

DISSERTATION

GUNNISON SAGE-GROUSE DEMOGRAPHY AND CONSERVATION

Submitted by

Amy Jane Davis

Department of Fish, Wildlife, and Conservation Biology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2012

Doctoral Committee:

Advisor: Paul F. Doherty Jr.

Michael L. Phillips

William Kendall

Liba Pejchar

Colleen Webb

Copyright by Amy Jane Davis 2012

All Rights Reserved

## ABSTRACT

### GUNNISON SAGE-GROUSE DEMOGRAPHY AND CONSERVATION

Gunnison Sage-grouse (*Centrocercus minimus*) have declined substantially from their historic range and are a candidate species under the U.S. Endangered Species Act. The status of Gunnison Sage-grouse highlights a need for effective management efforts. This species was only recognized as distinct from the Greater Sage-grouse (*Centrocercus urophasianus*) in 2000. Many of the details of the Gunnison Sage-grouse's demography and life history are not known. Although this species has many similarities with the Greater Sage-grouse, projecting the Gunnison Sage-grouse's population viability and instituting management plans should be based on demography estimates from Gunnison Sage-grouse and not on substitute Greater Sage-grouse estimates, as has been the case to date.

Gunnison Sage-grouse are distributed into seven isolated populations in the southwest of Colorado and stretching into the eastern part of Utah. One population, Gunnison Basin, comprises 85-90% of all Gunnison Sage-grouse and the other six populations are estimated to range in size from 20 to 150 individuals. Population index data have shown a decline in the San Miguel population. The same index data in Gunnison Basin have shown the population is currently declining after a population increase. Due to the inherent difference in population sizes and the fact the populations may be experiencing different ecological pressures, the population dynamics of these small populations may be considerably different from the GB population. In Chapters 1, 2, and 3, I investigated factors affecting fecundity and survival of Gunnison Sage-grouse in the two populations.

In Chapter 1, my objective was to compare the demography of these two populations by evaluating the relationship between nest success and (1) vegetation characteristics (e.g., sagebrush height, shrub cover, grass cover and forb cover), (2) temporal factors (e.g., year, timing of nest initiation, and nest age), and (3) age of the nesting female (yearling or adult). Although I expected nest success to be related to vegetation characteristics, my results did not suggest a strong connection. These results might be due, in

part, to measuring characteristics at a different scale than they are acting on the system. My results indicate that temporal factors were strongly related to nest success in both populations. Nest success varied considerably between years (21.4%-60.1%); the average was 38.8%. Within years, I found nests that initiated earlier in the season had higher success than those that were initiated later in the season. Nests were also at greater risk of failure the longer they had been incubated. I found no evidence for a difference in nest success with relation to hen age or between populations.

Juvenile recruitment is one of the most important vital rates influencing the population growth of many bird species, and is fundamental to understanding trends in population growth. In Chapter 2 my research focused on establishing baseline juvenile recruitment rates and testing population-level, individual (e.g., hatch date) and temporal (e.g., month) hypotheses associated with juvenile recruitment for the Gunnison Sage-grouse. I evaluated juvenile recruitment by combining both chick survival (hatch to 30 days of age) and juvenile survival (31 days of age to the start of the first breeding season). I found strong support for a difference between the two populations in the chick survival analysis, no chicks (n=8) survived to 30 days of age in San Miguel. Chick survival was 0.44 in Gunnison Basin (n=282). Thus no recruitment occurred in San Miguel. I found a slight negative trend in chick survival and a stronger negative trend in juvenile survival from 2005-2010 in Gunnison Basin. Overall, juvenile survival in Gunnison Basin ranged from 0.60 in 2005 to 0.11 in 2010 (n=87) and the juvenile recruitment rate declined from 0.26 in 2005 to 0.05 in 2010. These declines mimic declines observed in population index data which might suggest juvenile recruitment declines are contributing to population declines.

In Chapter 3, I evaluated differences in adult and yearling survival by population and tested hypotheses with regards to temporal effects (across years and within year) and individual effects (sex, age, breeding status). I also examined the effect of harsh winters on survival using average monthly snow depth as an indicator of winter harshness. The within-year pattern of survival is considerably different for males as compared to females. Males had the lowest survival during the lekking season (March –April), females had lowest survival during the nesting and chick rearing season (May – August). Survival also varied

among years: between 0.52 and 0.89 for females and between 0.30 and 0.71 for males. My data suggest that harsh winters have little effect on sage-grouse survival. I found no evidence for a difference in survival between yearlings and adults or between the Gunnison Basin and San Miguel population.

In Chapter 4, I brought together the survival and reproductive rates to create a population model for Gunnison Sage-grouse to assess the viability of, and sensitivity of growth rates to vital rates in the two populations. I also evaluated translocation strategies from the larger Gunnison Basin population to the smaller San Miguel population. Population projections for both populations suggest they are currently experiencing a population decline (the San Miguel population decline is more pronounced than the Gunnison Basin population). Juvenile survival had the largest sensitivity proportional to their variation suggesting it might be an ideal target for management actions. I found adult survival to be the most influential vital rate when the population is declining. Translocation strategies that move birds every five, or fewer, years result in an increase in population persistence. Moving more birds (e.g., > 400 over the course of 30 years) improves the expected population size, but does not improve the persistence probability as much as frequent translocation (e.g., moving birds every year or every other year).

In Chapter 5 I developed a Bayesian integrated model to combine two sources of data that are available for Gunnison Sage-grouse: population survey data (i.e., lek counts) and the demographic data from Chapters 1-3. Both of these data sources have their strengths and their weaknesses. The count data are long running population index data, but are lacking in statistical rigor as there has been a lack of consistent sampling effort, detectability has not been accounted for, and are complicated by observer bias. The demographic estimates are statistically rigorous however they span a much smaller time frame and thus biases are possible in evaluating long-term population viability. To utilize the strengths, and minimize the weaknesses of these two data types, I developed an integrated model that innovatively links population count data and population demographic data through population growth rate ( $\lambda$ ) for Gunnison Sage-grouse. I was able to reduce the variability in expected population growth rates across time, while correcting for potential small sample size bias in the demographic data. I found the population of

Gunnison Sage-grouse to be slightly declining over the past 16 years ( $\lambda = 0.94$ , 95% CI 0.90,1.00).

However, it is important to keep in mind that these results are preliminary as this methodology is novel and further simulation is probably needed to fully understand the method's limitations.

Through my dissertation I was able to establish baseline demographic rates for Gunnison Sage-grouse that will aid in the management of this species of concern. I found strong evidence for a difference between the two populations (Gunnison Basin and San Miguel); which suggests that management plans for these two populations should be developed separately to address the dynamics specific to each population. The complete lack of observed chick survival in San Miguel should be a primary target for that population. The declining juvenile survival in Gunnison Basin coupled with the high sensitivity of this parameter implies it should be a main focus for management in that population. Population projections based solely on the six years of demographic data suggest that the species is in decline. However, when those demographic data are integrated with long-term count data my analyses suggest the populations of Gunnison Sage-grouse are currently experiencing a decline, but that that decline is likely balanced by a recent increase in the population, suggesting the population, on average, has been experiencing only a slight decline over the past 16 years. Only the future will tell if this recent decline is part of a natural cycle or something about which to be concerned.

## ACKNOWLEDGEMENTS

I have sincerely enjoyed my time here at Colorado State University. There are so many people who have helped me throughout my graduate career. First, I have to thank my advisor, Paul Doherty. Having been a member of my Master's committee, he proposed this Ph.D. opportunity to me, for which I will always be grateful. Paul has always been extremely supportive and encouraging and I feel very lucky to have had him as my advisor. However, my goal in life, now that I have completed my degree, is to have Paul finally tell me that I deserve a day off.

I was exceptionally privileged to have such great people on my committee: Mike Phillips, Bill Kendall, Liba Pejchar, and Colleen Webb. They pushed me to become a better scientist. My research is stronger due to their advice and support.

This project was funded by the Colorado Division of Parks and Wildlife (CPW). I am also extremely grateful for Mike Phillips, the PI on this project, and I was fortunate to be a part of this research. I benefited from Mike's knowledge and experience both in the field and as a member of my committee. Another important person I need to thank is Phillip Street. He was the field crew leader for this project and another of Paul Doherty's student. Therefore, he not only ensured that quality data were collected during the field seasons, he was also handy for me to pester when questions came up in the off season. Among the many CPW employees who helped with this project I would also like to thank Jim Gammonley and J Wenum for their help and support.

I am indebted to Gabriele Engler in the Colorado Cooperative Fish and Wildlife Research Unit and Joyce Pratt in the Fish, Wildlife, and Conservation Biology Department for their assistance with logistics, travel, and ensuring that all of the details of being a graduate student and earning my degree are taken care of, and whose help I would have been lost without.

I owe a special thanks to Gary White. He was extraordinarily helpful (and patient) when I would come to him with some issue or another I was having with Program MARK. He, not only, would sit there and figure out a problem with me, he would often update MARK to make that specific issue go away.

Another person I would like to thank is Mevin Hooten. My 5<sup>th</sup> chapter would not have been possible without Mevin's help. He spent many hours discussing conditional distributions with me. These are types of interactions I will miss when I leave here.

You do not really realize how many people you interact with until you sit down and try to thank them all, and I apologize if I forget to mention anyone. Thanks to: Viviana Ruiz-Gutierrez for always being able to solve my R problems, André Breton for his help managing the data in Access, Michael Buhnerkempe for writing amazing R code for a stranger, and the "Wagar 113 Superpopulation" for all of their help reviewing my dissertation chapters and making them stronger.

My research would not have been possible without the hard work from the field crews: Kristina Kasik, Laura Beard, Nick Meyers, Lisa Stoorza, Clare Mix, Andy Braun, Brian Delight, Corbin Niell, Brett Owsley, Joy Felio, Jessie Miller, Jen Peters, Jacob Way, Kendall Siebert, Marla Koberstien, and Randy Everett.

Finally, I would like to thank my parents, Tim and Karen, and my sister, Nancy. They have always been there to support me and encourage me. Without them I would not be where I am today.

TABLE OF CONTENTS

**CHAPTER 1: FACTORS AFFECTING NEST SUCCESS OF GUNNISON SAGE-GROUSE IN TWO POPULATIONS IN SOUTHWEST COLORADO..... 1**

INTRODUCTION ..... 1

METHODS ..... 4

    Study areas ..... 4

    Capture and monitoring ..... 5

    Habitat data ..... 5

    Model set..... 6

    Auxiliary models..... 6

RESULTS ..... 7

    Raw data..... 7

    Model results..... 7

    Auxiliary results..... 8

DISCUSSION ..... 9

LITERATURE CITED ..... 21

APPENDIX 1.A..... 25

APPENDIX 1.B..... 26

**CHAPTER 2: ESTIMATION AND EVALUATION OF GUNNISON SAGE-GROUSE JUVENILE RECRUITMENT IN SOUTHWEST COLORADO..... 27**

INTRODUCTION ..... 28

METHODS ..... 30

    Study areas ..... 30

    Capture and monitoring ..... 31

    Statistical analysis ..... 32

    Bootstrap analysis ..... 33

RESULTS ..... 34

    Chick Survival Analysis..... 35

    Juvenile Survival Analysis..... 36

    Recruitment Analysis..... 37

DISCUSSION ..... 37

LITERATURE CITED: .....	48
APPENDIX 2.A.....	52
APPENDIX 2.B.....	54
<b>CHAPTER 3: ADULT AND YEARLING SURVIVAL OF GUNNISON SAGE-GROUSE IN SOUTHWEST COLORADO .....</b>	<b>55</b>
INTRODUCTION .....	56
METHODS .....	57
Study areas .....	57
Capture and monitoring .....	58
Statistical analysis .....	59
RESULTS .....	60
Raw data.....	60
Model results.....	61
DISCUSSION .....	63
LITERATURE CITED: .....	74
APPENDIX 3.A.....	77
<b>CHAPTER 4: EVALUATING VIABILITY AND TRANSLOCATION STRATEGIES OF GUNNISON SAGE-GROUSE USING A POPULATION PROJECTION MODEL.....</b>	<b>79</b>
INTRODUCTION .....	79
METHODS .....	81
Study areas .....	81
Matrix model.....	82
Environmental stochasticity .....	83
Demographic stochasticity .....	84
Data uncertainty .....	84
Sensitivity analyses .....	84
Transient sensitivity .....	85
Translocation methods .....	86
RESULTS .....	87
Sensitivity analysis.....	88
Translocation results .....	90
DISCUSSION .....	91
Translocation.....	96
LITERATURE CITED .....	112

APPENDIX 4.A.....	116
APPENDIX 4.B.....	117
APPENDIX 4.C.....	118
APPENDIX 4.D.....	119
APPENDIX 4.E.....	122
APPENDIX 4.F.....	123
APPENDIX 4.G.....	124
<b>CHAPTER 5: AN INTEGRATED MODELING APPROACH TO ESTIMATING GUNNISON SAGE-GROUSE POPULATION DYNAMICS: COMBINING INDEX AND DEMOGRAPHIC DATA .....</b>	<b>125</b>
INTRODUCTION .....	125
METHODS .....	128
Data.....	128
Integrated population model .....	129
RESULTS .....	133
DISCUSSION .....	135
LITERATURE CITED .....	151
APPENDIX 5.A.....	155
APPENDIX 5.B.....	156
APPENDIX 5.C.....	157
APPENDIX 5.D.....	159
APPENDIX 5.E.....	160
APPENDIX 5.F.....	161
<b>MANAGEMENT IMPLICATIONS .....</b>	<b>162</b>
<b>COMPLETE LITERATURE CITED .....</b>	<b>166</b>

## LIST OF TABLES

Table 1.1: Explanation of covariates and hypothesized effects on Gunnison Sage-grouse nest success....	14
Table 1.2: Number of nests found by year and population with the proportion of successful nests by group for Gunnison Sage-grouse.....	15
Table 1.3: Cumulative AICc weights by factor for Gunnison Sage-grouse nest success analysis .....	16
Table 1.4: Proportion of hens that nest by age of the hen and by the population for Gunnison Sage-grouse .....	17
Table 2.1: List of covariates and hypothesized effects on Gunnison Sage-grouse chick and juvenile survival.....	41
Table 2.2: Number of birds per year in the chick and juvenile analyses for Gunnison Sage-grouse .....	42
Table 2.3: Cumulative covariate weights for Gunnison Sage-grouse chick and juvenile survival analyses .....	43
Table 2.4: 30-day survival rate of Gunnison Sage-grouse chicks by population.....	44
Table 3.1: Explanation of covariates and hypothesized effects on Gunnison Sage-grouse adult and yearling survival.....	67
Table 3.2: Age and sex distribution of Gunnison Sage-grouse monitored per year in the Gunnison Basin and San Miguel populations.....	68
Table 3.3: Cumulative AICc weights for each covariate used in the Gunnison Sage-grouse adult and yearling survival models .....	69
Table 4.1: Matrix components and corresponding equations for a Gunnison Sage-grouse population model .....	99
Table 4.2: Parameter estimates and standard errors for Gunnison Sage-grouse vital rates .....	100
Table 4.3: Covariance matrix for Gunnison Sage-grouse vital rates calculated from six years of data ...	101
Table 5.1: Posterior means and 95% credible intervals for parameter values from the integrated model for Gunnison Sage-grouse in Gunnison Basin , Colorado.....	141
Table 5.2: Prior values used in the integrated model on Gunnison Sage-grouse.....	142

## LIST OF FIGURES

Figure 1.1: Map of the Gunnison Sage-grouse nest success study area.....	18
Figure 1.2: Estimated nest success rates ( $\phi$ ) by year for Gunnison Sage-grouse.....	19
Figure 1.3: Gunnison Sage-grouse daily nest survival rates (%) by nest initiation week.....	20
Figure 2.1: Map of Gunnison Sage-grouse chick and juvenile survival study area.....	45
Figure 2.2: Chick and juvenile survival and juvenile recruitment for Gunnison Sage-grouse across years.....	46
Figure 2.3: Juvenile survival rates by month for Gunnison Sage-grouse .....	47
Figure 3.1: Map of Gunnison Sage-grouse adult and yearling survival study area .....	70
Figure 3.2: Monthly survival estimates and standard errors by sex for Gunnison Sage-grouse.....	71
Figure 3.3: Annual survival estimates for Gunnison Sage-grouse adult and yearling survival .....	72
Figure 3.4: Annual adult and yearling survival by population for Gunnison Sage-grouse.....	73
Figure 4.1: Map of study area for Gunnison Sage-grouse population model .....	102
Figure 4.2: Life cycle and population matrix model for Gunnison Sage-grouse .....	103
Figure 4.3: Deterministic Gunnison Sage-grouse population projections and population growth rates ( $\lambda$ ) .....	104
Figure 4.4: Gunnison Sage-grouse population projections with environmental stochasticity .....	105
Figure 4.5: Gunnison Sage-grouse population projections with demographic stochasticity .....	106
Figure 4.6: Plots of Gunnison Sage-grouse vital rate distributions based on simulations with and without correlations.....	107
Figure 4.7: Box plots of variance-stabilized sensitivities (VSS) for Gunnison Sage-grouse.....	108
Figure 4.8: Relationship between variance-stabilized sensitivity (VSS) and population growth rate ( $\lambda$ ) .....	109
Figure 4.9: Life-table Response Experiment (LTRE) results by vital rate for Gunnison Sage-grouse ....	110
Figure 4.10: Results of Gunnison Sage-grouse translocation options on the destination and source population .....	111
Figure 5.1: Plot of high male lek counts by year and survey effort for Gunnison Sage-grouse in Gunnison Basin, Colorado.....	143
Figure 5.2: Directed acyclic graph of the integrated population model for Gunnison Sage-grouse .....	144
Figure 5.3: Plot of the distribution of population growth rate ( $\lambda$ ) values for the lek count data compared to the demographic values.....	145
Figure 5.4: Plot of the posterior means for the population growth rate ( $\lambda$ ) values of Gunnison Sage-grouse from 1996-2011 .....	146
Figure 5.5: Plot of bias vs variance trade-off for integrated model of Gunnison Sage-grouse.....	147

Figure 5.6: Posterior means of population growth for fixed values of  $\sigma\lambda^2$ ..... 148

Figure 5.7: Population projections from the integrated model on Gunnison Sage-grouse for 1996-2011 149

Figure 5.8: Plot of posterior means for the population growth rate ( $\lambda$ ) values for Gunnison Sage-grouse from 1953-2011 ..... 150

## **CHAPTER 1**

### **FACTORS AFFECTING NEST SUCCESS OF GUNNISON SAGE-GROUSE IN TWO POPULATIONS IN SOUTHWEST COLORADO**

I investigated factors affecting nest success at two dynamically different populations of Gunnison Sage-grouse (*Centrocercus minimus*) to determine what selection pressures may be acting on these different populations. The Gunnison Basin population is believed to comprise 85-90% of all Gunnison Sage-grouse and is relatively stable. The San Miguel population is one of six relatively small populations, which contains 3-5% of Gunnison Sage-grouse and is on the decline. My objective was to compare the demography of these two populations by evaluating the relationship between nest success and (1) vegetation characteristics (e.g., sagebrush height, shrub cover, grass cover and forb cover), (2) temporal factors (e.g., year, timing of nest initiation, and nest age), and (3) age of the nesting female (yearling or adult). Although expecting nest success to be related to vegetation characteristics is logical, my results did not suggest a strong connection. These results may be due, in part, to measuring characteristics at a different scale than they are acting on the system. My results indicate that temporal factors were strongly related to nest success in both populations. Nest success varied considerably between years (21.4%-60.1%); the average was 38.8%. Within years, I found nests that initiated earlier in the season had higher success than those that were initiated later in the season. Nests were also at greater risk of failure the longer they had been incubated. I found no evidence for a difference in nest success with relation to hen age or between populations.

