different in that all badger depredations occurred while incubating grouse were present, perhaps increasing the probability of badgers using scent to detect females and their nests. Similarly, dense cover does not affect waterfowl nest predation by olfactory-cued mammals (Crabtree and Wolfe 1988, Fleskes and Klaas 1991, Sargeant et al. 1993). However, loss of understory cover in these areas likely would have a negative effect on nest success. Sage-grouse will choose areas of increased herbaceous cover for

nesting (Wakkinen 1990, Connelly et al. 1991) and these areas may be important habitats for source populations, especially at the landscape scale (Aldridge 2005).

Areas that lose key habitat features (caused by natural or anthropogenic effects) may experience changes in predation rates but still may be selected by grouse as nest sites. These areas can become ecological traps (Battin 2004, Shochat et al. 2005) creating sink populations, as suggested for sage-grouse in areas of Alberta, Canada (Aldridge 2005). Badger predation appears to be a natural component of grouse reproduction. However, habitat change may interact with predation pressure (Evans 2004) by increasing opportunities for subsidized generalist predators (e.g., ravens) (Boarman 1993, 2003, 2006) to depredate nests.

Differences in habitat measurements at nests between badgers and ravens explain why I did not identify single habitat features universally associated with nest success. Variables that were strongly correlated to nest predation, i.e., ravens (decreased canopy cover) and badgers (increased forb biomass and understory obstruction), differed significantly between ravens and badgers, indicating the relative importance of habitat characteristics varies with predator composition. Interactions between habitat features and predator communities should be evaluated when measuring factors that influence nest success. Otherwise, differences in predator communities between study areas may confound results and lead to inconsistencies in the apparent relative importance of variables on nest success. Authors have documented grass height (Gregg et al. 1994, Aldridge and Brigham 2002, Holloran et al. 2005), shrub height (Gregg et al. 1994, DeLong et al. 1995), canopy cover (Wallestad and Pyrah 1974, Watters et al. 2002), understory cover (Gregg et al. 1994, DeLong et al. 1995), and species of nesting shrub

(Connelly et al. 1991) to be central sage-grouse nest success, while others have found negative or no relationships between nest success and grass height (Wakkinen 1990), shrub height (Autenrieth 1981, Sveum et al. 1998), canopy cover (Ritchie et al. 1994), understory cover (Aldridge and Brigham 2002), and species of nesting shrub (Autenrieth 1981, Sveum et al. 1998). These discrepancies may be explained by predator composition and abundance.

The direct relationship I detected between probability of depredation and the indices of abundance and activity of ravens and badgers, respectively, supports the hypothesis that nest depredation increases with increasing predator densities (Angelstam 1986, Ritchie et al. 1994). Raven abundance indices were highest at lek-routes with low badger activity and vice versa. These findings are similar to those reported about badger and crow relationships in the Canadian prairie pothole region (Johnson et al. 1989).

One important distinction between sage-grouse predators is that ravens, unlike badgers, thrive in human-altered landscapes (Boarman 1993, Luginbuhl et al. 2001, Boarman 2003) and appear to forage in degraded sage-grouse nesting habitat. Well designed studies are needed to identify the most important human alterations that influence raven abundances in sage-grouse habitat. Raven indices were highly correlated to nest failure and raven numbers appear higher in areas of degraded habitat. Loss of suitable nesting habitat coupled with greater abundance of ravens may result in increased raven predation on sage-grouse nests. The inflection points of models using raven abundance to predict nest success and raven-caused depredation were similar, 7.3 and 7.7 ravens (per 10 km), respectively. This indicates that landscapes with greater raven

abundances may be at risk to increased raven depredation rates at least in the habitat types evaluated in this study.

An interaction between habitat loss and raven abundance may lead to hyperpredation (Crooks and Soule 1999, Courchamp et al. 2000) of sage-grouse nests, as ravens are thought to do to desert tortoise (*Gopherus agassizii*) (Kristan and Boarman 2003) and other prey, and may result in declines in local sage-grouse populations. This combination may be especially acute in areas of northeastern Nevada that have high raven numbers and low shrub cover, such as the northernmost portion of my study. Research that identifies the degree of overlap in distributions of ravens and sage-grouse, estimates raven densities, and measures relative effects of possible raven overabundance would be beneficial to local sage-grouse population management.

Table 4.1. Explanatory variables characterizing predators, age of grouse, and microhabitat used in an information theoretic approach to model nest success and used in exact regression models to predict probability of depredation by each predator species of greater sage-grouse in northeastern Nevada during 2002-2005.

| Variables | Description | n ^a | mean | ±SE ^b |
|---------------------------|---|----------------|--------|------------------|
| Predator variables | | | | |
| RVN | Index of raven abundance in relation to sage-grouse nests (No. of ravens /10 km) | 77 | 2.88 | 0.28 |
| BDG ^c | Index of badger activity (# of dens and digs per 3.2 km) | 47 | 13.11 | 1.97 |
| Age variable | | | | |
| AGE | Age of grouse (< or >1 year of age) | 77 | | |
| Timing variables | | | | |
| NI | Nest initiation ordinal date (days elapsed between 1 January and nest initiation date) | 77 | 120.40 | 1.26 |
| YR | Year of nest (2002-2005) | | | |
| Nesting habitat variables | | | | |
| LR | Nearest lek route to nest (grouse were captured from 4 lek routes) | | | |
| NVO | Nest understory visual obstruction (% visual obstruction using checkered board at zero and 45° angles) | 77 | 76.10 | 0.82 |
| 50VO | 50 m understory visual obstruction (% obstruction using checkered board in nest area) | 77 | 56.50 | 0.81 |
| MFB ^d | Biomass of forbs (average dry mass [g] of 16 micro-plots within 50 m of each other centered around nests) | 58 | 1.90 | 0.09 |
| MGR ^d | Biomass of grass (average dry mass [g] of 16 micro-plots within 50 m of each other at nest areas) | 58 | 3.08 | 0.38 |
| CC | Shrub canopy cover (%) along four, 25 m line transects measured using line-intercept method | 77 | 40.50 | 1.08 |
| HT | Height of shrubs (cm) along four, 25 m line transects intersecting at nest bowl | 77 | 39.32 | 1.40 |
| HT ² | Quadratic function of HT | | | |
| NHT | Height of shrub (cm) directly above nest bowl | 77 | 66.19 | 2.44 |
| NHT ² | Quadratic function of NHT | | | |

^a Represents sample size.

^b Represents standard error of the sample mean.

^c Index of badger activity was not included as an explanatory variable using information criterion because badger activity did not vary with incubation period within transects.

^d Dry biomass of forbs and grasses were measured during 2004-2005 only and the effects of these variables were tested against the best-fit model representing data from 2002-2005.

Table 4.2. Logistic models explaining nest success of greater sage-grouse in relation to predators, age of grouse, and microhabitat variables in northeastern Nevada, during 2002-2005.

| Model ^a | Variables | K ^b | -2LL ^c | L R ² ^d | ΔAIC ^e | ω _i ^f |
|---------------------|-----------|----------------|-------------------|-------------------------------|-------------------|-----------------------------|
| Step 1 ^g | | | | | | |
| 1* | RVN AGE | 3 | 86.33 | 0.22 | 0.00 | 0.62 |
| 2 | LR AGE | 6 | 81.92 | 0.26 | 2.46 | 0.18 |
| 3 | RVN | 2 | 94.13 | 0.14 | 5.63 | 0.04 |
| 4 | RVN NI | 3 | 91.96 | 0.16 | 5.63 | 0.04 |
| 5 | RVN 50VO | 3 | 93.50 | 0.14 | 7.17 | 0.02 |
| Step 2 ^h | | | | | | |
| 6 | RVN AGE | 3 | 68.71 | 0.18 | 0.00 | 0.29 |
| 7 | RVN MFB | 3 | 69.42 | 0.17 | 0.71 | 0.21 |
| 8* | RVN | 2 | 72.62 | 0.12 | 1.69 | 0.13 |
| 9 | RVN MGR | 3 | 70.58 | 0.15 | 1.87 | 0.12 |
| 10 | AGE MGR | 3 | 71.61 | 0.13 | 2.90 | 0.07 |

^a Top 5 models from steps 1 and 2. Asterisks (*) denotes *post hoc* model selection using stepwise procedures. Main effects were retained in all models with quadratic functions.

^b Number of parameters estimated in model (Anderson and Burnham 2002).

^c -2 Log-likelihood

^d R² based on likelihood-ratio test, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where LogL_m, and LogL_o are log-likelihood of models of interest and intercept, respectively, and *n* is number of observations (Magee 1990).

^e ΔAIC represents difference between model of interest and best-fit model of those considered.

^f Akaike's ω_i represents the probability that model is best among those considered (Anderson et al. 2000).

^g Step 1 compared models of variables collected during 2002-2005. Best-fit models had ΔAIC ≤ 2 because of substantial support from the data (Anderson and Burnham 1998). I used 63 candidate models.

^h Step 2 challenged the variables from the best-fit model derived from step 1 with additional for variables collected during 2004-2005. I used 15 candidate models.

Table 4.3. Relative importance of estimated parameters from logistic regression models of nest success of greater sage-grouse in northeastern Nevada during 2002-2005.

| Variable | Estimate ^a | ±SE ^b | L R ² ^c | P L ^d |
|----------|-----------------------|------------------|-------------------------------|------------------|
| AGE | -0.803 | 0.290 | 0.07 | 0.81 |
| RVN | -0.149 | 0.049 | 0.14 | 0.77 |
| MFB | -0.028 | 0.016 | 0.04 | 0.34 |
| MGR | -0.258 | 0.131 | 0.07 | 0.26 |
| CC | 0.036 | 0.024 | 0.02 | 0.19 |

^a Averaged parameter estimate across all models and corrected using Akaike's weights (ω_i).