## **INTRODUCTION**

Nest success (the probability that at least one egg hatches) is a primary factor in determining avian reproductive success, and thus population growth rates. Consequently, declines in nest success are thought to correspond to population declines for fast life-history bird species (Wisdom and Mills 1997).

Understanding the relationship between nest success and additional factors (e.g., vegetation structure, weather) enables better understanding of the selection pressures that may be affecting a species (e.g., Connelly et al. 2000). Johnson et al. (2010) noted that selection pressures can vary between populations of the same species. This variation suggests that successful management actions may be different among populations.

Gunnison Sage-grouse (*Centrocercus minimus*, GUSG) have declined substantially from their historic range (Schroeder et al. 2004) and are a candidate species under the U.S. Endangered Species Act (ESA, United States Fish and Wildlife Service 2010). GUSG are distributed into seven isolated populations. One population, Gunnison Basin (GB), comprises 85-90% of all GUSG and the other six populations are estimated to range in size from 20 to 170 individuals (Kathy Griffin, Colorado Parks and Wildlife (CPW), Grouse Coordinator, pers. comm.). Due to the inherent small sizes of these other populations and the fact they have been declining in recent years, the population dynamics of these small populations may be very different from the GB population.

In addition to a difference between populations, there are many factors that are commonly thought to be related to sage-grouse nest success. Previous work on GUSG has been limited; only three studies have examined GUSG nest success (Young 1994, Apa 2004, Stiver 2007). However, work on the closely related Greater Sage-grouse (*Centrocercus urophasianus*, GRSG) has been extensive (e.g., Schroeder et al. 1999). Adult GRSG females generally have a higher nest initiation rate than yearlings (Connelly et al. 1993, Schroeder 1997, Sveum et al. 1998). Adults have been more successful in nesting than yearlings (Wallestad and Pyrah 1974) or nest success has been similar between ages (Connelly et al. 1993). Adults have been more likely to renest following an early failure than yearlings (Connelly et al. 1993); and reneests have usually been more successful than first nesting attempts (Schroeder et al. 1999). Daily nest survival has been negatively correlated with nest age (Kolada et al. 2009). Numerous studies have examined the relationship between nest success rates and vegetation structure for GRSG (e.g., Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Holloran et al. 2005, Moynahan et al. 2007,

Herman-Brunson et al. 2009). However, the effects of vegetation on nest success vary from population to population. Percent shrub cover is thought to be an important factor for concealing a nest and thus related positively to nest success in GRSG in North Dakota and Oregon (Gregg et al. 1994, Herman-Brunson et al. 2009). Percent grass cover has been found to be positively correlated with nest success in Washington, Wyoming, Montana, and Southern Canada (Sveum et al. 1998, Aldridge and Brigham 2002, Holloran et al. 2005, Moynahan et al. 2007). Some studies on GRSG indicated that grass height is more likely related to nest success than just grass cover (Gregg et al. 1994, Holloran et al. 2005, Herman-Brunson et al. 2009). Lane (2005), however, found no difference in successful or non-successful nests with respect to vegetation characteristics in Montana and Wyoming for GRSG.

A desire to improve the population growth rate of GUSG exists, and nest success is thought to be one of the most influential factors in the population growth rate of sage-grouse (*Centrocercus sp.*, Schroeder et al. 2004). The amount of variability present in nesting success of sage-grouse, coupled with the potential importance of nesting success to population viability spotlights the need for an in depth analysis of GUSG nesting success.

I analyzed nest success rates for GUSG in two isolated populations in southwestern Colorado. My objective was to determine if a strong correlation between vegetation structure and nest success exists, and if so, to determine the direction and magnitude of that relationship to better direct future management. I also analyzed additional factors, e.g., temporal effects and the age of the nesting female, to better understand what effects might be related to GUSG nest success. My study provides much needed species-specific demographic data, which are important for successfully managing an Endangered Species Act (ESA) candidate species like the GUSG.

## METHODS

### Study areas

I captured and radiomarked GUSG hens in two of seven isolated populations of GUSG: Gunnison Basin (GB) and San Miguel (SM). Over 85% of the existing individuals are thought to be in the GB population (Kathy Griffin, CPW Grouse Coordinator, pers. comm.). My study encompasses the Gunnison Basin, in Gunnison County and Saguache County, Colorado, USA excluding the western edge (Figure 1.1).

Gunnison Basin is a 2,000km<sup>2</sup> intermontane basin ranging in elevation from 2,300 to 2,900m (Hupp and Braun 1989). Mountainous terrain borders the north, east, and south-east sides of the study area. These areas contain habitat not commonly used by sage-grouse (Connelly et al. 2000). The western edge of the Gunnison Basin is comprised mostly of land managed by the Bureau of Land Management, the National Park Service and the Ute Mountain Ute Tribe; these areas were not included in our study area. The study area is sagebrush steppe dominated by sagebrush (*Artemisia spp.*) interspersed with rabbitbrush (*Chrysothamnus spp.*) antelope bitterbrush (*Purshia tridentate*) serviceberry (*Amelanchier spp.*) and mountain snowberry (*Symphoricarpos oreophilus*). Black sagebrush (*Artemisia nova*) is common on xeric ridge tops and south-facing slopes.

Of the six small populations, my research was conducted in the SM population. This is the largest of the small populations and therefore the best chance of obtaining a decent sample size. The SM population is located in Montrose and San Miguel counties, Colorado, USA. The SM population is comprised of six, interconnected subpopulations over a 400km<sup>2</sup> area. The elevation of this area ranges from 1,900 to 2,800m (Gunnison Sage-grouse Rangewide Steering Committee 2005). The vegetation characteristics vary between the six subpopulations in the SM population. The data for this study were collected from the Dan Noble State Wildlife Area (site of one of the subpopulations of the SM population). The shrubs in this study area are mostly low sagebrush (*Artemisia arbuscula*) and black sagebrush (*Artemisia nova*), with some mountain big sagebrush (*Artemisia tridentate*) along drainages.

## **Capture and monitoring**

I used spot-lighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) to trap sage-grouse (mid-March through early-May) from 2005-2010. Sage-grouse were fitted with a 17g necklace-style radiotransmitter (Advanced Telemetry Systems, Inc.) and a numbered leg band (National Brand and Tag Company). The transmitter weight is <2% of the average adult female GUSG's body weight ( $\bar{y} = 1230\text{g}, \pm 10.5 \text{SD}$ ).

Each bird was weighed and plumage characteristics were used to determine age (Beck et al. 1975). Each GUSG was categorized as either an adult ( $\geq 2$  years old) or a yearling (1 year old, first breeding season).

Females were tracked through the breeding season to determine nesting status. If a female remained in the same location for three consecutive days we assumed she was nesting. While the female was on the nest, the location of the nest was determined by telemetry triangulation using maximum likelihood estimates in program LOCATE II (Nams 1990). Locations were recorded using UTM coordinates (with the CONUS NAD 27 datum). Multiple bearings were taken (a minimum of 3, but usually  $>3$ ) to ensure errors around the nest were less than  $100\text{m}^2$ . Visual observations of the females on nest were avoided to minimize flushing birds and therefore risking interfering with nesting behavior. Nesting females were monitored from at least 30 m from the nest to minimize disturbance. Nests were monitored 6-7 days a week to determine when, either eggs in a nest hatched, or the nest was abandoned or destroyed by predation. Once a female moved from the nest, the nest was located to assess the fate (e.g., hatched, depredated, abandoned, other) and record a GPS location to compare with the location estimated by triangulation. A nest was considered successful if at least one egg hatched (Mayfield 1975). If a nest was abandoned or depredated, the female was tracked to determine if she re-nested.

## **Habitat data**

Vegetation characteristics were measured at all nest locations using techniques described by Connelly (2003). After the female moved from the nest (regardless of the nest fate), a 30m north-south transect was established, centered at the nest. The line intercept method (Canfield 1941) was used to estimate the amount of sagebrush canopy cover. Sagebrush height was estimated at 7 sample points along the transect

(5 m intervals - including the start and end of the transect). A 20 x 50 cm frame was used to estimate the percent cover, height and frequency of grass and forb understory at the 7 sample points along the transect (Daubenmire 1959). The percentage of bare ground, and litter were also recorded as the 7 sample points.

### **Model set**

I used nest survival models (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999) to estimate rates of daily nest survival and examine the relationship between nest success and vegetation and temporal covariates (Table 1.1). Based on my method of monitoring, the hen had been incubating the nest for approximately three days before I determined she was nesting. Therefore my nest success estimates are conditional on the nest surviving to the third day and my nest initiation rates are also conditional on a nest surviving until day three. I examined four vegetation covariates: average shrub height, percent shrub cover, percent grass cover, and percent forb cover. I evaluated several additional covariates (Table 1.1).

I evaluated the relative importance of each model using Akaike Information Criterion with the small sample size correction (AICc, Burnham and Anderson 2002). Following the recommendation of Doherty et al. (2012) I ran all additive combinations of factors in Table 1.1 (with the stipulation that models with interaction terms had to include the main effect terms) for a balanced model set. To evaluate the relative importance of each factor I calculated the cumulative AICc weight (Burnham and Anderson 2002) for each factor and covariates with a cumulative AICc weight above 0.5 were considered to be important (Barbieri and Berger 2004).

### **Auxiliary models**

*One meter vegetation cover:* I created a second vegetation data set by truncating the original data to only include information within 1m of the nests. I calculated the Pearson correlation coefficient for the two types of vegetation data. I compared our top model from the above analysis and compared it to the same

model but with the addition of each of the 1m vegetation covariates in turn. The results were compared using AICc.

*Analysis by population:* In a separate analysis I divided the data by population. Then I ran all combinations as above, but for each population separately. These models were also run in MARK and compared using AICc. Models that were run using different data sets were not compared to each other, but the cumulative AICc weights were used to compare relative importance between each model set.

## **RESULTS**

### **Raw data**

From 2005-2010 in GB and 2007-2010 in SM, I tracked a total of 192 hens (181 in GB and 11 in SM). I located 177 nests in the GB population and 20 nests in the SM population (Table 1.2). During that time I found 11 renesting attempts, all by adult hens, five in GB and six in SM.

### **Model results**

According to the cumulative AICc weights, the three factors that dominated the analysis were temporal covariates: year effect, nest age, and initiation week (Table 1.3). The interaction between the year effect and the initiation week was also considered important with a cumulative model weight of 0.68.

Nest success fluctuated between years (Figure 1.2). 2008 had the highest nest success rate. The smallest sample size was in 2005 (N=10), which corresponds to the largest error bars (Figure 1.2). The effect of 'nest age' was negative (-0.04, SD=0.1); the older the nest, the lower the daily nest survival. I examined a quadratic effect of nest initiation date. The result suggests that birds that initiate nests early in the season have greater success than those that nest later in the nesting season, but that the worst time to initiate a nest is the last week in May (Figure 1.3).

The cumulative AICc weights for the vegetation covariates were all well below the 0.5 cutoff, and thus are not considered influential in determining nest success (Table 1.3). The shrub cover ranged from 0 to 76% ( $\bar{y} = 26.5 \pm 10.6$  SD). The average shrub height ranged from 0 to 86.5 cm, ( $\bar{y} = 39.4 \pm 16.6$  SD). The grass cover ranged from 0.0% to 60.0%, ( $\bar{y} = 11.7 \pm 8.8$  SD). The ranges for each vegetation covariate and their corresponding nest fates also strongly overlapped (Appendix 1.A). The parameter estimates for vegetation characteristics were close to zero and their 95% confidence interval overlapped zero suggesting a weak effect (Appendix 1.A).

The age of the nesting female was not an important factor, with a cumulative AICc weight of 0.27 (Table 1.3). The parameter estimate for hen age was near zero, indicating the difference in nest success between yearlings and adults was small. The nest initiation rates were slightly higher for adults (0.93) than juveniles (0.89) in GB (Table 1.4). The nest initiation rates for SM were slightly less than GB for adults, 0.88; however, no yearlings were captured in SM (Table 1.4).

### **Auxiliary results**

*One meter vegetation cover:* The Pearson correlation coefficient between the 1m and 15m vegetation data was 0.74. The addition of the 1m vegetation covariates did not increase the AICc by 2 or more (Burnham and Anderson 2002). The estimates of the 1m vegetation covariates were still near zero and their confidence intervals overlapped with zero.

*Analysis by population:* The factors that had a cumulative AICc weight above 0.5 for the GB only analysis were: initiation week, year, nest age, and year by initiation week interaction (with cumulative AICc weights of 0.9999, 0.9998, 0.9954, and 0.7407 respectively). The factors for the SM population that were above 0.5 were: nest age, initiation week, and grass cover (with cumulative AICc weights of 0.9952, 0.6011, and 0.5420 respectively). The effect of nest age for the SM population was negative, similar to that for the model with both populations combined. The 95% CIs for the beta estimates of the initiation week and grass cover overlapped zero. The effect of grass cover was slightly positive.

## **DISCUSSION**

Gunnison Sage-grouse nest success varied substantially from year to year within the same population. During my six-year study the nest success ranged from 21% to 60%, with an average of 39%. My estimates and the variability between them are similar to other sage-grouse research. Nest success rates from the work on GUSG range from 21% to 43% (Young 1994, Apa 2004, Stiver 2007). Previous studies on GRSG nest success show a wide range of success rates, 14%-86% (Schroeder et al. 1999) with most nest success estimates between 25%-50% (Connelly et al. 1993, Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Holloran et al. 2005, Moynahan et al. 2007, Herman-Brunson et al. 2009, Kolada et al. 2009).

Temporal covariates dominated my analysis. The year in which a bird nested and the timing of the nesting within that year had a large influence on the probability of nest success. These temporal covariates may be accounting for factors that I did not explicitly examine, such as: variation in habitat quality, weather conditions, or predator levels and/or predator demands on grouse (e.g., variations in availability of buffer species). One example of this possibility is the success rates from 2008. The 2007-2008 winter in Colorado was extremely harsh with heavy snowfall that persisted late into spring. However, 2008 was the best year for GUSG nest success. The high success rate might be a result of better habitat quality due to the increased moisture, and/or less predation pressure due to predators requiring fewer GUSG nests as a prey source because of the abundance of winter killed deer and elk, and/or the harsh winter may have led to fewer predators overall. Therefore, monitoring some of these other factors would be beneficial to more fully understanding factors related to nest success.

The age of the nest is an important determinant of daily survival rates. Previous work on other bird species has found the relationship between daily nest survival and nest age to be positive (Dinsmore et al. 2002) or negative (Kolada et al. 2009) depending on the species. Kolada et al. (2009) found a negative

relationship between nest age and daily survival rates for GRSG in California. My analysis shows a strong negative relationship as well. Coates & Delehanty (2008) monitored incubation patterns of GRSG, and found that incubation constancy (percentage of time spent at the nest in a 24-hour period) is lower in later incubation stages. An increase in movement to and from the nest might increase the chance a predator will be alerted to the nest's location and thus its predation. This might contribute to the negative relationship between daily nest survival and nest age that we found.

Understanding the relationship between nest success and vegetation characteristics is important in order to implement effective management actions. I focused on four vegetation characteristics for my analysis: percent shrub cover, average shrub height, percent grass cover, and percent forb cover around the nest. However, none of these vegetation covariates were found to be strongly correlated with nest success. When added to the top model separately, the parameter estimates for shrub height, % grass cover, and % forb cover were all near zero (Appendix 1.A). The estimate for percent shrub cover was positive, but the standard error was relatively large and the 95% CI greatly overlapped with zero (Appendix 1.A). Young (1994) found a positive relationship between nest success and shrub cover for GUSG. My results suggest that more shrub cover may tend to coincide with higher nest success; however, the parameter estimates show this is not a strong relationship, and the cumulative AICc weight suggest this effect is not important relative to other factors I examined.

I considered the fact that I might not be measuring vegetation at the same scale as is important for nest concealment. I had not collected data at a broader spatial scale, but I could truncate the data to evaluate vegetation effects at a finer scale. My data were collected using a 30m transect centered on the nest. I compared this 15m radius data to data within 1m from the nest. The vegetation data were correlated between the two scales, but not so highly correlated as to suggest the analyses would necessarily return identical results (Pearson correlation coefficient = 0.74). When I compared my best model (year + nest age + nest initiation) to a model that added the 1m data, I found my original model still performed better. Therefore, narrowing the scale of the vegetation sampling did not appear to improve my detection of a

nest site level relationship. Future studies could examine the relationship between nest success and vegetation characteristics at a broader scale. I also examined histograms of the vegetation covariates and the related nest fates to determine if there was a pattern I was missing in the vegetation effect (Appendix 1.B). These plots show that the hatch/fail rates are similar across all levels of vegetation cover. These results suggest that differences in vegetation cover are not explaining why some nests fail and others are successful.

The role vegetation plays in GUSG nesting may be more pronounced with respect to the location of a nest on a landscape (i.e., nest sites have different vegetation structure than random sites) than to nest success (i.e., the vegetation structure corresponds highly with the success of a nest). Several studies have found a difference between vegetation cover at nest sites compared to random sites (Gregg et al. 1994, Young 1994, Apa 2004, Moynahan 2004). Shrub cover was greater and average shrub height was higher for nesting sites than for random sites for GUSG (Young 1994, Apa 2004).

The considerable variability in previous studies on nest success and vegetation structure for sage-grouse demonstrate that there is no overarching role that vegetation plays in nest success. The effects of vegetation structure likely reflect the different ecosystem dynamics at play in one population versus another. My results suggest that factors other than vegetation covariates (as measured in my study) are more crucial gauges of nest success in these populations. Previous studies have predominantly worked on GRSG. Although GRSG and GUSG are closely related, there are noted behavioral and genetic differences (Young et al. 2000b). These differences may also contribute to the divergent results I found. Furthermore, southwest Colorado (including Gunnison and San Miguel counties) were recovering from drought conditions during years prior to 2003 (NOAA Climate Prediction Center), which may contribute to the results I found.

Generally, the age of the female is thought to play a role in the reproductive success of sage-grouse. That role can be played through nest initiation rates, nest success rates, or the probability of re-nesting.

Although adults seem to initiate nests at a slightly higher rate than yearlings this is not a strong difference (Table 1.4), and my results also do not suggest a difference in nest success with respect to age (Table 1.3). Interestingly, no yearlings were observed in the SM populations. This is likely related to the fact that there has been no recruitment observed during the course of my study (Mike Phillips, CPW Gunnison Sage-grouse Researcher, pers. comm., Chapter 2).

The variability in previous work on GRSG suggests selection pressures may be acting on each population differently. Johnson et al. (2010) determined that ideal management of a species was different between populations when variability existed between the vital rates of those populations. This concept emphasizes the need for species-specific demographic rates, but also suggests population-level demographic rates are necessary to implement optimal management strategies. I analyzed data from two different populations. These populations are different in the vegetation species composition, range of elevations (2,300-2,900 in GB and 1,900-2,800 in SM), soil properties, and population size (Gunnison Sage-grouse Rangewide Steering Committee 2005). Spatial distribution and abundance of predators and predator communities are likely to vary as well. Therefore, a difference might be expected in the dynamics of the two populations (e.g., the effects of demographic and environmental stochasticity). However, our analysis did not suggest a difference between the two populations (cumulative AICc weight of 0.37, Table 1.3).