^b Averaged standard error across all models and corrected using Akaike's weights (ω_i).

^c Likelihood R²-value is based on likelihood-ratio test of the variable under consideration alone, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where LogL_m is log-likelihood of the single-variable model, LogL_o is intercept-only model, and n is number of observations (Magee 1990).

^d Parameter likelihoods were sums of model weights for models in which the tested variable was present (Burnham and Anderson 1998). Parameter likelihood indicates relative importance of the explanatory variable in the presence ≤ 2 other variables. Values < 0.05 were not included in the table.

Table 4.4. Parameter estimates and 95% CI describing relationships between probability of greater sage-grouse nest depredation by common ravens and explanatory variables measured in northeastern Nevada in 2002-2005.

Videography was used to identify predators.

| Explanatory Variable | Parameter Estimate | \pm SE ^a | 95% CI | | <i>P</i> ^b |
|----------------------|--------------------|-----------------------|--------|--------|-----------------------|
| | | | lower | upper | |
| RVN | 0.234 | 0.078 | 0.105 | 0.411 | 0.001 |
| CC | -0.078 | 0.031 | -0.146 | -0.022 | 0.004 |
| MGR | 0.167 | 0.117 | -0.626 | 0.408 | 0.148 |
| MFB | 0.157 | 0.276 | -0.403 | 0.703 | 0.564 |
| AGE | -1.046 | 0.745 | -2.756 | 0.741 | 0.300 |
| 50VO | 0.015 | 0.030 | -0.043 | 0.077 | 0.633 |
| NVO | -0.008 | 0.038 | -0.081 | 0.070 | 0.811 |
| NI | 0.001 | 0.028 | -0.056 | 0.057 | 0.968 |
| 50HT | 0.000 | 0.031 | -0.064 | 0.060 | 0.977 |
| NHT | -0.002 | 0.017 | -0.038 | 0.030 | 0.982 |

^a Standard error of parameter estimate.

^b Probability value.

Table 4.5. Parameter estimates and 95% CI describing relationships between probability of greater sage-grouse nest depredation by American badger and explanatory variables measured in northeastern Nevada using videography to identify predators during 2002-2005.

| Explanatory Variable | Parameter Estimate | \pm SE ^a | 95% CI | | <i>P</i> ^b |
|----------------------|--------------------|-----------------------|--------|-------|-----------------------|
| | | | lower | upper | |
| 50VO | 0.103 | 0.042 | 0.030 | 0.197 | 0.002 |
| MFB | 0.700 | 0.321 | 0.131 | 1.426 | 0.014 |
| BDG ^c | 0.061 | 0.031 | 0.007 | 0.121 | 0.047 |
| MGR | 0.226 | 0.126 | -0.021 | 0.489 | 0.071 |
| CC | 0.021 | 0.020 | -0.016 | 0.062 | 0.285 |
| AGE | -0.731 | 0.587 | -2.046 | 0.696 | 0.343 |
| NHT | 0.013 | 0.014 | -0.014 | 0.421 | 0.346 |
| NUC | 0.030 | 0.034 | -0.021 | 0.111 | 0.433 |
| NI | 0.009 | 0.025 | -0.030 | 0.070 | 0.810 |
| HT | -0.079 | 0.068 | -0.244 | 0.057 | 0.269 |

^a Standard error of parameter estimate.

^b Probability value.

^c Indices of badger activity at nearest transect. No nests were >300 m from transects.

Table 4.6. Comparison of means (independent t-tests) of microhabitat variables of sage-grouse nests that were unambiguously confirmed to have been depredated by ravens or badgers in northeastern Nevada during 2002-2005.

| Variable | Raven ^a | | Badger ^b | | t-value | df ^d | P ^e |
|----------|--------------------|------------------|---------------------|------------------|---------|-----------------|----------------|
| | Mean | ±SE ^c | Mean | ±SE ^c | | | |
| MGR | 4.1 | 3.4 | 9.1 | 2.5 | -3.48 | 10 | 0.006 |
| 50VO | 56.9 | 2.8 | 71.2 | 4.8 | -2.56 | 9 | 0.031 |
| CC | 23.8 | 6.3 | 46.8 | 6.9 | -2.46 | 11 | 0.032 |
| MFB | 1.7 | 1.4 | 5.4 | 4.0 | -2.02 | 4 | 0.114 |
| 50HT | 38.8 | 2.8 | 45.2 | 4.2 | -1.27 | 10 | 0.232 |
| NHT | 66.3 | 3.2 | 73.7 | 8.4 | -0.83 | 7 | 0.435 |
| NVO | 85.6 | 3.0 | 88.4 | 3.6 | -0.60 | 12 | 0.561 |
| NI | 119.9 | 3.6 | 120.1 | 2.8 | -0.05 | 14 | 0.959 |

^a Nine ravens were video identified with camouflaged, miniature cameras and time-lapse, continuous-recording VCRs. One raven was directly observed depredating nests in the field.

^b Seven badgers were identified using videography described above.

^c Standard error of sample mean.

^d Degrees of freedom.

^e Probability value.

Table 4.7. Pearson's correlation describing relationships between predator indices in relation to nest sites and nest microhabitat characteristic in northeastern Nevada during 2002-2005.

| Variable | Badger Activity ^a | | Raven Abundance ^b | |
|----------|------------------------------|----------------|------------------------------|----------------|
| | r ^c | P ^d | r ^c | P ^d |
| MFB | 0.489 | 0.001 * | -0.018 | 0.894 |
| MGR | 0.154 | 0.326 | 0.317 | 0.016 * |
| 50VO | 0.45 | 0.002 * | 0.023 | 0.864 |
| CC | 0.261 | 0.092 | -0.477 | 0.001 * |
| HT | 0.258 | 0.100 | 0.182 | 0.175 |
| NHT | 0.2 | 0.200 | -0.033 | 0.806 |
| NVO | 0.294 | 0.055 | -0.049 | 0.497 |

^a Analyses were performed at the transect level for badgers because indices of badger activity did not vary with incubation periods. Habitat features were averaged for each transect.

^b Analyses were performed at the nest level for ravens because indices of raven abundance varied with incubation periods of each grouse.

^c Pearson's product moment correlation.

^d Probability value.

* denotes a statistical significant correlation ($\alpha = 0.05$).

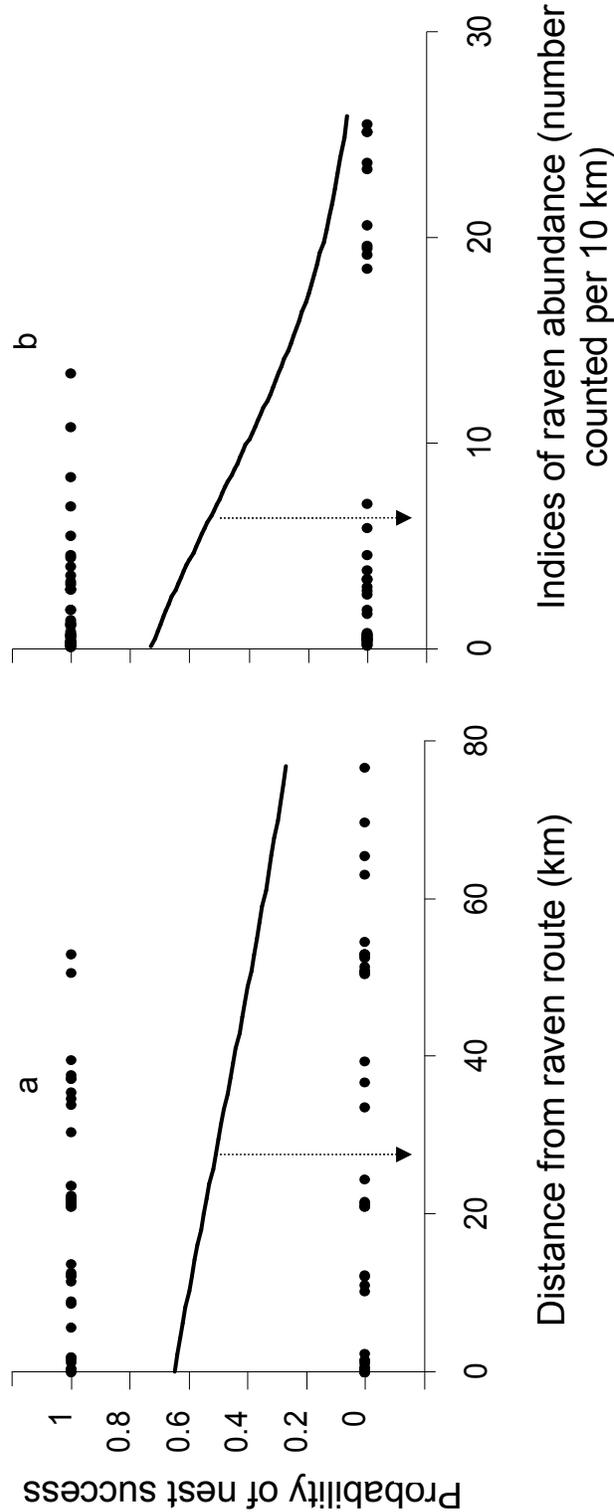


Figure 4.1. Logistic response curves predicting the probability of greater sage-grouse nest success in relation to (a) distance from common raven removal area and (b) indices of raven abundance in northeastern Nevada, 2002-2005. Dots represent observations of individual nests, 0 = failed nests and 1 = successful nests, by species of interest. Arrows represent points of inflection of response curve, which is associated to a 50% probability of nesting successfully. The point of inflection was approximately (a) 29.5 km from the raven removal route and (b) 7.3 ravens counted per 10 km.