The lack of a strong population difference may be a consequence of the small sample size from the SM population (SM: N=20, GB: N=177). In order to ensure the data from SM were not being overwhelmed by the Gunnison Basin data, I constructed models for the two populations separately. Predictably the results from Gunnison Basin alone were similar to the full data set (the same four variables were dominant with nearly the same cumulative AICc weights). The SM results showed three factors were above the 0.5 threshold (nest age, initiation week, and % grass cover). The effect of nest age and initiation week showed similar trends to those of the combined data set, indicating these effects are important across populations. The year effect was not important in the SM results; small sample sizes

within years for SM might make detecting a year effect difficult. These results suggest that more grass cover corresponds to higher nest success, however, the effect was not strong (AICc weight 0.54, and the 95% CIs overlap zero); this is of primary interest as it is divergent from the Gunnison Basin data. Perhaps with a larger sample size in SM this might indicate a key difference between the populations.

One of the primary goals of this study was to estimate reliable, baseline nest success rates for GUSG, which I was able to do. Another motivation for this study was to examine the differences between two characteristically different populations. The small sample size in the SM population prevented me from being able to make any definitive conclusions about the relationship, but the data I do have suggest that a difference in the importance of vegetation characteristics between populations may exist. This implies a need for more effort in SM. Additionally, I was unable to detect a relationship between vegetation characteristics where one was expected. However, I do not think the role that vegetation in nest success should be dismissed, and future work should examine this relationship at different scales.

**Table 1.1:** Explanation of covariates and hypothesized effects on Gunnison Sage-grouse nest success

<b>Factors</b>	<b>Explanation/Hypothesis</b>
<b>Location Factor</b>	
Population	Nest success will be higher for Gunnison Basin (GB) than for San Miguel (SM) because GB is larger and potentially more stable
Year by Population interaction	The yearly variation will not be the same in the two populations, e.g., 2007 might be a good year in SM but not in GB
<b>Temporal Factors</b>	
Year	Nest success will vary by year
Initiation Week (Quadratic)	Nests initiated either early or late in the season will have a lower success rate than those that are initiated in the middle of the season.
Year by Initiation Week	This interaction will take into account the fact that the nesting season starts earlier in some years than others. Thus allowing the ‘initiation week’ factor to correspond to the start of the nesting season and not the same calendar date each year.
Nest age	Daily nest survival will increase with age of the nest (number of days the nest has been incubated)
<b>Nest Site Factors</b>	
% Shrub cover	Percent shrub cover will be positively correlated with nest success
Shrub height (cm)	Shrub height will have a positive correlation with nest success
% Grass cover	Percent grass cover will have a positive correlation with nest success
% Forb cover	Percent forb cover will have a positive correlation with nest success
<b>Individual Factors</b>	
Age of nesting female	Yearling females will have lower nest success than adults, this is often the case in GRSG

**Table 1.2:** Number of nests found by year and population with the proportion of successful nests by group for Gunnison Sage-grouse. Research was conducted in the Gunnison Basin population from 2005-2010 and in the San Miguel population from 2007-2010.

<b>Year</b>	<b>Gunnison Basin Population</b>		<b>San Miguel Population</b>	
	<b>Number of nests</b>	<b>Proportion successful</b>	<b>Number of nests</b>	<b>Proportion successful</b>
2005	10	0.20	-	-
2006	23	0.48	-	-
2007	24	0.29	2	0.00
2008	35	0.60	4	0.50
2009	38	0.47	7	0.29
2010	47	0.43	7	0.00
<b>Total</b>	<b>177</b>	<b>0.45</b>	<b>20</b>	<b>0.20</b>

**Table 1.3:** Cumulative AICc weights by factor for Gunnison Sage-grouse nest success analysis.

<b>Factor</b>	<b>Cumulative AICc Weight</b>
Year <sup>a</sup>	1.000
Nest age <sup>b</sup>	0.999
Initiation week <sup>c</sup>	0.999
Year by initiation week interaction <sup>d</sup>	0.678
Population <sup>e</sup>	0.368
Shrub height <sup>f</sup>	0.326
% Grass cover <sup>g</sup>	0.284
% Shrub cover <sup>h</sup>	0.280
Hen age <sup>i</sup>	0.271
Year by population interaction <sup>j</sup>	0.096

<sup>a</sup> ‘Year’ allows nest success to be estimated for each year in the study separately

<sup>b</sup> ‘Nest age’ is a linear trend relating the age of the nest (days of incubation) to nest success

<sup>c</sup> ‘Initiation week’ is a quadratic effect relating the week in which the nest was initiated with nest success

<sup>d</sup> ‘Year by initiation week interaction’ allows for a yearly shift in the quadratic initiation week effect

<sup>e</sup> ‘Population’ denotes a 0 for the Gunnison Basin population and a 1 for the San Miguel population

<sup>f</sup> ‘Shrub height’ is a linear relationship between nest success and the shrub height around the nest

<sup>g</sup> ‘% Grass cover’ is a linear relationship between nest success and the percent grass cover around the nest

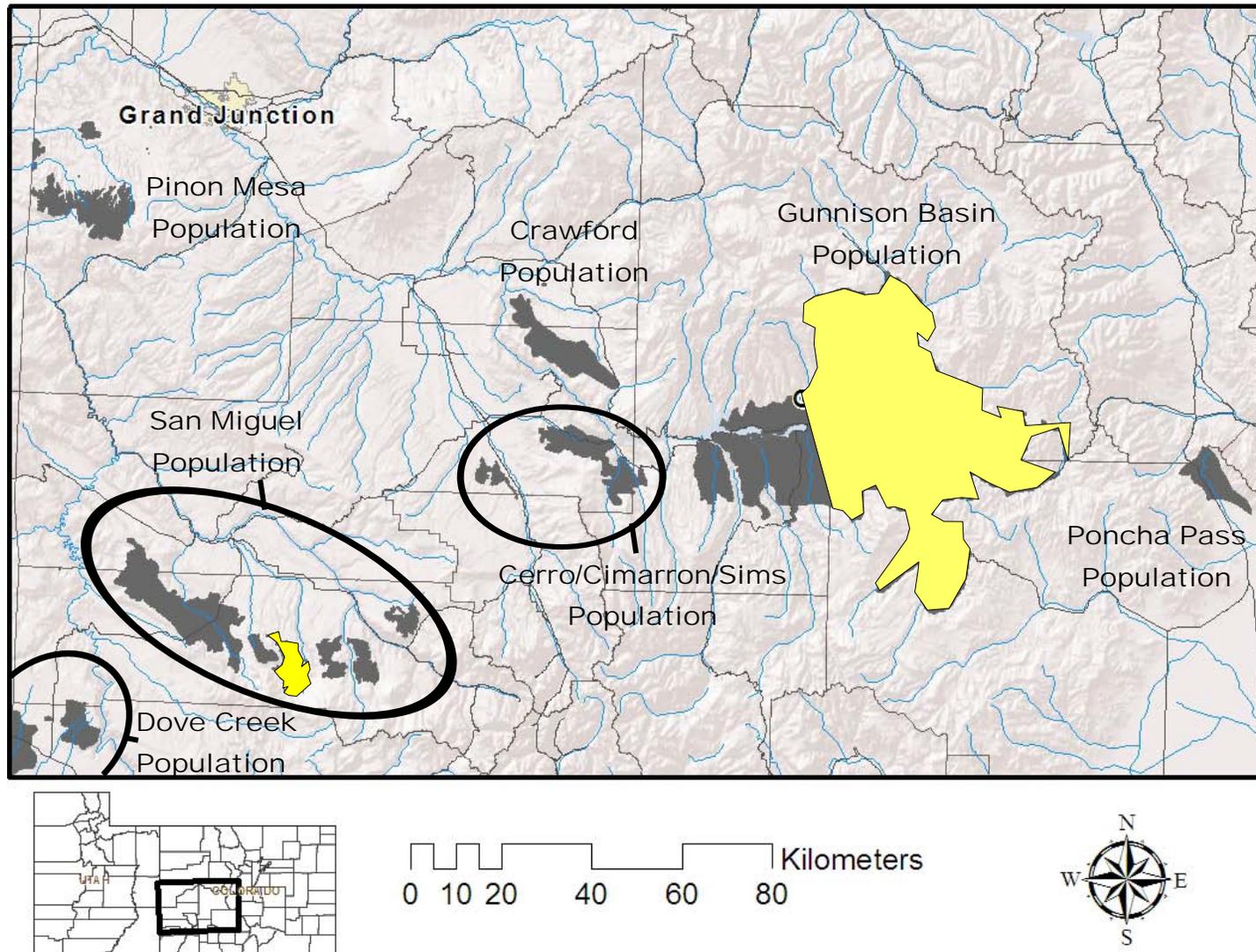
<sup>h</sup> ‘%Shrub cover’ is a linear relationship between nest success and the percent shrub cover around the nest

<sup>i</sup> ‘Hen age’ denotes a 0 for a yearling hen and a 1 for an adult hen, referring to the bird that is nesting

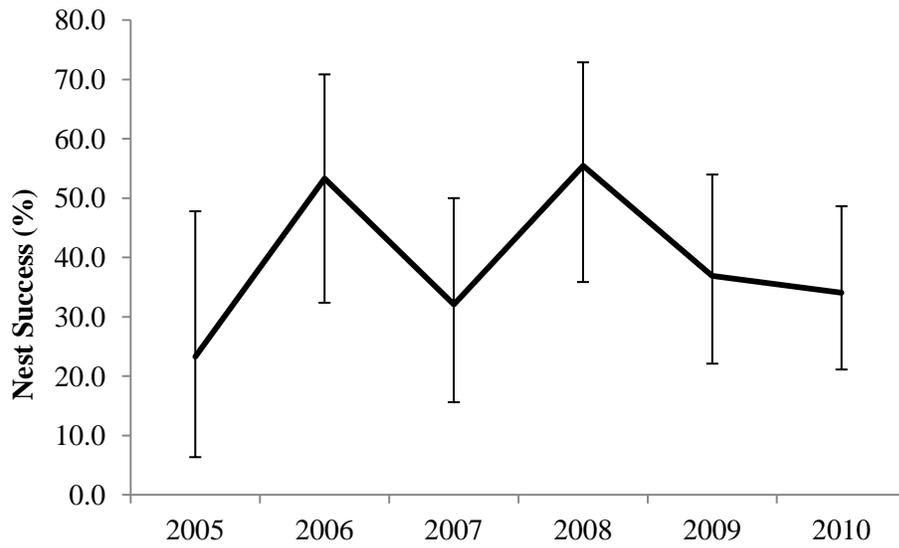
<sup>j</sup> ‘Year by population interaction’ allows for the nest success to vary by both year and population

**Table 1.4:** Proportion of hens that nest by age of the hen and the population.

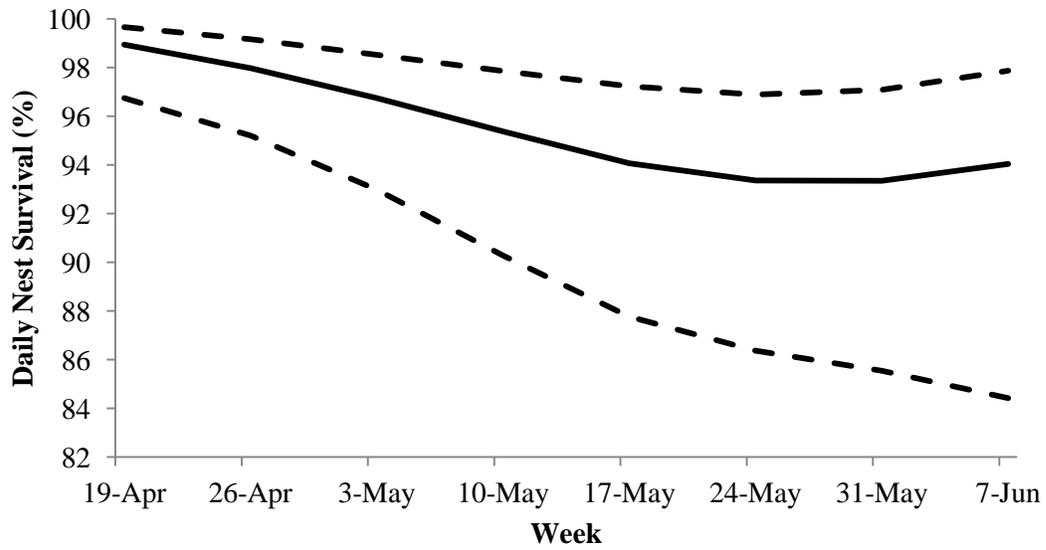
<b>Age</b>	<b>Gunnison Basin Population</b>		<b>San Miguel Population</b>	
	<b>Proportion that Nested</b>	<b>N</b>	<b>Proportion that Nested</b>	<b>N</b>
Adult	0.93	(128)	0.88	(16)
Yearling	0.89	(80)	-	(0)
Overall	0.91	(208)	0.88	(16)



**Figure 1.1:** The seven populations of Gunnison Sage-grouse. The two areas highlighted in yellow are the study areas.



**Figure 1.2:** Estimated nest success rates (%) by year for Gunnison Sage-grouse (for both the Gunnison Basin and San Miguel populations). Errors bars are 95% confidence intervals.



**Figure 1.3:** Gunnison Sage-grouse daily nest survival rates (%) by nest initiation week (for both the Gunnison Basin and San Miguel populations). Error bars are 95% confidence intervals.

## LITERATURE CITED

- Aldridge, C. L. and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. *Journal of Wildlife Management* **66**:433-444.
- Apa, A. D. 2004. Habitat use, movements, and survival of Gunnison Sage-Grouse in southwestern Colorado. Unpublished Report. Colorado Division of Wildlife, Colorado, USA.
- Barbieri, M. M. and J. O. Berger. 2004. Optimal predictive model selection. *Annals of Statistics* **32**:870-897.
- Beck, T. D. I., R. B. Gill, and C. E. Braun. 1975. Sex and age determination of sage grouse from wing characteristics. *in* C. D. o. Wildlife, editor. Game Information Leaflet, Fort Collins, CO, USA.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference- a practice information-theoretic approach. 2nd edition. Springer, New York.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* **39**:388-394.
- Coates, P. S. and D. J. Delehanty. 2008. Effects of Environmental Factors on Incubation Patterns of Greater Sage-grouse. *Condor* **110**:627-638.
- Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting by Sage Grouse in Southeastern Idaho. *Condor* **95**:1041-1043.
- Connelly, J. W., Reese, K.P., and Schroeder, M.A. 2003. Monitoring of Greater Sage-Grouse Habitats and Populations. University of Idaho, Moscow, Idaho.
- 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.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* **33**:43-64.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**:3476-3488.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* **152**:317-323.

- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for Trapping Sage Grouse in Colorado. *Wildlife Society Bulletin* **10**:224-231.
- Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. Delong. 1994. Vegetational Cover and Predation of Sage Grouse Nests in Oregon. *Journal of Wildlife Management* **58**:162-166.
- Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-Grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Herman-Brunson, K. M., K. C. Jensen, N. W. Kaczor, C. C. Swanson, M. A. Rumble, and R. W. Klaver. 2009. Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. *Wildlife Biology* **15**:395-404.
- Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management* **69**:638-649.
- Hupp, J. W. and C. E. Braun. 1989. Topographic Distribution of Sage Grouse Foraging in Winter. *Journal of Wildlife Management* **53**:823-829.
- Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. *Ecological Applications* **20**:1753-1765.
- Kolada, E. J., M. L. Casazza, and J. S. Sedinger. 2009. Ecological Factors Influencing Nest Survival of Greater Sage-Grouse in Mono County, California. *Journal of Wildlife Management* **73**:1341-1347.
- Lane, V. R. 2005. Sage-grouse (*Centrocercus urophasianus*) nesting and brood rearing sagebrush habitat characteristics in Montana and Wyoming. Montana State University, Bozeman, MT.
- Mayfield, H. F. 1975. Suggestions for Calculating Nest Success. *Wilson Bulletin* **87**:456-466.
- Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. Dissertation. University of Montana, Missoula, Montana.

- Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. *Journal of Wildlife Management* **71**:1773-1783.
- Nams, V. O. 1990. Locate II. Pacer, Truro, Nova Scotia, Canada.
- Schroeder, M. A. 1997. Unusually high reproductive effort by Sage Grouse in a fragmented habitat in north-central Washington. *Condor* **99**:933-941.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-Grouse in North America. *Condor* **106**:363-376.
- Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Greater Sage-Grouse (*Centrocercus urophasianus*). The birds of North America. The Birds of Norther America Online, Ithiaca, NY: Cornell Lab of Ornithology.
- Stiver, J. A. 2007. Polygyny and effective population size in the lekking Gunnison Sage-grouse. University of Nebraska, Lincoln, Nebraska.
- 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.
- United States Fish and Wildlife Service, U. 2010. Determination of Gunnison Sage-grouse as a Threatened or Endangered Species. *in* D. o. t. Interior, editor. Federal Register
- 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. Pyrah. 1974. Movement and Nesting of Sage Grouse Hens in Central Montana. *Journal of Wildlife Management* **38**:630-633.
- White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Fort Collins, CO.
- Wisdom, M. J. and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: Prairie-chickens as an example. *Journal of Wildlife Management* **61**:302-312.

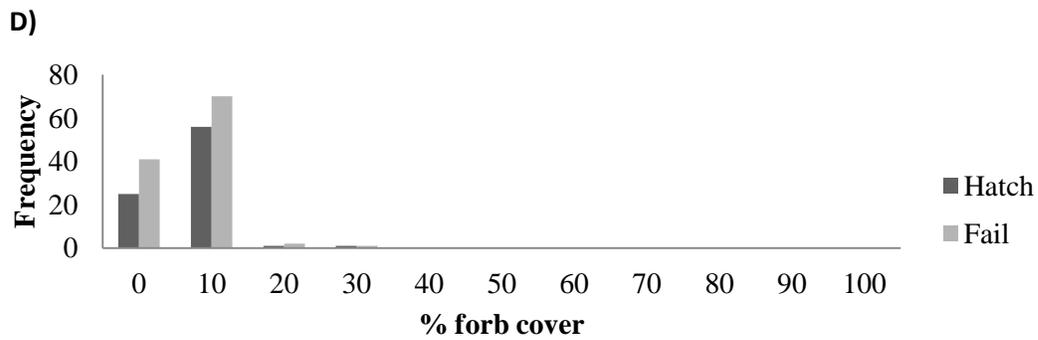
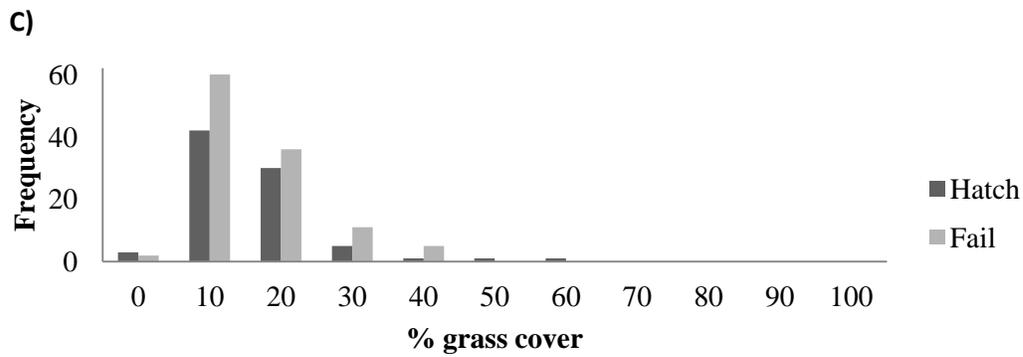
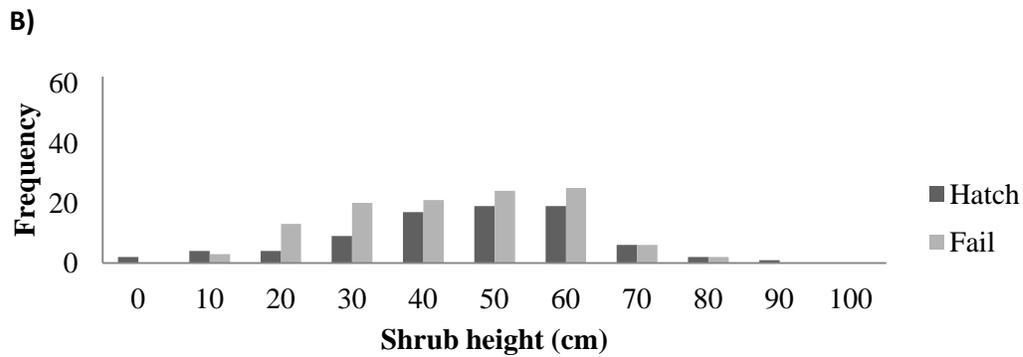
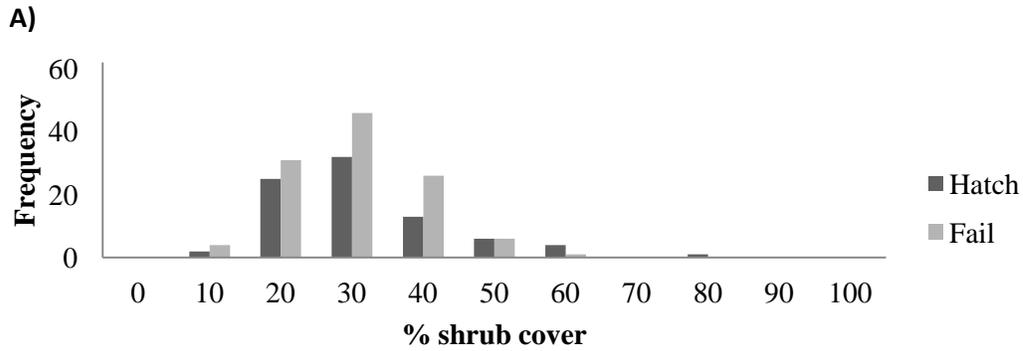
Young, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence among sage grouse populations. . Dissertation. Purdue University, West Lafayette, Indiana, USA.

Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000. A new species of sage-grouse (Phasianidae : *Centrocercus*) from southwestern Colorado. *Wilson Bulletin* **112**:445-453.

**APPENDIX 1.A:** Parameter estimates, standard errors, and 95% confidence intervals for the vegetation covariates. These estimates come from top model with each vegetation covariate added separately.

<b>Covariate</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>95% LCL</b>	<b>95% UCL</b>
Shrub Height	-0.0058	0.0090	-0.0234	0.0118
% Shrub cover	0.1918	1.1471	-2.0565	2.4401
% Grass cover	-0.0044	0.0124	-0.0287	0.0199
% Forb cover	0.0084	0.0318	-0.0539	0.0707

**APPENDIX 1.B.** Histograms of nest fate by vegetation covariates: A) % shrub cover, B) average shrub height, C) % grass cover, and D) % forb cover.



## CHAPTER 2

### ESTIMATION AND EVALUATION OF GUNNISON SAGE-GROUSE JUVENILE RECRUITMENT IN SOUTHWEST COLORADO

Juvenile recruitment is one of the most important vital rates influencing the population growth of many bird species, and is fundamental to understanding trends in population size. Gunnison Sage-grouse (*Centrocercus minimus*) have declined substantially from their historic range and are currently a candidate species under the U.S. Endangered Species Act. In order to assess the status of this species, my research focused on establishing baseline juvenile recruitment rates and testing population-level, individual (i.e., hatch date) and temporal hypotheses (i.e., month) associated with juvenile recruitment for the Gunnison Sage-grouse. I tested these hypotheses on data from two populations of Gunnison Sage-grouse in the southwest of Colorado: Gunnison Basin that was monitored from 2005-2010 and San Miguel that was monitored from 2007-2010. I evaluated juvenile recruitment by combining both chick survival (hatch-30 days of age) and juvenile survival (31 days of age to the start of the first breeding season). I found strong support for a difference between the two populations in the chick survival analysis, no chicks survived to 30 days of age in San Miguel (n=8). Chick survival was 0.44 in Gunnison Basin (n=282). Thus there was no recruitment in San Miguel. I found a slight negative trend in chick survival and a stronger negative trend in juvenile survival from 2005-2010 in Gunnison Basin. Juvenile survival ranged from 0.60 in 2005 to 0.11 in 2010 (n=87). The overall juvenile recruitment rate in Gunnison Basin declined from 0.26 in 2005 to 0.05 in 2010. These declines mimic declines observed in population index data which might suggest juvenile recruitment declines are contributing to population declines.

## INTRODUCTION

Accurate information about factors contributing to population declines is necessary for successful conservation and management of species. Effective management is particularly necessary for rare or declining species. Life-history theory often enables us to determine which vital rates are most influential on population growth rates (Pfister 1998). For many bird species juvenile recruitment (proportion of birds hatched that survive to join the breeding population) is a primary driver of population growth (e.g., Roff 1992). Detecting trends across time in recruitment may be key to understanding trends in population growth for bird species.

Gunnison Sage-grouse (*Centrocircus minimus*, GUSG) have declined substantially from their historic range (Schroeder et al. 2004) and are a candidate species under the US Endangered Species Act (ESA, United States Fish and Wildlife Service 2010). Juvenile recruitment has been indicated as possibly the most limiting demographic parameter of population growth of sage-grouse species (Connelly et al. 2004, Gunnison Sage-grouse Rangewide Steering Committee 2005, Gregg and Crawford 2009). However, very little information is known about GUSG juvenile recruitment (Gunnison Sage-grouse Rangewide Steering Committee 2005). Examining estimates and trends in juvenile recruitment is important to understanding population growth of this species of concern.

GUSG are distributed into seven isolated populations. One population, Gunnison Basin (GB), comprises 85-90% of all GUSG and the other six populations are estimated to range in size from 20 to 170 individuals (Kathy Griffin, Colorado Parks and Wildlife (CPW), pers. comm.). Population index data have shown a decline in one of the smaller populations (San Miguel, SM, Kathy Griffin, CPW, pers. comm.). The same index data in GB have shown a recent decline after a population increase (Chapter 5). Due to the inherent difference in population sizes and the fact the populations may be experiencing different ecological pressures; the population dynamics of these small populations may be considerably different from the GB population.

In sage-grouse species recruitment into the breeding population occurs in the first lekking season after hatching. I define juvenile recruitment as survival of a bird from hatching to recruitment to the breeding population. Previous research on the related Greater Sage-grouse (*Centrocercus urophasianus*, GRSG) is not standardized and has typically been conducted on chick survival from hatch to 18 - 50 days of age (Burkpile et al. 2002, Aldridge 2005, Thompson et al. 2006, Gregg and Crawford 2009, Dahlgren et al. 2010, Taylor et al. 2012). A few studies have examined survival of juvenile GRSG from the fall until the first breeding season (Connelly et al. 2004, Beck et al. 2006, Taylor et al. 2012).

GRSG chicks are known to have a high mortality rate for the first 30 days after hatch (Apa 2004, Aldridge 2005, Gregg et al. 2007) and chick survival research is typically analyzed on a daily scale (Schroeder 1997, Burkpile et al. 2002, Gregg et al. 2007). Juvenile GRSG have a higher survival and are typically analyzed on a monthly scale (Beck et al. 2006, Battazzo 2007, Walker 2008, Swanson 2009). To provide a more precise estimate of juvenile recruitment and to allow ease of comparison with research on GRSG, I evaluated both a 30-day chick survival analysis and a juvenile survival analysis from 30-days of age to the start of the first breeding season. For both the chick and juvenile survival analyses I tested several of the same hypotheses: whether there is year to year variability, whether there is a trend across time, and if there is a difference between the two populations. Additionally for both the chick and juvenile analyses I examined if they, like professional hockey players (Gladwell 2008), benefit from being born earlier in the year. For the chick analysis I also tested whether older chicks have a higher daily survival than younger chicks, which was found to be the case in at least one study on GRSG (Dahlgren et al. 2010). Curio (1983) found yearling breeding birds were less productive than adult birds. To examine this hypothesis I compared the survival of chicks with respect to the age of their hen.

For the juvenile survival analysis I included a within-year month to month variation of survival similar to that used in the yearling and adult survival analysis of GUSG (see Chapter 3). Additionally, the independence assumption is often violated in studies of sage-grouse chicks as many, if not most, of the individuals have siblings in the study. To account for this possible source of dependence I used the

methods developed by Bishop et al. (2008) to estimate an overdispersion parameter ( $\hat{c}$ ). My study will provide crucial information for understanding GUSG population dynamics, which is necessary for implementing effective conservation strategies.

## METHODS

### Study areas

I captured and radiomarked GUSG hens in two of seven isolated populations of GUSG: GB and SM. My study area in the GB population is located in Gunnison and Saguache County, Colorado, USA (Figure 2.1). Gunnison Basin is a 2,000km<sup>2</sup> intermontane basin ranging in elevation from 2,300 to 2,900m (Hupp and Braun 1989). Mountainous terrain borders the north, east, and south-east sides of the study area. These areas contain habitat not commonly used by sage-grouse (Connelly et al. 2000). The western edge of the Gunnison Basin is comprised of land managed by the Ute Mountain Ute Tribe. The study area is sagebrush steppe dominated by sagebrush (*Artemisia spp.*) interspersed with rabbitbrush (*Chrysothamnus spp.*) antelope bitterbrush (*Purshia tridentate*) serviceberry (*Amelanchier spp.*) and mountain snowberry (*Symphoricarpos oreophilus*). Black sagebrush (*Artemisia nova*) is common on xeric ridge tops and south-facing slopes.

The SM population is located in Montrose and San Miguel counties, Colorado, USA. The SM population is comprised of six, interconnected subpopulations over a 400km<sup>2</sup> area. The elevation of this area ranges from 1,900 to 2,800m (Gunnison Sage-grouse Rangewide Steering Committee 2005). The vegetation characteristics vary between the six subpopulations in the SM population. The data for this study were collected from the Dan Noble State Wildlife Area (site of one of the subpopulations of the San Miguel population). The shrubs in this study area are mostly low sagebrush (*Artemisia arbuscula*) and black sagebrush (*Artemisia nova*), with some mountain big sagebrush (*Artemisia tridentate*) along drainages.

## Capture and monitoring

Spot-lighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) were used to trap yearling and adult female sage-grouse (mid-March through early-May) from 2004-2010. Sage-grouse were fitted with a 17g necklace-style radiotransmitter (Advanced Telemetry Systems, Inc.) and a numbered leg band (National Brand and Tag Company). The transmitter weight was <2% of the average adult female GUSG's body weight (1270g, SD 90g). Each bird was weighed and plumage characteristics were used to determine age (Beck et al. 1975). Each GUSG was categorized as either an adult ( $\geq 2$  years old) or a yearling (1 year old, first breeding season).

Females were tracked through the breeding season to determine nesting status. Nesting females were monitored from at least 30 m from the nest to minimize disturbance. Nests were monitored 6-7 days a week. Once a female moved from the nest, the nest was located to assess the fate (e.g., hatched, depredated, abandoned, other). For any successful nest (at least one egg hatched) the resulting chicks were caught and tagged usually within 24-48 hours of hatching. Chicks were captured by locating and flushing the hen while she was brooding the young (just after dawn or just before dusk). Trapping was not attempted in inclement weather (i.e., rain or snow, or temperatures <20°F). Chicks were placed in a lidded plastic tub with a hot water bottle for warmth during handling. Each chick was weighed and half of the brood (up to 3 individuals) were tagged with 1g radiotransmitter with a guaranteed 18-day battery life (Advanced Telemetry Systems, Inc.) that was attached by suturing (Burkpile et al. 2002). The transmitter weight is <4% of the average 1-2 day old GUSG chick's body weight (28.9g, SD 3.7g, pers. Obs.). Transmitters were not placed on chicks that were 23g or less in weight. The hen was ensured to be nearby before releasing the chicks.

Chicks were recaptured two weeks after hatch and the 1g transmitters were replaced by 4g radiotransmitters (Advanced Telemetry Systems, Inc.), also attached by suturing. The 4g transmitters had a battery life guaranteed for 6 months. The 4g transmitter was <5% of the average 14-18 day old chick's body weight (100g, SD 28g, my results). Chicks that were less than 80g at recapture were tagged with

another 1g transmitter as the 4g transmitter would be greater than 5% of the bird's weight. In these cases the bird would be recaptured again within 18 days to replace with a 4g transmitter. Birds were recaptured again in the fall and the 4g transmitter was replaced with an adult 17g transmitter necklace-style radiotransmitter (Advanced Telemetry Systems, Inc.), as long as the bird was greater than 340g (ensuring the transmitter was not more than 5% of the bird's weight).

Chicks were located 6 days a week for the first 60 days using radio telemetry triangulation. After 60 days of age they were located 3-4 times a week through September also by triangulation. Aerial locations were obtained monthly during the fall and winter. Chick transmitters (1g and 4g) do not have a mortality signal. If a chick was located without the hen a visual location was attempted to determine if the chick was alive.

### **Statistical analysis**

I ran two separate analyses: a daily survival analysis on chicks up to 30 days of age ("chick survival"), and a monthly survival analysis on chicks 30 days old until the first breeding season ("juvenile survival"). For both the chick survival and juvenile survival analyses I used the known fate type (nest survival) models in Program MARK (White and Burnham 1999). These models allow for staggered entry and are ideal for radio-telemetry studies. Birds that went missing or those that slipped their collars were included as alive in the study area until their last encounter, then were censored from the study. Additionally, any birds that were removed from the study area or affected by handling were censored in this manner. To compare the relative importance of each model I evaluated the Akaike Information Criterion (AIC) with the small sample size correction factor (AICc, Burnham and Anderson 2002). To evaluate the relative importance of each individual factor I calculated the cumulative AICc weight (Burnham and Anderson 2002) for each factor and covariates with a cumulative AICc weight above 0.5 were considered to be important (Barbieri and Berger 2004).

For the juvenile survival analysis, I considered two within-year seasonal variation intervals. First, I considered that survival would vary from month to month throughout the year. Second, I assumed that fall and winter survival would be constant (October to March) and the rest of the year would have a monthly survival variation (this parameterization I called “season”). These are similar to the methods used for the yearling and adult survival analysis (Chapter 3).

I evaluated the relative importance of each model using Akaike Information Criterion with the small sample size correction (AICc, Burnham and Anderson 2002). Following the recommendation of Doherty et al. (2012) I ran all combinations of factors (described in Table 2.1) with the exception that the within-year temporal covariates (“Month” and “Season”) and the between year temporal covariates (“Year” and “Year trend”) cannot be in the same models due to un-identifiability of parameters. Based on these methods I ran 48 models for the chick survival analysis and 18 models for the juvenile survival analysis.

I calculated 30-day chick survival and juvenile survival (30 days of age to first breeding season) by multiplying the daily or monthly survival rates within each year period, the variance for those estimates were calculated using the delta method (Seber 1982). To calculate an estimate of juvenile recruitment (survival from hatch to first of the breeding season) I multiplied the chick and the juvenile survival rates (accounting for staggered entry into the analysis), the variance estimates were calculated using the delta method (Seber 1982).

### **Bootstrap analysis**

I used a data-bootstrap analysis to test for overdispersion due to sibling dependence. I followed methodologies described by Bishop et al. (2008) and as implemented in Program MARK (White and Burnham 1999). Each bootstrap analysis consisted of 2,000 replicates. I resampled broods with replacement (not individual chicks). The number of broods sampled equaled the number of broods in the original analysis; however, since the different broods were selected each time the total number of chicks in the analysis varied with each sample. I ran the survival analysis for the most parameterized model in

the analysis described above on each of the bootstrap replicates. I then calculated the mean and standard deviation from the 2,000 bootstrap replicates. The dependence among the broods is reflected in the standard deviation of the survival estimates. I estimated overdispersion in the data set as the ratio of the bootstrap estimate of standard deviation ( $[SD(\hat{S})]$ ) over the theoretical standard error (standard error from the survival estimate of the top model). Burnham and Anderson (2002) suggest that estimates of  $\hat{c}$  that are just above 1.0 show only slight overdispersion and judgment should be used for interpretation. I used estimates of  $\hat{c} < 1.2$  to be weak support for overdispersion for the chick survival and juvenile survival analysis (Bishop et al. (2008). If the resulting  $\hat{c}$  estimate was above the cutoff of 1.2 then the estimated  $\hat{c}$  was incorporated into Program MARK and the model estimates were compared using the Quasi-Akaike Information Criterion (QAICc, Burnham and Anderson 2002).

## **RESULTS**

From 2005-2010, 134 females with broods were tracked and a total of 328 chicks were marked. Over the six years, 15 chicks were found dead the day after capture at the capture site (all from the GB population). These birds may have died due to exposure after handling because they were not able to reunite with their hens, and they were censored from the study. Birds that were not able to be aged accurately were not included in the chick analysis. These included chicks that had been adopted by a marked hen (determined by obvious sized difference from brood mates) or chicks whose hatch date was unknown. This resulted in 290 chicks being included in the chick survival analysis (Table 2.2). Eighty-seven birds were included in the juvenile survival study (Table 2.2). Of those, 70 birds had survived from the chick survival study and 17 birds were of the group whose age was not known exactly. The ages of these birds were estimated based on their weights at capture and included in the juvenile study when they were estimated to be 31 days of age (the scale for the juvenile survival is monthly, therefore juveniles were included in the study in the month they were 32 days old). Only nine chicks were caught in the San Miguel population from

three broods. None of those chicks survived to 30 days and therefore no birds from SM were included in the juvenile survival analysis.

### **Chick Survival Analysis**

I evaluated the relative support for the 48 models in the candidate model set for chick survival (Appendix 2.A). The bootstrap analysis was run on the most parameterized model (10 parameters). The estimate of  $\hat{c}$  based on the ratio of the average bootstrap standard deviation over the standard error from the estimate of the full model was 2.036. This value is above 1.2 suggesting there is overdispersion in the data.

Therefore the models were compared using QAICc.

Six models were within two  $\Delta$ QAICc units of the top ranked model (Appendix 2.A). The population effect was the only factor in all of the top models, denoting its importance in chick survival. The age of the chick was included in five of the top six models suggesting it is also related to chick survival. Trend was in four of the top six models, including the top model, and is likely important. Hen age and hatch week were not as influential as they were only in two and one of the six top models, respectively. The year to year variation was not in any of these models and thus not influential on chick survival in my study.