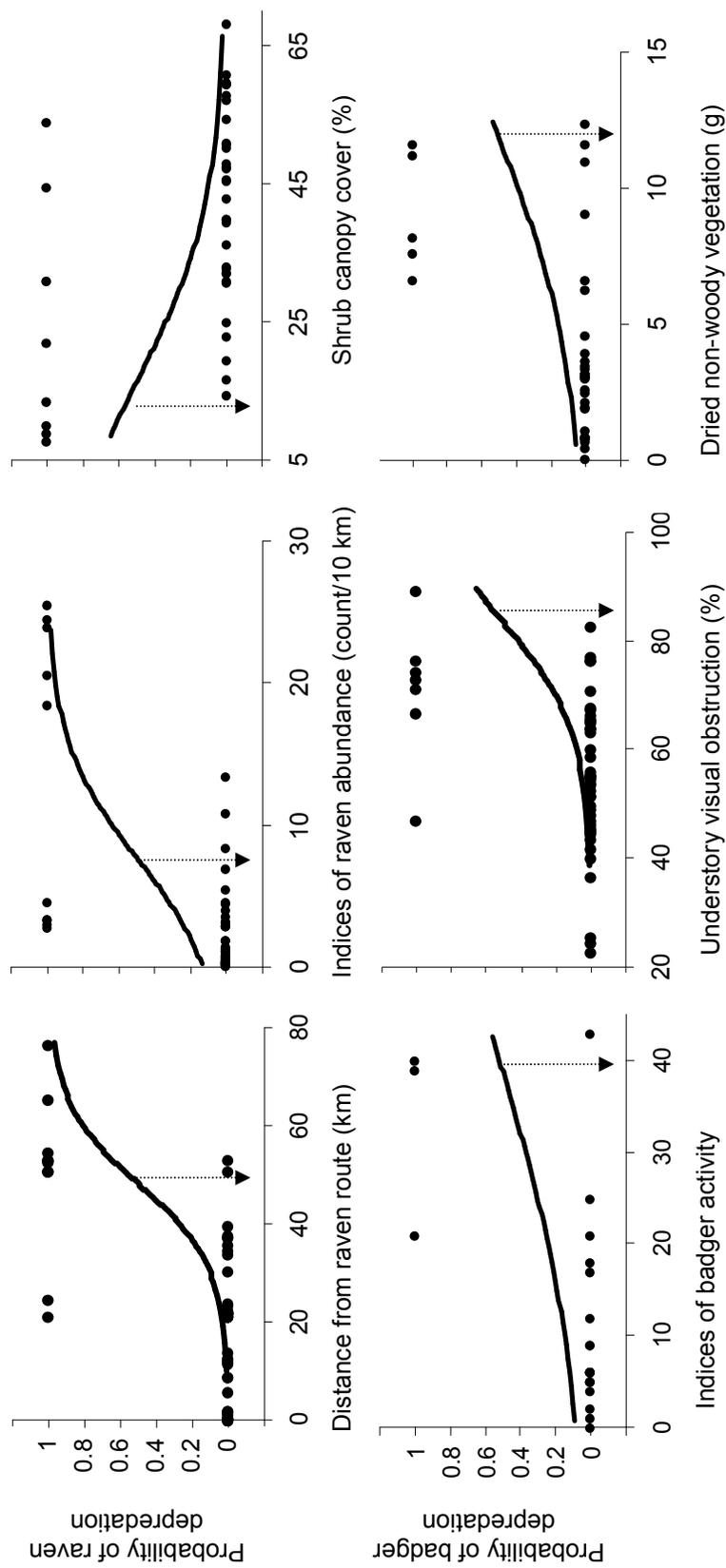


Figure 4.2. Logistic response curves predicting the probability of raven and badger depredation in relation to indices of abundance and activity, respectively, and microhabitat characteristics in northeast Nevada, 2002-2005. Dots represent observations of individual nests, 0 = successful nests and 1 = depredated nests by species of interest. Arrows represent points of inflection of response curves, which are associated to a 50% probability of species of predator depredating nests.

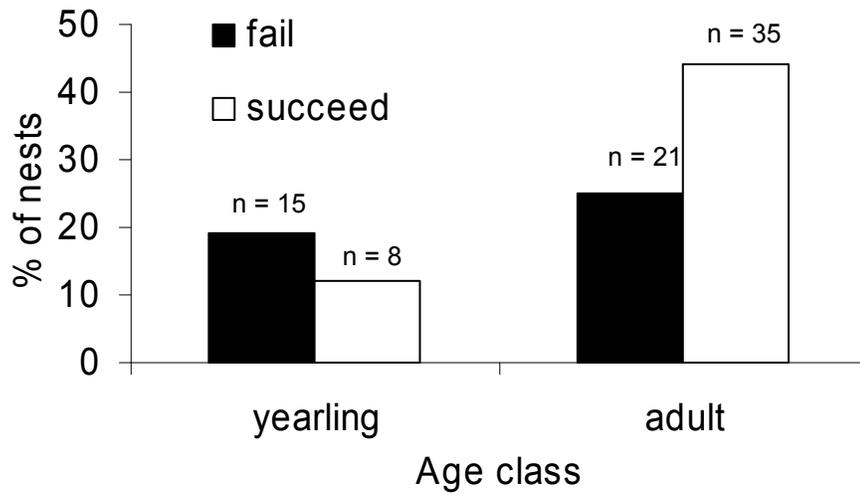


Figure 4.3. Percent of greater sage-grouse nests ($n = 79$) that were successful or failed in relation to age class in northeastern Nevada, 2002-2005.

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 R. M. Brigham. 2002. Sage-Grouse nesting and brood habitat use in southern Canada. *Journal of Wildlife Management* 66:433-444.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaksi, editors. *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, Hungary.
- Ammann, G. A. 1944. Determining the age of pinnated and sharp-tailed grouse. *Journal of Wildlife Management* 8:170-171.
- Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66: 912-918.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912-923.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794-804.
- Andrén, H., P. Angelstam, E. Lindstrom, and P. Widen. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. *Oikos* 45:273-277.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365-373.
- Ar, A., and Y. Sidis. 2002. Nest microclimate during incubation. Pages 143-160 in D. C. Deeming, editor. *Avian Incubation: Behavior, Environment, and Evolution*. Oxford University Press, New York.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game. *Wildlife Bulletin No. 9. Federal Aid in Wildlife Restoration Project W-125-R and W-160-R*. Boise, ID.

- Baines, D., R. Moss, and D. Dugan. 2004. Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology* 41:59-71.
- Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission, Oregon Fauna Service 1, Portland, Oregon. 29 pp.
- Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* 18:1482-1491.
- Bergerud, A. T. 1988. Population ecology of North American grouse. Pages 578-648 *in* A. T. Bergerud and M. W. Gratson, editors. *Adaptive Strategies and Population Ecology of Northern Grouse*. University of Minnesota Press, Minneapolis.
- 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. Miller, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. *Conservation and Resource Management*. Pennsylvania Academy of Science, Philadelphia.
- Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). *In* A. Poole and F. Gill, editors. *The Birds of North America*, No. 476. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, D.C.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing Common Raven predation on desert tortoises. *Environmental Management* 32:205-217.
- Boarman, W. I., M. A. Patten, R. J. Camp, and S. J. Collis. 2006. Ecology of a population of subsidized predators: Common ravens in the central Mojave Desert, California. *Journal of Arid Environments* 67:248-261.
- Bowman, G. B., and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest depredation. *Journal of Wildlife Management* 44:806-813.
- Braun, C. E. 1998. Sage-grouse declines in western North America: what are the problems? *Proceedings of the Western Association of State Fish and Wildlife Agencies* 78:139-156.
- Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. *Wilson Bulletin* 88:165-171.

- Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. *Wildlife Society Bulletin* 5:99-106.
- Burnham, K. P., and D. R. Anderson. 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.
- Canfield, R. H. 1941. Applications of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388-394.
- Chesness, R. A., M. M. Nelson, and W. H. Longley. 1968. The effect of predator removal on pheasant reproductive success. *Journal of Wildlife Management* 32:683-697.
- Clark, R. G., and T. D. Nudds. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. *Wildlife Society Bulletin* 19:534-543.
- Clark, R. G., D. E. Meger, and J. B. Ignatiuk. 1995. Removing American crows and duck nesting success. *Canadian Journal of Zoology* 73:518-522.
- Coates, P. S., J. O. Spencer, Jr., and D. J. Delehanty. In press. Efficacy of CPTH-treated egg baits for removing ravens. *Human Wildlife Conflicts*.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. *Journal of Wildlife Management* 55:521-524.
- Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967-985.
- Conover, M. R. 1989. Potential compounds for establishing conditioned food aversions in raccoons. *Wildlife Society Bulletin* 17:430-435.
- Conover, M. R. 1990. Reducing mammalian predation on eggs by using a conditioned taste aversion to deceive predators. *Journal of Wildlife Management* 54:360-365.
- Conway, C. J., and T. E. Martin. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* 54:670-685.