I also compared the relative importance of each covariate using the cumulative QAICc weights (Table 2.3A). Population and chick age are the only two effects that have a covariate weight above the 0.50 cutoff and population had considerable support for being correlated with chick survival (QAICc cumulative weight of 0.95). Chick survival in GB is substantially higher than in SM (Table 2.4). Chick age is marginally supported with a cumulative QAICc weight of 0.56 (Table 2.3A). The older a chick is the higher its survival ( $\hat{\beta} = 0.02$ , 95% CI -0.01, 0.06, estimates are on the logit scale). However, the confidence intervals overlap zero and thus the correlation is not definitively positive.

Trend across years was of borderline importance (cumulative QAICc weight of 0.49). However this factor is in fewer models than other covariates because it could not be run concurrently with the covariate

that fluctuates between years. A slight decline in chick survival may be apparent, however the confidence intervals overlap zero ( $\hat{\beta} = -0.141$ , 95% CI -0.332, 0.050, estimates are on the logit scale). The chick survival rates across years are shown with and without a trend effect in Figure 2A. The remaining main effects were relatively unsupported: hen age (QAICc cumulative weight = 0.28), hatch week (QAICc cumulative weight = 0.28), and year effect (QAICc cumulative weight = 0.04).

### **Juvenile Survival Analysis**

The relative support for the 18 candidate models are presented in Appendix 2.B. The bootstrap analysis was run on the most parameterized model (16 parameters). There was only weak evidence for overdispersion in the juvenile survival data ( $\hat{c} = 1.103$ ), therefore I did not use a  $\hat{c}$  adjustment and the models were compared using AICc.

The top model (AICc weight = 0.524) included a year trend and the season effect (Appendix 2.B). All of the other models were  $>2\Delta\text{AICc}$  from this model. The year trend and season effect were the only factors that had a cumulative AICc weight above 0.50 (Season 0.96 and Trend 0.74, Table 2.3B). Little support was evident for an effect of hatch week (cumulative AICc wt 0.30), year to year variation (0.21), or month (0.04).

Juvenile survival represents the survival rate from 31 days of age to the start of the first breeding season (April 1). Monthly estimates of juvenile survival are weighted by the proportion of individuals that entered into the study in each month (during June, July, and August; when juvenile turn 31 days old). The within-year variability shows that juvenile survival is lower and more variable from June to September and consistently higher from October thru March (Figure 2.3) and the among-year variability shows juvenile survival has declined from 2005-2010 (Figure 2.2B). The sample sizes vary between 8 and 27 (Table 2.2) individuals per year and thus the confidence intervals are wide for the survival estimates (Figure 2.2B).

## Recruitment Analysis

The recruitment estimates are based on the multiplication of the chick and juvenile survival analysis. Recruitment has declined from 2005-2010 (Figure 2.2C). The recruitment rates calculated from the chick survival estimates with and without a trend effect are shown in Figure 2.2C. Recruitment varies between 0.05 to 0.26 without a trend on chick survival and 0.02 to 0.28 with a trend effect on chick survival.

## DISCUSSION

Gunnison Sage-grouse are a species of concern. However, little is known about the species-specific demographic rates, which are important for assessing population viability and targeting management actions. My project focused on establishing baseline rates of juvenile recruitment for the species, and for two isolated and characteristically distinct populations of GUSG. In Chapters 1 and 3 I did not find a detectable difference in rates of nest success and adult survival between these two unique populations. However, my results in this chapter demonstrate a dramatic difference between GB and SM in chick survival (Table 2.3A, Table 2.4). There were no chicks that survived to 30 days of age in SM during the 4 years in which we conducted research while estimates in GB were 0.468 (SE 0.031). However, my sample size was low for the SM population ( $n=8$ ) and maybe the low rate of chick survival was a matter of chance. If the chick survival rate was actually similar to that in GB ( $\hat{S} = 0.44$ ) then the likelihood of having zero of eight chicks survive is around 10% (accounting for overdispersion). Therefore, I conclude that the survival rates between these populations are probably different and that SM has a lower chick survival than GB.

A decline in high male lek counts in SM has occurred over the last 10 years (the only population monitoring tool employed in SM). The lack of observed recruitment during this study may be a contributing factor to that decline. Juvenile recruitment has been shown to be a limiting factor in population growth for sage-grouse species (Chapter 4, Johnson and Braun 1999, Taylor et al. 2012).

Population-specific rates for juvenile survival were not able to be established for SM, due to no chicks surviving to 31 days of age in that population. The lack of surviving chicks also leads to the estimate of zero overall juvenile recruitment in SM.

In comparison, the chick survival and juvenile survival in GB were considerably higher than in SM and are similar to rates for GRSG (Aldridge 2005, Gregg and Crawford 2009, Swanson 2009). However, both the chick and juvenile survival estimates appear to be declining during our study in GB (Figure 2.2). The trend in chick survival is border line in importance; but is slightly negative over time which is important to be aware of in a species of concern like GUSG. I did find strong evidence of a decline in juvenile survival in GB over the past six years.

Gunnison Basin is considered to be a relatively stable population of GUSG (Gunnison Sage-grouse Rangewide Steering Committee 2005). My juvenile recruitment estimates coincide with estimated declining trends in the population (see Chapter 4). A decline across time in juvenile recruitment has been shown to be related to general population declines in sage-grouse species (Chapter 4, Connelly and Braun 1997, Gregg et al. 2007). The population indices of lek counts for GB do suggest that there has been a population decline during the time frame of my study, and the GB population might not be as stable as previously thought. However, I note that the time span of my study may not be long enough to encompass broader time trends/cycles that might be at play for such a population. The six years examined might only be showing the downward pattern in a larger cyclical time series.

The trend across time in juvenile recruitment is more pronounced in the juvenile survival component than in the chick survival in GB. Previous research on galliforms is often concentrated on chick survival (Connelly and Braun 1997, Schroeder et al. 2004, Taylor et al. 2012) with comparatively few studies examining juvenile survival (Beck et al. 2006, Swanson 2009). My results suggest that the pattern of decline is stronger in juvenile survival. The pattern of a decline in juvenile survival would have been masked had we only looked at chick survival. These results also highlight that a gap in demographic

information, such as a lack of species- or population-specific juvenile survival estimates, might skew population projections (e.g., Morris and Doak 2002).

Another interesting finding is that a high level of sibling dependence occurred in chicks but not in juveniles. When chicks are captured for the first time the majority have at least one sibling tagged at well ( $n=277/290$ ). Chicks during the first 30-days of life stay close to their mother and therefore sibling proximity and behavior are inherently linked (Huyer 2004). Therefore, I anticipated that there would be evidence of overdispersion in the chick survival data ( $\hat{c} = 2.036$ ). Sage-grouse young require protection against the elements at night by being brooded by a hen, typically up to 60 days of age, and juvenile grouse tend to remain in flocks with their hen and siblings into the fall (Mike Phillips, pers. Comm., Swanson 2009). However, there was no evidence for overdispersion in the juvenile survival analysis ( $\hat{c} = 1.103$ ). This may in part be due to brood mixing which occurs at a relatively high rate within sage-grouse (Dahlgren et al. 2010). Additionally, the proportion of juveniles with siblings is lower than chicks with siblings (36 juveniles with siblings of 87 total juveniles).

Sage-grouse chick survival has been linked to many external effects, primarily among them are factors relating to food and cover. Chick survival is generally better when there is greater forb cover (Drut et al. 1994, Huyer 2004, Gregg and Crawford 2009), greater shrub and herbaceous cover (Aldridge 2005), and when arthropods are abundant (Drut et al. 1994, Dahlgren et al. 2010). Drought conditions have been found to have a negative effect on chick survival (Aldridge 2005). Although my study did not focus on measuring vegetation and arthropods at hen and brood locations, these above associations might exist. Anecdotal evidence based on movement patterns of hens with chicks compared to hens without chicks suggest that forb and invertebrate availability is important for chicks as hens seemed to spend more time in drainages and hay meadows with greener vegetation.

Yearling hens appear to rear chicks with the same success rate as adults. This is contrary to typical results from GRSG research (Connelly et al. 1993, Gregg et al. 2006). However, research on GRSG suggests

that chicks with yearling hens are more likely to leave their own brood than chicks of adult hens, and that this likely enhances the survival rate of these chicks (Dahlgren et al. 2010). The rates of adoptions were not well monitored in my study and therefore I have no evidence to support this conjecture. However, if this is true then it may help explain why there was no discernable difference in survival of chicks hatched to yearling vs adult hens.

I found juvenile survival rates to be more variable and lower during the summer months (June-September) and consistently higher during the fall and winter (October-March, Figure 2.3). This within year pattern of survival is similar to that of adult and yearling GUSG (Chapter 3) where survival rates of yearling and adults is high and constant during the non-breeding season (fall-winter). This survival pattern suggests that juveniles that survive until October will likely survive to the breeding season. This highlights the potential that management efforts focused on juvenile survival during the summer months will likely be more efficient than working to improve fall and winter survival.

**Table 2.1:** List of covariates and hypothesized effects on Gunnison Sage-grouse chick and juvenile survival

<b>Chicks (0-30 days old)</b>		<b>Juveniles (30 days of age to first breeding season)</b>	
<b>Covariates</b>	<b>Hypothesis</b>	<b>Covariates</b>	<b>Hypothesis</b>
Year	Survival will vary year to year	Year	Survival will vary year to year
Year trend	Survival will show a trend across years (e.g., decreasing)	Year trend	Survival will show a trend across years (e.g., decreasing)
Population	Birds from Gunnison Basin will have higher survival than those from San Miguel	Population	Birds from Gunnison Basin will have higher survival than those from San Miguel
Hen	Sibling survival will be correlated	Hen	Sibling survival will be correlated
Hatch week	Chicks that hatch earlier in the year will have higher survival than those that hatch later in the year	Hatch week	Chicks that hatch earlier in the year will have higher survival than those that hatch later in the year
Age	Daily age of chick (1 -30 days of age), older chicks have higher survival	Month	Month to month variation in survival
Hen Age	Older hens will be more successful at raising young than yearling hens	Season	Fall and winter months (Oct-Mar) will have constant survival rates and the rest of the year will vary by month

**Table 2.2:** Number of birds per year in the chick and juvenile analyses for Gunnison Sage-grouse

<b>Year</b>	<b>Chick analysis</b>	<b>Juvenile analysis</b>
2005	19	8
2006	30	13
2007	40	9
2008	71	18
2009	79	27
2010	51	12
<b>Total</b>	<b>290</b>	<b>87</b>

**Table 2.3:** Cumulative covariate weights for Gunnison sage-grouse chick survival (**A**) and juvenile survival (**B**) analyses. The chick survival analysis used QAICc based on an estimated  $\hat{c}$  of 2.036. The juvenile survival analysis did not suggest overdispersion and thus models were evaluated with AICc. Bold numbers indicate cumulative weights above 0.50.

**A)**

<b>Covariate</b>	<b>Cumulative Quasi-AICc Weight</b>
Population <sup>a</sup>	<b>0.950</b>
Age <sup>b</sup>	<b>0.566</b>
Trend <sup>c</sup>	0.494
Hen age <sup>d</sup>	0.281
Hatch week <sup>e</sup>	0.275
Year <sup>f</sup>	0.042

**B)**

<b>Covariate</b>	<b>Cumulative AICc Weight</b>
Season <sup>g</sup>	<b>0.962</b>
Trend <sup>c</sup>	<b>0.739</b>
Hatch week <sup>e</sup>	0.296
Year <sup>f</sup>	0.210
Month <sup>h</sup>	0.038

<sup>a</sup> ‘Population’ denotes a 0 for the Gunnison Basin population and a 1 for the San Miguel population

<sup>b</sup> ‘Age’ is a linear trend relating the age (1-30 days old) of a chick to the daily chick survival rate

<sup>c</sup> ‘Trend’ is a linear relationship between the years in the study and the survival rate

<sup>d</sup> ‘Hen age’ denotes a 0 for a yearling hen and a 1 for an adult hen, referring to the mother of the chick

<sup>e</sup> ‘Hatch week’ is a linear relationship between chick survival and the week the chick was hatched

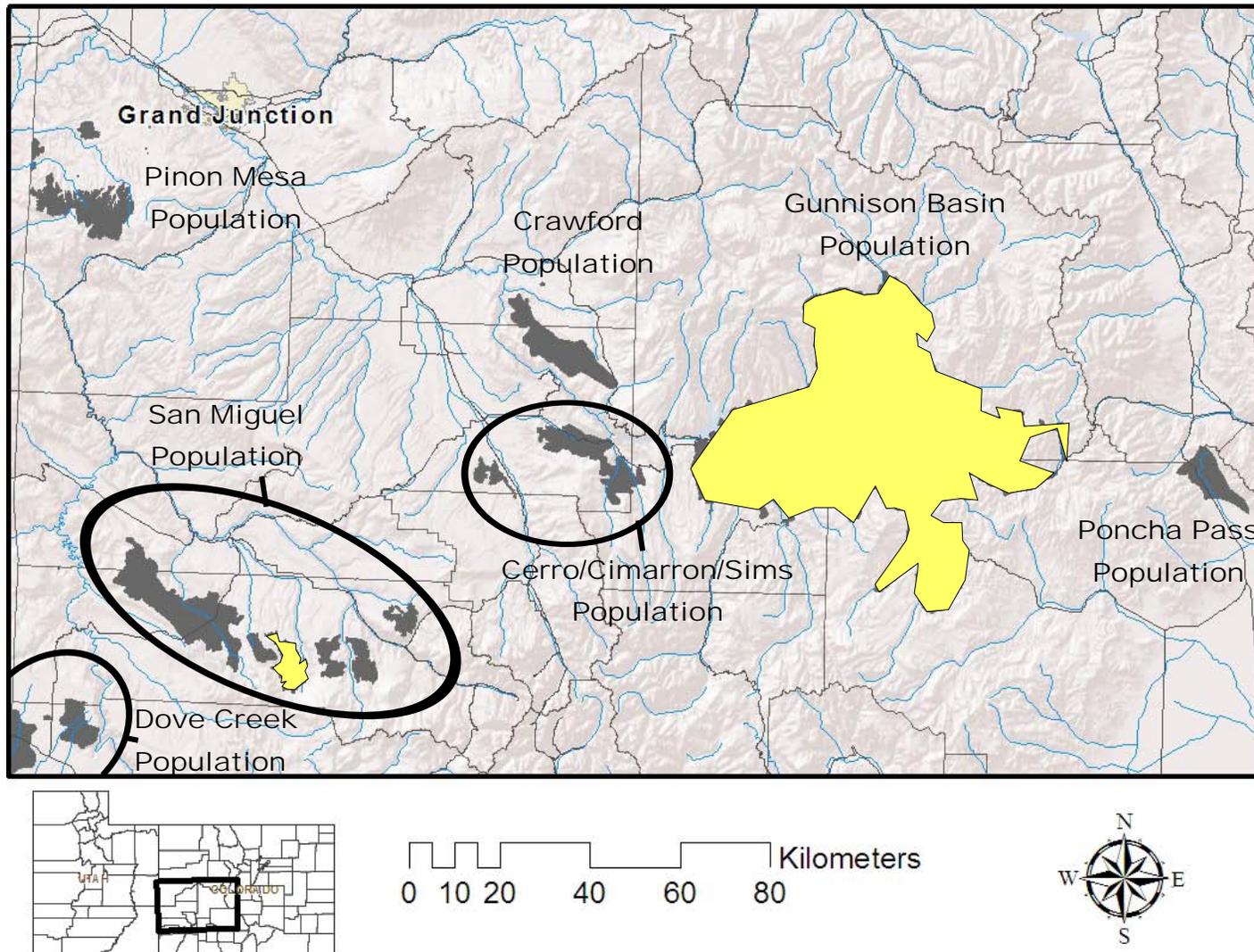
<sup>f</sup> ‘Year’ allows for survival to vary for each year in the study

<sup>g</sup> ‘Season’ allows for monthly variability in survival from Jun-Sept and constant survival from Oct-Mar

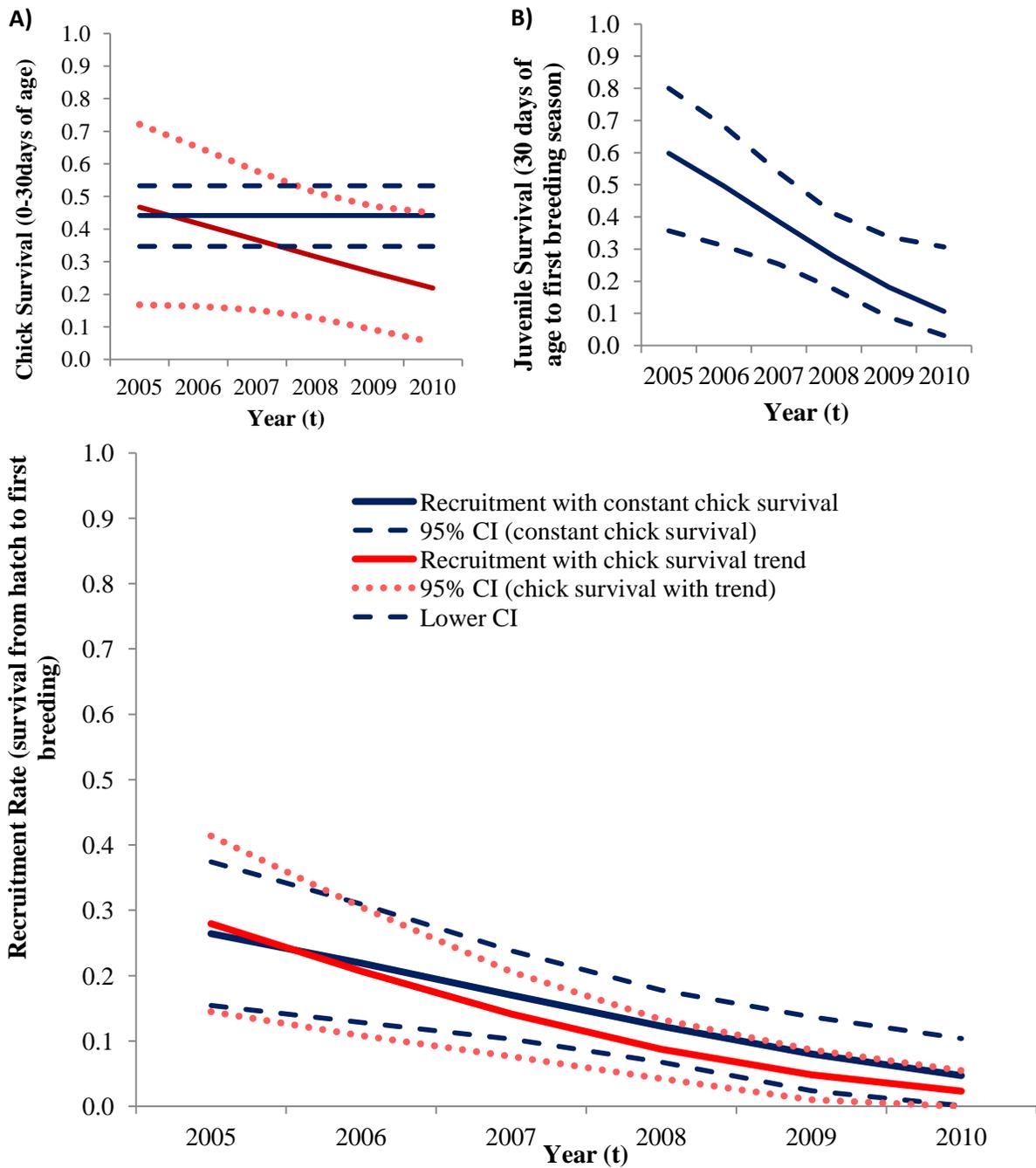
<sup>h</sup> ‘Month’ allows for monthly variability in survival for all months