- Côté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11:395-405.
- Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modeling the hyperpredation process. *Journal of Animal Ecology* 69:154-164.
- Crabtree, R. L., and M. L. Wolfe. 1988. Effects of alternate prey on skunk predation of waterfowl nests. *Wildlife Society Bulletin* 16:163-169.
- Crooks, K. R., and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563-566.
- Deeming, D. C. 2002. Behavior patterns during incubation. Pages 63-87 *in* D. C. Deeming, editor. *Avian Incubation: Behavior, Environment, and Evolution*. Oxford University Press, New York.
- DeLong, A. K., J. A. Crawford, and D. C. DeLong. 1995. Relationship between vegetational structure and predation of artificial sage grouse nests. *Journal of Wildlife Management* 59:88-92.
- Dobson, F. S., and J. D. Kjelgaard. 1985. The influence of food resources on population dynamics in Columbian ground squirrels. *Canadian Journal of Zoology* 63:2095-2104.
- Duebbert, H. F., and J. T. Lokemoen. 1980. High duck nesting success in a predator-reduced environment. *Journal of Wildlife Management* 44:428-437.
- Ellis, K. L. 1984. Behavior of lekking sage grouse in response to a perched Golden Eagle. *Western Birds* 15:37-38.
- Engel K. A., and L. S. Young. 1992. Movements and habitat use by common ravens from roost sites in southwestern Idaho. *Journal of Wildlife Management* 56:596-602.
- Erikstad, K. E., R. Blom, and S. Myrberget. 1982. Territorial hooded grows as predators on willow ptarmigan nests. *Journal of Wildlife Management* 46:109-114.
- 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.

- Fleskes, J. P., and E. E. Klaas. 1991. Dabbling duck recruitment in relation to habitat and predators at Union Slough National Wildlife Refuge, Iowa. U. S. Fish and Wildlife Service Technical Report 32, Washington, D. C. 19 pp.
- Garrott, R. A., P. J. White, and C. A. V. White. 1993. Overabundance: An issue for conservation biologists? *Conservation Biology* 7:946-949.
- Garton, E. O., J. T. Ratti, and J. H. Giudice. 2005. Research and experimental design. Pages 43-71 in C. E. Braun, editor. *Techniques for Wildlife Investigations and Management*. Sixth Edition. The Wildlife Society, Bethesda.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- Goodrich J. M., and S. W. Buskirk. 1998. Spacing and ecology of North American badgers (*taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex. *Journal of Mammalogy* 79:171-179.
- Greenwood, R. J. 1986. Influence of striped skunk removal on upland duck nest success in North Dakota. *Wildlife Society Bulletin* 14:6-11.
- 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.
- Hartley, M. J., and M. L. Hunter, Jr. 1998. A meta-analysis of forest cover, edge effects, and artificial nest rates. *Conservation Biology* 12:465-469.
- Heinrich, B., D. Kaye, T. Knight, and K. Schaumburg. 1994. Dispersal and association among common ravens. *Condor* 96:545-551.
- Herranz, J., M. Yanes, and F. Suárez. 2002. Does photo-monitoring affect nest predation? *Journal Field Ornithology* 73:97-101.
- Hirji, K. F., C. R. Mehta, and N. R. Patel. 1987. Computing distributions for exact logistic regression. *Journal of the American Statistical Association* 82:1110-1117.
- Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. 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., B. J. Heath, A. J. Lyon, S. J. Slater, and J. L. Kuipers, S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal Wildlife Management* 69:638-649.
- Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to arcview. Alaska Biological Science Center, U.S. Department of the Interior, Geological Survey, Anchorage.
- Johnson, D. H., A. B. Sargeant, and R. J. Greenwood. 1989. Importance of individual species of predators in nesting success of ducks in the Canadian Prairie Pothole Region. *Canadian Journal of Zoology* 67:291-297.
- Jones, R. E. 1968. A board to measure cover used by prairie grouse. *Journal of Wildlife Management* 32:28-31.
- Klimstra, W. D., and J. L. Roseberry. 1975. Nesting ecology of the bobwhite in southern Illinois. *Wildlife Monographs* No. 41. 37 pp.
- Klett, A. T., T. L. Shaffer, and D. H. Johnson. 1988. Duck nest success in the Prairie Pothole Region. *Journal of Wildlife Management* 52:431-440.
- Kristan, W. B., and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84:2432-2443.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.
- Knight, L. R., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management* 57:266-271.
- Kullback, S., and R. A. Leibler. 1951. On information and sufficiency. *Annals of Mathematical Statistics* 22:79-86.
- Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. *Journal of Animal Science* 76:1216-1231.

- Littlefield, C. D. 2003. Sandhill crane nesting success and productivity in relation to predator removal in southeastern Oregon. *Wilson Bulletin* 115:263-269.
- Lowe, B. S. 2006. Greater sage-grouse use of three-tip sagebrush and seeded sagebrush-steppe. Thesis, Idaho State University, Pocatello.
- Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael, and D. E. Varland. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. *Journal of Field Ornithology* 72:556-572.
- Magee, L. 1990. R^2 measures based on Wald and likelihood ratio joint significance tests. *American Statistician* 44:250-253.
- Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. *Journal Wildlife Management* 69:110-123.
- Martin, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. *BioScience* 43:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65:101-127.
- Messick, J. P. 1987. North American badger. Pages 586-597 in M. Novak, J. A. Baker, M. E. Obbard, B. Mallock, editors. *Wild Furbearer Management and Conservation in North America*. Ontario Trappers Association Ministry of Natural Resources, Toronto, Ontario.
- Messick, J. P., and M. G. Hornocker. 1981. Ecology of the badger in southwestern Idaho. *Wildlife Monographs* 76. 53 pp.
- Messick, J. P., M. C. Todd, and M. G. Hornocker 1981. Comparative ecology of two badger populations. Pages 1290-1304 in J. Chapman and D. Pursley, editors. *Proceedings of the World-wide Furbearer Conference*. International Association of Fish and Wildlife Agencies, Washington, D.C.
- Minta, S. C. 1990. The badger, *Taxidea taxus* (Carnivora: Mustelidae): spatial—temporal analysis, dimorphic territorial polygyny, population characteristics, and human influences on ecology. Dissertation, University of California, Davis.

- Nelson, O. C. 1955. A field study of sage grouse in southeastern Oregon with special reference to reproduction and survival. Thesis, Oregon State University, Corvallis.
- Parmenter, R. R., and J. A. MacMahon. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. *Oecologia* 59:145-156.
- Parker, H. 1984. Effect of corvid removal on reproduction of willow ptarmigan and black grouse. *Journal of Wildlife Management* 48:1197-1205.
- Parr, R. 1993. Nest predation and numbers of Golden Plovers *Pluvialis apricaria* and other moorland waders. *Bird Study* 40:223-231.
- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal Wildlife Management* 64:71-87.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecological Systematics* 28:289-316.
- Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *Auk* 120: 371-383.
- Ritchie, M. E., M. L. Wolfe, and R. Danvir. 1994. Predation of artificial sage grouse nests in treated and untreated sagebrush. *Great Basin Naturalist* 54:122-129.
- Sargeant, A. B., and P. M. Arnold. 1984. Predator management of ducks on waterfowl production in areas in the northern plains. *Proceedings of the Eleventh Vertebrate Pest Conference* 59:328-336.
- Sargeant, A. B., R. J. Greenwood, M. A. Sovada, and T. L. Shaffer. 1993. Distribution and abundance of predators in the Prairie Pothole Region that affect duck production. U.S. Fish and Wildlife Service Resource Publication 194. 96pp.
- 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, and J. Fallon. 2004. The North American Breeding Bird Survey, Results and Analysis 1966-2003. Version 2004.1. United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
- Schneider, M. F. 2001. Habitat loss, fragmentation, and predator impact: spatial implications for prey conservation. *Journal of Applied Ecology* 38:720-735.
- Schroeder, M. A., J. A. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In A. Poole and F. Gill, editors. *The Birds of North America*. No. 425. Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. B. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deirbert, S. C. Gardner, M. A. Hilliard, G. D. Kobridger, 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
- Shochat, E., M. A. Patten, D. W. Morris, D. L. Reinking, D. H. Wolfe, and S. K. Sherrod. 2005. Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos* 111:159-169.
- Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* 12:564-575.
- Spencer, J. O., Jr. 2002. DRC-1339 use and control of common ravens. *Proceedings of the Vertebrate Pest Conference* 20:110-113.
- Staller, E. L., W. E. Palmer, J. P. Carroll, R. P. Thornton, and D. C. Sisson. 2005. Identifying predators at northern bobwhite nests. *Journal Wildlife Management* 69:124-132.
- Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. *Journal of Wildlife Management* 57:271-281.

- Summers, R. W., R. E. Green, R. Proctor, D. Dugan, D. Lambie, R. Moncrieff, R. Moss, and D. Baines. 2004. An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *Journal of Applied Ecology* 41:513-525.
- Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage grouse in south-central Washington. *Journal of Range Management* 51:265-269.
- Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. *Biological Conservation* 41:125-132.
- Van Horne, B., G. S. Olson, R. L. Schooley, J. G. Corn, and K. P. Burnham. 1997. Effects of drought and prolonged winter on Townsend's ground squirrel demography in shrubsteppe habitats. *Ecological Monographs* 67:295-315.
- 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. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. Thesis. University of Idaho. Moscow.
- 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., and D.P. Pyrah. 1974. Movement and nesting of sage grouse hens in Central Montana. *Journal of Wildlife Management* 38:630-633.
- Watters, M. E., T. L. McLash, C. L. Aldridge, and R. M. Brigham. 2002. The effect of vegetation structure on predation of artificial greater sage-grouse nests. *Ecoscience* 9:314-319.
- Watson, M., and S. J. Thirgood. 2001. Could translocation aid hen harrier conservation in the UK? *Animal Conservation* 4:37-43.
- Webb, C. W., W. I. Boarman, and J. T. Rotenberry. 2004. Common raven juvenile survival in a human-augmented landscape. *Condor* 106:517-528.

- Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation biology* 13:1424-1436.
- Yensen, E., and D. L. Quinney. 1992. Can Townsend's ground squirrels survive on a diet of exotic annuals? *Great Basin Naturalist* 52:269-277.
- Yensen, E., D. L. Quinney, K. Johnson, K. Timmerman, and K. Steenhof. 1992. Fire vegetation changes, and population fluctuations of Townsend's ground squirrels. *American Midland Naturalist* 128:299-312.