**Table 2.4:** 30-day survival rate of Gunnison Sage-grouse chicks by population

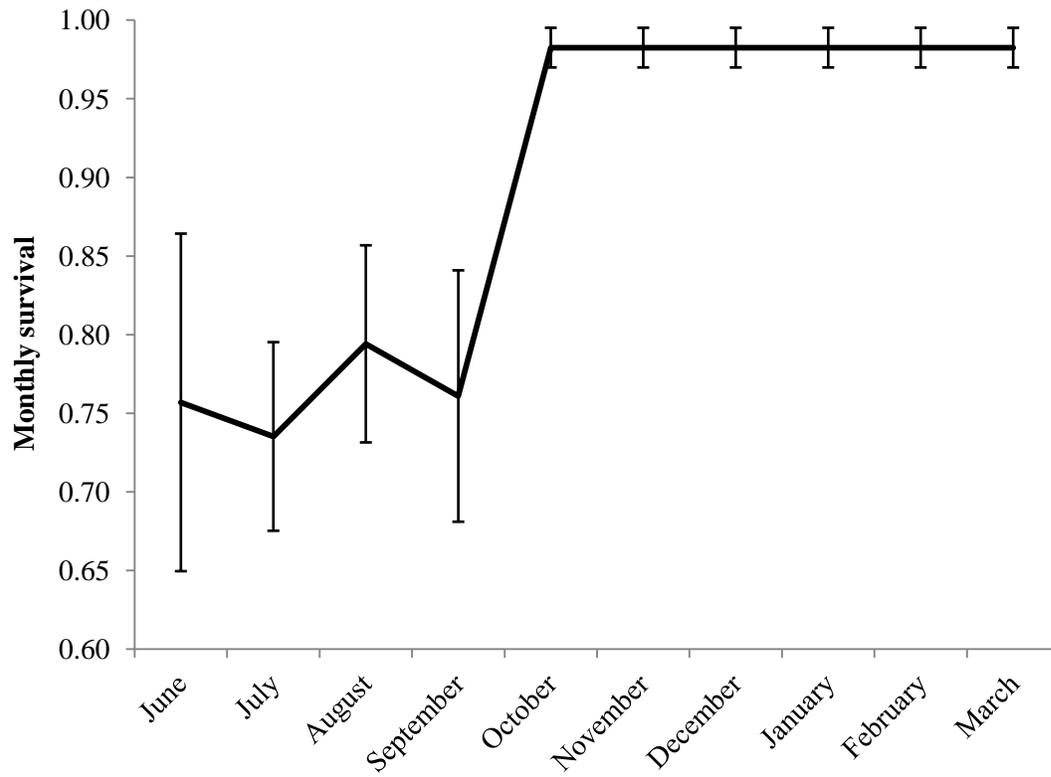
<b>Population</b>	<b>30-day survival rate</b>	<b>Standard Error</b>
Gunnison Basin	0.468	0.031
San Miguel	0.008	0.105



**Figure 2.1.** The seven populations of Gunnison Sage-grouse. The two areas highlighted in yellow are the study areas.



**Figure 2.2:** Chick survival (A), Juvenile survival (B), and Recruitment rate (C) with 95% confidence intervals across years. The chick survival and recruitment rates are show when a trend is included in the chick survival analysis and without.



**Figure 2.3:** Juvenile monthly survival rates from 30 days of age to the first breeding season (April 1) with standard errors for Gunnison Sage-grouse

## LITERATURE CITED:

- Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. University of Alberta, Alberta, Canada.
- Apa, A. D. 2004. Habitat use, movements, and survival of Gunnison Sage-Grouse in southwestern Colorado. Unpublished Report. Colorado Division of Wildlife, Colorado, USA.
- Barbieri, M. M. and J. O. Berger. 2004. Optimal predictive model selection. *Annals of Statistics* **32**:870-897.
- Battazzo, A. M. 2007. Winter Survival and Habitat Use by Female Greater Sage-grouse (*Centrocercus urophasianus*) in South Phillips County, Montana 2004-2006. University of Montana, Missoula, MT USA.
- Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin* **34**:1070-1078.
- Beck, T. D. I., R. B. Gill, and C. E. Braun. 1975. Sex and age determination of sage grouse from wing characteristics. *in* C. D. o. Wildlife, editor. Game Information Leaflet, Fort Collins, CO, USA.
- Bishop, C. J., G. C. White, and P. M. Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. *Journal of Wildlife Management* **72**:1085-1093.
- Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. *Wildlife Society Bulletin* **30**:93-96.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference- a practice information-theoretic approach. 2nd edition. Springer, New York.
- 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., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting by Sage Grouse in Southeastern Idaho. *Condor* **95**:1041-1043.

- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies Unpublished Report, Cheyenne, Wyoming, USA.
- Connelly, J. W., 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.
- Curio, E. 1983. Why Do Young Birds Reproduce Less Well. *Ibis* **125**:400-404.
- Dahlgren, D. K., T. A. Messmer, and D. N. Koons. 2010. Achieving Better Estimates of Greater Sage-Grouse Chick Survival in Utah. *Journal of Wildlife Management* **74**:1286-1294.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* **152**:317-323.
- Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Technical Note- Diets and Food Selection of Sage Grouse Chicks in Oregon. *Journal of Range Management* **47**:90-93.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for Trapping Sage Grouse in Colorado. *Wildlife Society Bulletin* **10**:224-231.
- Gladwell, M. 2008. *Outliers: The Story of Success*. Little, Brown and Company Hachette Book Group, New York, NY USA.
- Gregg, M. A. and J. A. Crawford. 2009. Survival of Greater Sage-Grouse Chicks and Broods in the Northern Great Basin. *Journal of Wildlife Management* **73**:904-913.
- Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted radiotransmitters to estimate survival of greater sage-grouse chicks. *Journal of Wildlife Management* **71**:646-651.
- Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and reneating by greater sage-grouse. *Journal of Wildlife Management* **70**:472-478.
- Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-Grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Hupp, J. W. and C. E. Braun. 1989. Topographic Distribution of Sage Grouse Foraging in Winter. *Journal of Wildlife Management* **53**:823-829.

- Huwer, S. L. 2004. Evaluating greater sage-grouse brood habitat using human-imprinted chicks. Colorado State University, Fort Collins, CO.
- Johnson, K. H. and C. E. Braun. 1999. Viability and conservation of an exploited sage grouse population. *Conservation Biology* **13**:77-84.
- Morris, W. F. and D. F. Doak. 2002. *Quantitative Conservation Biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America* **95**:213-218.
- Roff, D. A. 1992. *Evolution of Life Histories*. Prentice-Hall, New York.
- Schroeder, M. A. 1997. Unusually high reproductive effort by Sage Grouse in a fragmented habitat in north-central Washington. *Condor* **99**:933-941.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-Grouse in North America. *Condor* **106**:363-376.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Second edition. Macmillan, New York, New York, USA.
- Swanson, C. C. 2009. *Ecology of greater sage-grouse in the Dakotas*. Ph.D. South Dakota State University, United States -- South Dakota.
- Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* **76**:336-347.
- Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. *Western North American Naturalist* **66**:332-342.

- United States Fish and Wildlife Service, U. 2010. Determination of Gunnison Sage-grouse as a Threatened or Endangered Species. *in* D. o. t. Interior, editor. Federal Register
- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An Improved Spotlighting Technique for Capturing Sage Grouse. *Wildlife Society Bulletin* **20**:425-426.
- Walker, B. L. 2008. Greater Sage-grouse Response to Coal-bed Natural Gas Development and West Nile Virus in the Powder River Basin, Montana and Wyoming, USA. University of Montana, Missoula, MT.
- White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Fort Collins, CO.

**APPENDIX 2.A.** Full table of model results from the chick survival analysis for Gunnison Sage-grouse from the Gunnison Basin and San Miguel populations.

<b>Model</b>	<b>QAICc</b>	<b>Δ QAICc</b>	<b>QAICc Weights</b>	<b>Likelihood</b>	<b>K*</b>	<b>Q Deviance</b>
Trend <sup>a</sup> +Age <sup>b</sup> +Population <sup>c</sup>	452.24	0.000	0.139	1.000	4	444.23
Age+Population	452.43	0.186	0.127	0.911	3	446.42
Trend+Population	452.75	0.511	0.108	0.774	3	446.75
Population	452.87	0.632	0.101	0.729	2	448.87
Trend+Hatch <sup>d</sup> +Age+Population	454.12	1.875	0.054	0.392	5	444.10
Age+Population+HenAge <sup>e</sup>	454.19	1.952	0.052	0.377	4	446.18
Trend+HenAge+Age+Population	454.24	1.996	0.051	0.369	5	444.22
Age+Population+Hatch	454.42	2.183	0.047	0.336	4	446.41
Population+HenAge	454.64	2.395	0.042	0.302	3	448.63
Trend+Hatch+Population	454.65	2.404	0.042	0.301	4	446.64
Trend+ HenAge +Population	454.75	2.510	0.040	0.285	4	446.74
Population+Hatch	454.86	2.622	0.037	0.270	3	448.86
Trend+Age+Population+Hatch+HenAge	456.12	3.879	0.020	0.144	6	444.10
Age+Population+Hatch+HenAge	456.20	3.957	0.019	0.138	5	446.18
Population+Hatch+HenAge	456.64	4.398	0.015	0.111	4	448.63
Trend+Hatch+ HenAge +Population	456.65	4.408	0.015	0.110	5	446.63
Year <sup>f</sup> +Age+Population	457.27	5.029	0.011	0.081	8	441.24
Year+Population	457.49	5.251	0.010	0.072	7	443.47
Trend+Age	457.62	5.375	0.009	0.068	3	451.61
Age	457.93	5.684	0.008	0.058	2	453.92
Year+Age+Population+Hatch	459.22	6.982	0.004	0.030	9	441.18
Year+Age+Population+HenAge	459.23	6.984	0.004	0.030	9	441.18
Age+HenAge	459.26	7.020	0.004	0.030	3	453.26
Year+Population+Hatch	459.43	7.188	0.004	0.028	8	443.39
Year+Population+HenAge	459.45	7.213	0.004	0.027	8	443.42
Trend	459.54	7.295	0.004	0.026	2	455.53
Trend+ HenAge +Age	459.56	7.318	0.004	0.026	4	451.55
Trend+Hatch+Age	459.60	7.364	0.004	0.025	4	451.60
Intercept only	459.75	7.511	0.003	0.023	1	457.75
Age+Hatch	459.82	7.581	0.003	0.023	3	453.82
HenAge	461.06	8.817	0.002	0.012	2	457.06
Year+Age+Population+Hatch+HenAge	461.18	8.937	0.002	0.011	10	441.13
Age+Hatch+HenAge	461.24	9.003	0.002	0.011	4	453.23
Year+Population+Hatch+HenAge	461.39	9.151	0.001	0.010	9	443.35
Trend+ HenAge	461.46	9.216	0.001	0.010	3	455.45
Trend+Hatch	461.53	9.292	0.001	0.010	3	455.53
Trend+Hatch+Hen+Age	461.54	9.298	0.001	0.010	5	451.52
Hatch	461.62	9.378	0.001	0.009	2	457.62
Hatch+HenAge	463.03	10.785	0.001	0.005	3	457.02

Year+Age	463.40	11.158	0.001	0.004	7	449.37
Trend+Hatch+ HenAge	463.45	11.207	0.001	0.004	4	455.44
Year	465.05	12.804	0.000	0.002	6	453.03
Year+Age+Hatch	465.38	13.142	0.000	0.001	8	449.35
Year+Age+HenAge	465.41	13.165	0.000	0.001	8	449.37
Year+Hatch	467.02	14.776	0.000	0.001	7	452.99
Year+HenAge	467.05	14.807	0.000	0.001	7	453.02
Year+Age+Hatch+HenAge	467.39	15.150	0.000	0.001	9	449.35
Year+Hatch+HenAge	469.02	16.781	0.000	0.000	8	452.99

\* k is the number of parameters in the model

<sup>a</sup> ‘Trend’ represents a linear trend across years (k=1)

<sup>b</sup> ‘Age’ represents a linear trend on the age of the chick from 1-30 days of age (k=1)

<sup>c</sup> ‘Population’ represents Gunnison Basin if it is a 0 and San Miguel if it is a 1 (k=1)

<sup>d</sup> ‘Hatch’ represents a linear trend based on the week the chick was hatched (k=1)

<sup>e</sup> ‘HenAge’ denotes the age of the hen: 0 for yearlings and 1 for adults (k=1)

<sup>f</sup> ‘Year’ denotes a separate parameter for each year in the study allowing for annual variability (k=6)

**APPENDIX 2.B.** Full table of model results from juvenile survival analysis for the Gunnison Basin population of Gunnison Sage-grouse.

<b>Model</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>AICc Weights</b>	<b>Model Likelihood</b>	<b>K*</b>	<b>Deviance</b>
Trend <sup>a</sup> +Season <sup>b</sup>	227.38	0	0.524	1	6	215.11
Trend+Season+Hatch <sup>c</sup>	229.46	2.075	0.186	0.354	7	215.09
Season+Year <sup>d</sup>	230.39	3.005	0.117	0.223	10	209.66
Year+Season+ Hatch	230.99	3.611	0.086	0.164	11	208.12
Season	232.73	5.342	0.036	0.069	5	222.53
Trend+Month <sup>e</sup>	233.76	6.380	0.022	0.041	11	210.89
Season+ Hatch	234.76	7.375	0.013	0.025	6	222.48
Trend+Month+Hatch	235.91	8.527	0.007	0.014	12	210.88
Year+Month	237.06	9.678	0.004	0.008	15	205.45
Year+Month+ Hatch	237.81	10.427	0.003	0.005	16	203.98
Month	238.90	11.520	0.002	0.003	10	218.18
Hatch +Month	241.00	13.619	0.001	0.001	11	218.13
Year+ Hatch	255.76	28.379	0.000	0.000	7	241.40
Trend	256.63	29.245	0.000	0.000	2	252.59
Trend+ Hatch	257.33	29.947	0.000	0.000	3	251.25
Year	260.73	33.351	0.000	0.000	6	248.46
Intercept only	266.85	39.471	0.000	0.000	1	264.84
Hatch	268.43	41.049	0.000	0.000	2	264.39

\* k is the number of parameters in the model

<sup>a</sup> ‘Trend’ represents a linear trend across years (k=1)

<sup>b</sup> ‘Season’ denotes the parameterization that allows for monthly variation in survival during the reproductive season (Jun-Sept) and a constant survival during the non-reproductive season (k=5)

<sup>c</sup> ‘Hatch’ represents a linear trend based on the week the chick was hatched (k=1)

<sup>d</sup> ‘Year’ denotes a separate parameter for each year in the study allowing for annual variability (k=6)

<sup>e</sup> ‘Month’ denotes the parameterization that allows for full monthly variability in survival (k=10)

## CHAPTER 3

### ADULT AND YEARLING SURVIVAL OF GUNNISON SAGE-GROUSE IN SOUTHWEST COLORADO

Gunnison Sage-grouse (*Centrocercus minimus*) populations have declined from their historic numbers and range and recent monitoring has suggested that some populations are continuing to decline. The evaluation of long-term, population-specific survival estimates is important to evaluate population stability; which is necessary for conservation of this species of concern. I evaluated adult and yearling survival in two populations of Gunnison Sage-grouse. The Gunnison Basin population is believed to comprise 85-90% of all Gunnison Sage-grouse and is relatively stable; the San Miguel population is one of six relatively small populations and contains 3-5% of the species and is on the decline. I examined the relationship between survival and population and tested hypotheses with regards to temporal effects (across years and within year) and individual effects (sex, age, breeding status). I also examined the effect of harsh winters on survival using average monthly snow depth as an indicator of winter harshness. I evaluated monthly survival using known-fate models in Program MARK on 217 radiomarked birds in the Gunnison Basin from 2004-2010 and 25 birds in San Miguel from 2007-2010. I compared the relative support for each covariate using cumulative AICc model weights. The within year pattern of survival is different for males compared to females (cumulative AICc weight 0.878). Males had the lowest survival during the lekking season (March –April), females had lower survival during the nesting and chick rearing season (May – August). Survival also varied among years: between 0.52 and 0.89 for females and between 0.30 and 0.71 for males. My data suggest that harsh winters have little effect on sage-grouse survival. I found no evidence for a difference in survival between yearlings and adults or between the Gunnison Basin and San Miguel population.

## INTRODUCTION

Gunnison Sage-grouse (*Centrocercus minimus*, GUSG) have declined substantially from their historic numbers and range (Zablan et al. 2003, Schroeder et al. 2004) and are a candidate species under the US Endangered Species Act (United States Fish and Wildlife Service 2010). One key factor that contributes to such listing decisions is population growth rate. Depending on the life-history of a species, population growth rates can be influenced by different demographic parameters. For birds with moderate to long life-spans, such as GUSG, adult survival is thought to be influential in determining population growth rates (Gunnison Sage-grouse Rangewide Steering Committee 2005, Desholm 2009). Estimates of survival for GUSG have been limited and population viability analyses have had to rely on the closely related greater sage-grouse (*Centrocercus urophasianus*, GRSG). This situation has created uncertainty in determining the status of GUSG and my goal was to examine overall trends in, and relationships between explanatory variables and survival to better inform management for this species.

GUSG are distributed among seven isolated populations. One population, Gunnison Basin (GB), comprises 85-90% of all GUSG and the other six populations are estimated to range in size from 20 to 170 individuals (Kathy Griffin, Colorado Parks and Wildlife (CPW), pers. comm.). Due to the inherent small sizes of these other populations and the fact they have declined recently, the population dynamics of these small populations may be considerably different from the GB population.

Two previous studies estimated survival rates for GUSG, but neither of them have been longitudinal studies. Survival estimates for GUSG range between 0.45-0.71 for females and 0.27-0.51 for males (Apa 2004, Stiver et al. 2008). Apa (2004) examined survival in all seven of the populations and survival appeared to vary between the populations, however the sample sizes were too small to make definitive comparisons among the populations.

Few correlates with survival have been examined for GUSG. However work on the closely related GRSG has been more extensive with sex, age, and winter severity being common survival correlates. As

with GUSG, females have been found to have higher survival rates than males (Connelly et al. 1994, Schroeder et al. 1999, Zablan et al. 2003). Moynahan et al. (2006) found that females that initiated nests had a higher survival probability during the breeding season than those that did not. Yearling birds have higher survival than adult birds (Zablan et al. 2003, Moynahan et al. 2006). Historically, harsh winters are not thought to affect sage-grouse survival (Connelly et al. 2000). However, several recent studies have found a negative relationship between harsh winters and survival (Zablan et al. 2003, Moynahan et al. 2006, Anthony and Willis 2009).

My objective was to evaluate differences in GUSG survival for two populations (GB and San Miguel (SM) - one of the smaller populations) and whether there were trends in survival across time. I was also interested in testing several hypotheses about what factors are correlated with survival (e.g., sex, age, winter severity). My study will provide needed information on GUSG survival and trends in survival. This information will help guide future studies on population growth of this species of conservation concern.

## **METHODS**

### **Study areas**

I captured and radiomarked GUSG hens in two of seven isolated populations of GUSG: GB and SM. Over 85% of the existing individuals are thought to be in the GB population (Kathy Griffin, CPW, pers. comm.). My study area in the GB population is located in Gunnison and Saguache counties, Colorado, USA excluding the western edge (Figure 3.1). Gunnison Basin is a 2,000km<sup>2</sup> intermontane basin ranging in elevation from 2,300 to 2,900m (Hupp and Braun 1989). Mountainous terrain borders the north, east, and south-east sides of the study area and these border areas contain habitat not commonly used by sage-grouse (Connelly et al. 2000). The western edge of the Gunnison Basin is comprised mostly of land managed by the Bureau of Land Management, the National Park Service and the Ute Mountain Ute Tribe;

these areas were not included in our study area. The study area is sagebrush steppe dominated by sagebrush (*Artemisia spp.*) interspersed with rabbitbrush (*Chrysothamnus spp.*) antelope bitterbrush (*Purshia tridentate*) serviceberry (*Amelanchier spp.*) and mountain snowberry (*Symphoricarpos oreophilus*). Black sagebrush (*Artemisia nova*) is common on xeric ridge tops and south-facing slopes.

The SM population is located in Montrose and San Miguel counties, Colorado, USA. The SM population is comprised of six, interconnected subpopulations over a 400km<sup>2</sup> area. The elevation of this area ranges from 1,900 to 2,800m (Gunnison Sage-grouse Rangewide Steering Committee 2005). The vegetation characteristics vary between the six subpopulations in the SM population. The data for this study were collected from the Dan Noble State Wildlife Area (site of one of the subpopulations of the San Miguel population). The shrubs in this study area are mostly low sagebrush (*Artemisia arbuscula*) and black sagebrush (*Artemisia nova*), with some mountain big sagebrush (*Artemisia tridentate*) along drainages.

### **Capture and monitoring**

Spot-lighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) were used to trap sage-grouse (mid-March through early-May) from 2004-2010. Sage-grouse were fitted with a 17g necklace-style radiotransmitter (Advanced Telemetry Systems, Inc.) and a numbered leg band (National Brand and Tag Company). The transmitter contained a mortality signal that would initiate after four hours of inactivity. The transmitter weight is <2% of the average adult female GUSG's body weight ( $\bar{y} = 1270\text{g}, \pm 90\text{g}$ ) and <1% of the average adult male's ( $\bar{y} = 2110\text{g}, \pm 190\text{g}$ ). Each bird was weighed and plumage characteristics were used to determine age and sex (Beck et al. 1975). Each GUSG was categorized as either an adult ( $\geq 2$  years old) or a yearling (1 year old, first breeding season). Yearling birds that survived to the following March were then classified as adults.

Survival was recorded for radiomarked birds from April 2004 - March 2011. Birds were located using radio telemetry triangulation from April to September. Aerial locations were obtained monthly during the fall and winter. Females were tracked extensively throughout the breeding season. Males were located 1-

2 times a month during the spring and summer. Cause of mortality was assigned to one of three categories: predation (based on field signs of a predator, feathers or partial carcass near collar, or bite marks on the collar itself), power line collision (carcass found under power line), and unknown (whenever field signs were unclear).

### **Statistical analysis**

I analyzed monthly survival data using nest survival models (Dinsmore et al. 2002, Anthony and Willis 2009) in Program MARK (White and Burnham 1999). These models allow for staggered entry, as well as unequal sampling intervals. Birds that go missing or those that slipped their collars were included as alive in the study area until their last encounter, then are censored from the study. Additionally, any birds that were moved from the study area or affected by handling were censored in this manner.

I considered two within-year intervals for survival. First, I considered that survival would vary from month to month throughout the year (I labeled this parameterization “Month”). Second, I assumed that survival would be constant across the non-breeding season (September to February) and vary by month during the rest of the year (this parameterization I called “Season”). I examined the effect of average monthly snow cover on survival. Since including a temporal covariate in the same model as a fully time varying model is inappropriate, I only included snow depth in models without the “Month” effect. The full set of covariates I examined is described in Table 3.1.

I evaluated the relative importance of each model using Akaike Information Criterion with the small sample size correction (AICc, Burnham and Anderson 2002). Following the recommendation of Doherty et al. (Doherty et al. 2012), I ran all combinations of covariates with the two within-year parameterizations and three interactions to obtain a model set. However, I never included “Month” structures with monthly snow depth which results in a total of 272 models. I then evaluated the relative importance of each covariate by calculating the cumulative AICc weight (Burnham and Anderson 2002) for each covariate and considered covariates with a cumulative AICc weight above 0.50 to be important

(Barbieri and Berger 2004). Interactions that had a cumulative AICc weight above 0.50 were considered important and if an interaction was important the main effects were not considered outside of the interaction.

I calculated the annual survival rates from one breeding season to the next by multiplying the monthly survival rates within each year period, the variance for those estimates were calculated using the delta method (Seber 1982). However, we had no birds marked during March 2004 (the month prior to the start of our study). Therefore, I used the average survival rate from the months of March during the rest of the study to substitute for the March 2004 value when calculating annual survival for 2004.

Since managers are interested in trend across years in survival I ran two models in Program MARK that incorporate a trend. In the first year of the study, 2004, birds were not captured in March (the first time period) but in April. For the first trend model I set the survival rate for March in 2004 to the average survival rate calculated from the other months of March from the study. For the second trend model I evaluated the trend only from 2005-2010.

## **RESULTS**

### **Raw data**

From 2004-2010 217 birds were caught in GB, the age and sex distribution of those birds are shown in Table 3.2. I collected mortality data for 135 birds (69 known predation, 2 power line collisions, and 64 unknown mortalities). Nine birds either slipped their collars or the batteries died on the collar before they could be replaced and were right-censored in the analysis. Three birds were censored from the study because they were moved from the study area. The remaining 70 birds were known to be alive when last encountered. From 2007-2010 25 birds were caught in SM. All of the birds from this population were adults (10 females, 15 males, Table 3.2). Eighteen of these birds are known to have died (10 known

predations and 8 unknown mortalities). The other seven birds were known to be alive when last encountered.

### **Model results**

Six models are within 2  $\Delta$ AICc of the top model (typical cutoff for strongly supported models, Burnham and Anderson 2002, Appendix 3.A). Thirty models contain at least 0.01 of the AICc weight, but only two contain more than 0.05 AICc weight. The covariate 'sex' is in all of the top 30 models. Season and the sex by season interactions are in all but two of the top 30 models. The year covariate is in 24 of those top 30 models. Breeding status of females, age, population, and snow depth were in about half of the models. The month effect was not in any of these models.

The AICc cumulative weights for all the variables in the model set are shown in Table 3.3. The cumulative AICc weight for the season by sex interaction is 0.86 (Table 3.3). Since this is above 0.50 (importance cutoff described above) the effects of season and sex should only be considered within the context of the interaction. The month by sex interaction and the sex by age interaction had little cumulative AICc weight (Table 3.3) and the main effects can be from this interaction. Aside from the covariates included in the season by sex interaction there are two covariates with a cumulative AICc weight above 0.50, the year effect (cumulative AICc wt 0.80) and the breeding status of females (cumulative AICc wt 0.53). The remaining main effects were relatively unsupported: age (0.46), snow depth (0.38), population (0.32), and month (0.001).

The sex by season interaction was strongly supported suggesting the within year pattern of survival is different between the sexes. Generally, survival was higher for females than for males. Males have a consistent survival rate except during the month of March when the survival is lower than the rest of the year Figure 3.2. Females have a lower survival from April to August, with May being the lowest survival rate. During the non-breeding season (September to February) the sexes appear to have similar survival rates. The standard errors for the males are consistently wider than those of the females.

Year was also an important covariate according to the cumulative AICc weight (Table 3.3). Overall a decreasing trend in survival rates is apparent (Figure 3.3). To evaluate the trend across years, two trends were fit to the data in Program MARK. The estimated slope of the trend from 2004-2010 was -0.053 (95% CI -0.163, 0.044). When a trend is fit from 2005-2010 the slope is estimated to be -0.007 (95% CI -0.118, 0.104).

The breeding status of a female was marginally important with a cumulative AICc weight of 0.53. The beta estimate (0.601; 95% CI -0.142, 1.343) indicated that females that nested had a slightly higher survival during that period than those that did not nest, but the confidence interval for this parameter overlaps slightly with zero. The effect of the population had a cumulative covariate weight of less than 0.50 and the parameter estimate for this covariate (0.177; 95% CI -0.403, 0.758) was slightly positive suggesting that survival in San Miguel was slightly higher than in Gunnison Basin, but the confidence interval also strongly overlapped zero. Because of the interest in this covariate, I have plotted the annual survival rates for each population (allowing for independent year to year variation) in Figure 3.4. The age of the bird was not a strong covariate based on the cumulative AICc weight (Table 3.3). The beta estimate for this parameter was slightly negative (-0.173) implying adult birds have slightly lower survival than yearlings; however the 95% confidence interval overlapped zero (-0.596, 0.249).

I examined climatological data collected from the NOAA weather stations in Gunnison Basin and San Miguel in order to evaluate the effects of harsh winters on grouse survival. I used average monthly snow depth as a measurement of winter harshness. The average winter snow depth in Gunnison Basin ranged from 8.6 to 31.0 cm, excluding the 2007-2008 winter. In 2007-2008 the average snow depth was 58.9 cm; 3.54 times as deep as any other year in the study in GB (NCDC 2004-2010). The average snow depth in SM ranged from 12.7cm to 36.0cm. The winter with the deepest snow on average in SM was 2009-2010. The covariate for snow depth was not supported, with a cumulative AICc weight lower than 0.50 (Table 3.3). The beta estimate is -0.022, suggesting the deeper the snow the lower the survival. However, the confidence interval overlaps zero (95% CI -0.074, 0.029).

## DISCUSSION

The 2004 survival rates from my study were high (0.89 for females and 0.64 for males, compared to average estimates of 0.57 for females and 0.48 for males (Apa 2004)). This was the first year of the study and the sample size was markedly lower than other years (n=16) additionally there were mostly males in the study (13 of 16). Based on the small sample size and the timing of initial capture the 2004 estimates may not be representative of the species for that year. The survival rates from 2005-2010 are similar to those found in previous research on GUSG (Apa 2004, Stiver et al. 2008). The lower bounds for annual survival are noticeably lower than estimates for GRSG annual survival rates (GUSG: 0.54 for females and 0.30 for males, GRSG: 0.68 for females and 0.46 for males (Schroeder et al. 1999)). This may indicate another distinction between the two species of sage-grouse (Young et al. 2000a).

The trend in survival across time is of particular interest in species of concern like the GUSG. For that reason I evaluated the linear trend across time in my survival data. 2004 was the first year in the study and had one fewer months of estimable survival data than each other year in the study. In addition, the 2004 estimates are unusually high. Outlier values can have a disproportionate effect on trends when they occur at end points of a data series (Ott and Longnecker 2001). Therefore, I examined a linear trend across time both including and omitting the 2004 estimates. The linear trend tended to be slightly negative for both the data with and without 2004 and somewhat steeper when 2004 was included; but the data do not strongly suggest either trend (the 95% confidence intervals for both slope estimates included zero).

On average males had a lower survival probability than females (Figure 3.3), which is consistent with previous research on sage-grouse species (Connelly et al. 1994, Zablan et al. 2003). Males have the lowest survival during the months of March and April (Figure 3.2); this is the lekking season. Males congregate on flat tracts of land, or leks, to display and compete for breeding opportunities. Fighting between males for breeding opportunities had been known to result in mortality for GUSG (Wiechman, unpublished data from a GUSG captive breeding program), which is likely to add to the high mortality

rate of males at this time. Males' prominent displays in large groups, on highly visible tracts of land, coupled with the fact that they return daily to the same location for more than a month in a row probably expose males to substantial predation risk during this time of year. Although cause of mortality was often unable to be determined, predation was the cause in 98% of the cases where it was able to be determined.

In contrast to males, females have the lowest survival during the months of May to August (Figure 3.2). This is the nesting and chick rearing time of the year. Hens are limited by their broods as to where they forage, how fast they travel, and how visible/detectable they are to potential predators. All of these factors may contribute to the higher mortality rates of females during this time of year. Interestingly a previous study on GRSB suggested that survival during the nesting season was higher for females that initiated a nest than for those hens that did not initiate a nest (Moynahan et al. 2006). I examined this same relationship and found a similar pattern. However, this effect was not as influential as compared to that of sex, season, and year (Table 3.3). Perhaps a hen sitting on a nest for 28 days limits her probability of being detected during that time compared to her counterparts that are probably more active. This survival benefit is in contrast to the traditional cost/benefit trade-off of electing to reproduce. The benefit to the hen's individual survival likely does not carry over to the chick rearing season based on the generally lower survival rates of females during this time of year. Another explanation of this finding might be that good individuals are good all-around. Cam et al. (2002) found a strong correlation between survival probability and breeding probability, suggesting that the higher survival for those birds that elect to nest might have more to do with the quality of the individual than a possible correlation with a benefit to nesting.

Although the survival rates vary between the sexes during the reproductively active times of the year, the survival rates of both sexes remains fairly constant during the non-breeding season (Figure 3.2). At this time of year birds congregate in large, mixed-sex flocks. Males are larger and less flighty in general (they are easier to trap than females, pers. obs.), thus they may be easier prey to predators as well. This

may explain why even during the non-breeding season when predation risk is similar males have lower survival than females.

During the non-breeding season predation is not the only threat to survival for sage-grouse; harsh winters have also been suggested as potentially deleterious to sage-grouse survival. Some research on GRSG has suggested that there is a negative effect of harsh winters (Zablan et al. 2003, Moynahan et al. 2006, Anthony and Willis 2009), other research indicates there is no effect of harsh winters unless snow cover reduces access to sagebrush (Connelly et al. 2000). The winter between 2007 and 2008 was particularly extreme in Colorado (snow depths were over three times that of any other year in the study). If there is a negative impact of increased snow depth on grouse survival this should have been detected during this extreme winter. The effect of snow depth was found to be negatively associated with survival; however, my data do not suggest that increased snow cover has a large effect on GUSG survival.

Previous work on GUSG has not examined a difference between yearling and adult survival rates. Two studies on GRSG have suggested that yearlings have higher survival rates than adults (Zablan et al. 2003, Moynahan et al. 2006) while another has not (Wallestad 1975). My results suggest that age is a relatively unimportant factor (cumulative covariate weight of 0.46, estimate near zero). I also examined an age by sex interaction; potentially the effect of age could be more pronounced or different in one sex over the other as was found in Zablan (1993) and Zablan et al. (2003). This interaction was not found to be influential (cumulative covariate weight of 0.20). The difference in survival rates between yearlings and adults may be a factor that is more important in some populations of sage-grouse than others. On the other hand this may indicate another subtle difference between GUSG and GRSG.

Another factor in which I expected to be a strong effect, but was not, was that of population. The two populations of GUSG that I examined are different in population size, population stability, elevation, habitat structure, and weather conditions. This set of different characteristics leads one to believe that the survival rates of adult and yearling GUSG might be different between the two populations. However

there was not a strong population effect on survival (Figure 3.4). Lek counts in this smaller population have shown a decline in recent years (Mike Phillips, pers. comm.). The fact that this decline is not echoed in the survival rates is surprising given that adult survival may be one of the driving factors in population growth for sage-grouse (Saether and Bakke 2000, Gunnison Sage-grouse Rangewide Steering Committee 2005, Moynahan et al. 2006). However, evidence has suggested that there has been almost no juvenile recruitment over the last few years (Chapter 2). Since adult survival is not showing a marked decline in SM this may suggest that falling lek count numbers might be due more to the lack of recruitment than to a change in adult mortality.

Future work on GUSG survival should investigate cause of mortality more explicitly. Identifying the primary predators would help us better understand the cause of variation in sage-grouse survival rates. The largest hindrance in my study was the small sample size in the SM population. Although no substantial difference between the populations was found for adults and yearling survival, the variance around the survival estimates for SM are large and better precision can be gained from a larger sample size in this population. Additionally, work should concentrate on estimating juvenile recruitment in this smaller population to determine if that is where conservation efforts should be focused.

**Table 3.1.** Explanation of covariates and hypothesized effects on Gunnison Sage-grouse survival.

<b>Covariate</b>	<b>Description/Hypothesis</b>
Age	Yearling survival will be higher than adult survival
Sex	Females will have higher survival than males
Age*Sex	The magnitude of the Age difference will differ by sex
Year	Survival will fluctuate between years (e.g., 2008 will be lower due to the severe winter)
Breeding status	Females that nest will have higher survival during the breeding season than those that do not nest
Population	Survival will be lower in San Miguel than in Gunnison Basin
Season	Survival will be relatively consistent during the non-breeding season but fluctuate monthly from March to September
Sex*Season	Survival will be lower during the lekking months for males, and lower for the chick rearing months for females
Snow Depth	Survival will be lower during months with greater snow cover
Month	Survival will fluctuate within year on a monthly scale
Sex*Month	Survival will be lower during the lekking months for males, and lower for the chick rearing months for females

**Table 3.2:** Age and sex distribution of birds monitored per year in the Gunnison Basin and San Miguel populations. Number of mortalities per year is shown in parentheses. Birds were monitored in San Miguel from 2007-2010. There were no yearling birds monitored in San Miguel and therefore no birds that were of unknown sex.

	Gunnison Basin									San Miguel				Total		
	Adult			Yearling			Adult									
	Female	Male	Unknown	Female	Male	Unknown	Female	Male	Female	Male						
<b>2004</b>	2	(1)	11	(1)	0	(0)	1	(0)	2	(0)	0	(0)		16	(2)	
<b>2005</b>	4	(0)	15	(7)	0	(0)	7	(1)	0	(0)	0	(0)		26	(8)	
<b>2006</b>	26	(8)	11	(3)	0	(0)	14	(6)	7	(4)	1	(0)		59	(21)	
<b>2007</b>	36	(12)	12	(5)	0	(0)	16	(8)	0	(0)	2	(0)	4	(2)	8	(4)
<b>2008</b>	43	(19)	4	(3)	2	(1)	10	(4)	1	(0)	0	(0)	4	(0)	7	(4)
<b>2009</b>	57	(14)	3	(2)	1	(1)	7	(2)	1	(0)	3	(1)	6	(1)	4	(2)
<b>2010</b>	58	(24)	7	(3)	2	(1)	17	(4)	0	(0)	0	(0)	6	(0)	4	(3)
<b>Total</b>	<b>226</b>	<b>(78)</b>	<b>63</b>	<b>(24)</b>	<b>5</b>	<b>(3)</b>	<b>72</b>	<b>(25)</b>	<b>11</b>	<b>(4)</b>	<b>6</b>	<b>(1)</b>	<b>20</b>	<b>(3)</b>	<b>23</b>	<b>(13)</b>

**Table 3.3.** Cumulative AICc weights for each covariate used in Gunnison sage-grouse survival models. Bold numbers indicate cumulative weights above 0.50.

Covariate	Cumulative AICc Weight
Sex <sup>a</sup>	<b>0.995</b>
Season <sup>b</sup>	<b>0.888</b>
Season by sex interaction <sup>c</sup>	<b>0.863</b>
Year <sup>d</sup>	<b>0.799</b>
Breeding status of hen <sup>e</sup>	<b>0.534</b>
Age <sup>f</sup>	0.459
Snow depth <sup>g</sup>	0.373
Population <sup>h</sup>	0.319
Age by sex interaction <sup>i</sup>	0.197
Month <sup>j</sup>	0.001
Month by sex interaction <sup>k</sup>	0.000

<sup>a</sup> ‘Sex’ denotes a 0 for females and 1 for males

<sup>b</sup> ‘Season’ allows for monthly variability in survival from Mar-Sept and constant survival from Oct-Feb.

<sup>c</sup> ‘Season by sex interaction’ allows for different patterns of season survival by sex

<sup>d</sup> ‘Year’ allows for survival to vary by year

<sup>e</sup> ‘Breeding status of hen’ denotes a 1 if a hen is nesting in that month and a 0 otherwise

<sup>f</sup> ‘Age’ denotes a 0 for yearlings and a 1 for adults

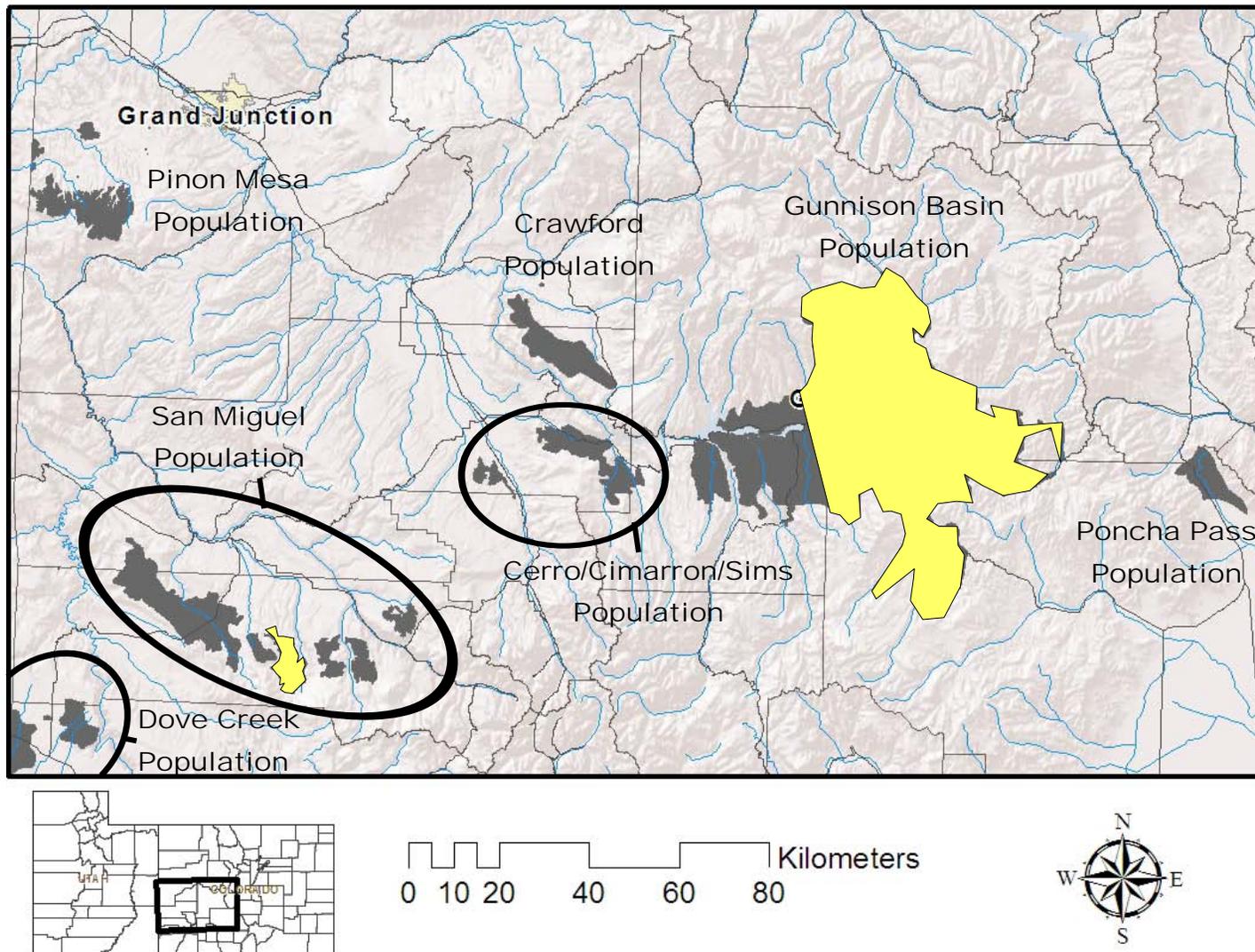
<sup>g</sup> ‘Snow depth’ is a linear relationship between average monthly snow depth and survival

<sup>h</sup> ‘Population’ denotes a 0 for the Gunnison Basin population and a 1 for the San Miguel population

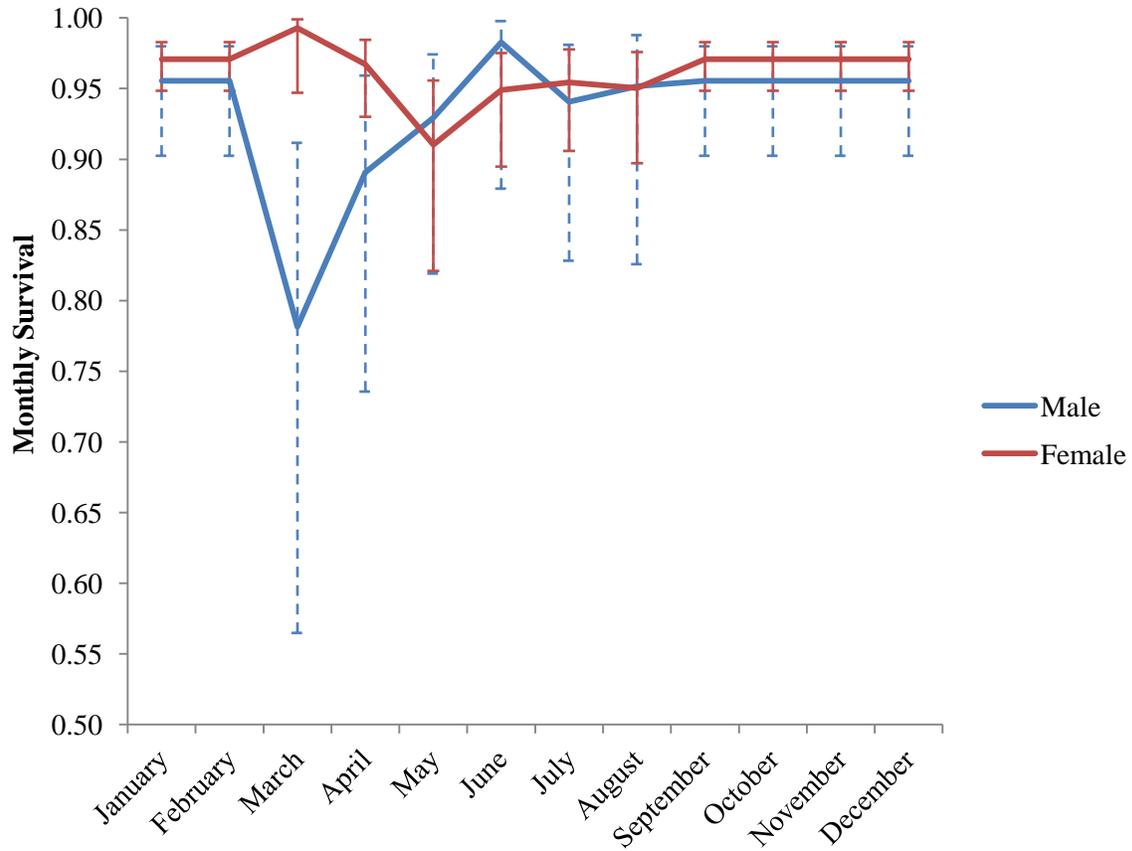
<sup>i</sup> ‘Age by sex interaction’ allows for a males and females to have a different effect of age

<sup>j</sup> ‘Month’ allows for survival to vary monthly

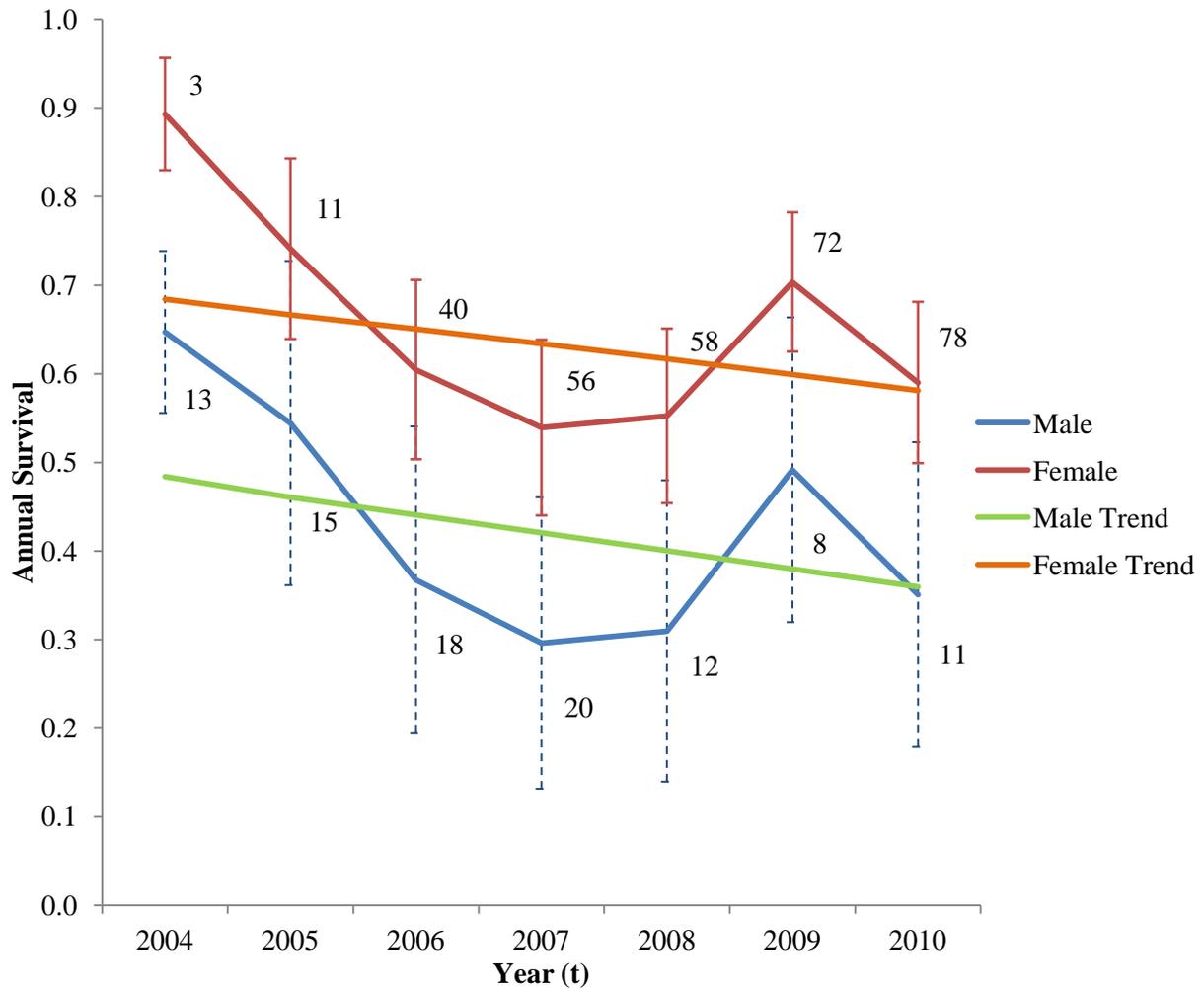
<sup>k</sup> ‘Month by sex interaction’ allows for monthly patterns of survival to vary by sex



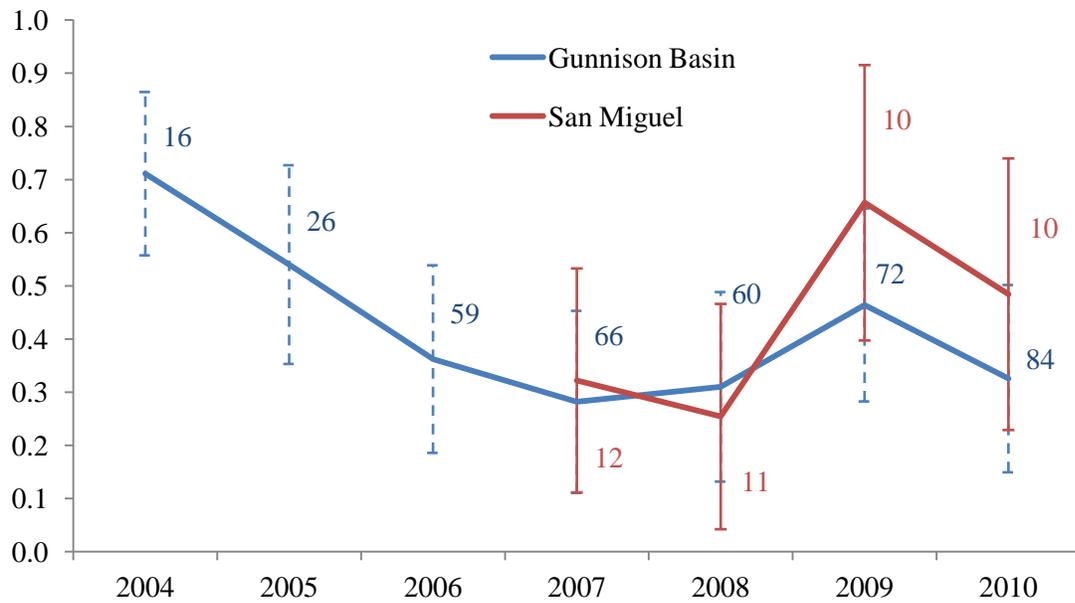
**Figure 3.1.** Gunnison Sage-grouse distribution map. The seven populations are labeled. The two areas highlighted in yellow are the study areas.



**Figure 3.2:** Monthly survival estimates and standard errors by sex for Gunnison Sage-grouse from a model with the sex by season interaction.



**Figure 3.3.** Annual adult and yearling survival estimates (March 1 of year t to Feb 28 of year t+1) and standard errors by sex for Gunnison Sage-grouse. Sample sizes are shown next to the data points. The trend lines are shown by sex.



**Figure 3.4.** Annual adult and yearling survival estimates and standard errors for Gunnison Sage-grouse by population for a model that contains a year by population interaction. Sample sizes are shown next to data points.

## LITERATURE CITED:

- Anthony, R. G. and M. J. Willis. 2009. Survival Rates of Female Greater Sage-Grouse in Autumn and Winter in Southeastern Oregon. *Journal of Wildlife Management* **73**:538-545.
- Apa, A. D. 2004. Habitat use, movements, and survival of Gunnison Sage-Grouse in southwestern Colorado. Unpublished Report. Colorado Division of Wildlife, Colorado, USA.
- Barbieri, M. M. and J. O. Berger. 2004. Optimal predictive model selection. *Annals of Statistics* **32**:870-897.
- Beck, T. D. I., R. B. Gill, and C. E. Braun. 1975. Sex and age determination of sage grouse from wing characteristics. *in* C. D. o. Wildlife, editor. *Game Information Leaflet*, Fort Collins, CO, USA.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multimodel inference- a practice information-theoretic approach*. 2nd edition. Springer, New York.
- Cam, E., W. A. Link, E. G. Cooch, J. Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: Seeing the trees despite the forest. *American Naturalist* **159**:96-105.
- Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage-grouse ecology final report. Idaho Department of Fish and Game.
- 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.
- Desholm, M. 2009. Avian sensitivity to mortality: Prioritising migratory bird species for assessment at proposed wind farms. *Journal of Environmental Management* **90**:2672-2679.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**:3476-3488.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* **152**:317-323.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for Trapping Sage Grouse in Colorado. *Wildlife Society Bulletin* **10**:224-231.

- Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-Grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Hupp, J. W. and C. E. Braun. 1989. Topographic Distribution of Sage Grouse Foraging in Winter. *Journal of Wildlife Management* **53**:823-829.
- Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female Greater Sage-Grouse in Montana. *Ecological Applications* **16**:1529-1538.
- NCDC. 2004-2010. Climatological Data Annual Summary Colorado. National Oceanic and Atmospheric Administration (NOAA).
- Ott, L. and M. Longnecker. 2001. An introduction to statistical methods and data analysis. Duxbury.
- Saether, B. E. and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642-653.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-Grouse in North America. *Condor* **106**:363-376.
- Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Greater Sage-Grouse (*Centrocercus urophasianus*). The birds of North America. The Birds of Norther America Online, Ithiaca, NY: Cornell Lab of Ornithology.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.
- Stiver, J. R., A. D. Apa, T. E. Remington, and R. M. Gibson. 2008. Polygyny and female breeding failure reduce effective population size in the lekking Gunnison sage-grouse. *Biological Conservation* **141**:472-481.
- United States Fish and Wildlife Service, U. 2010. Determination of Gunnison Sage-grouse as a Threatened or Endangered Species. *in* D. o. t. Interior, editor. Federal Register

- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An Improved Spotlighting Technique for Capturing Sage Grouse. *Wildlife Society Bulletin* **20**:425-426.
- Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Game Management Division, Montana Dept. of Fish and Game, Helena, MT.
- White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Fort Collins, CO.
- Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000. A new species of sage-grouse (Phasianidae : *Centrocercus*) from southwestern Colorado. *Wilson Bulletin* **112**:445-453.
- Zablan, M. A. 1993. Evaluation of sage grouse banding program in North Park, Colorado. Colorado State University, Fort Collins, CO.
- 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.

**APPENDIX 3.A.** The 30 most supported models from a set of 272 candidate models describing the survival of adult and yearling Gunnison Sage-grouse. Only models with an AICc wt  $\geq 0.01$  are shown.

<b>Model</b>	<b>AICc</b>	<b><math>\Delta</math> AICc</b>	<b>AICc Weights</b>	<b>Likelihood</b>	<b>K*</b>	<b>Deviance</b>
Season <sup>a</sup> +Sex <sup>b</sup> +Sex*Season <sup>c</sup> +Year <sup>d</sup> +BreedingStatus <sup>e</sup>	1078.68	0.000	0.092	1.000	21	1036.38
Season+Sex+Sex*Season+Year	1079.22	0.541	0.070	0.763	20	1038.95
Sex+Season+Sex*Season+Snow <sup>e</sup> +Year+BreedingStatus	1080.00	1.320	0.047	0.517	22	1035.67
Season+Sex+Sex*Season+Year+Age <sup>f</sup> +BreedingStatus	1080.05	1.365	0.046	0.506	22	1035.72
Season+Sex+Sex*Season+Year+Population+BreedingStatus	1080.34	1.658	0.040	0.437	22	1036.01
Sex+Season+Sex*Season+Snow+Year	1080.54	1.862	0.036	0.394	21	1038.24
Season+Sex+Age+Age*Sex+Year+BreedingStatus+Sex*Season	1080.70	2.014	0.033	0.365	23	1034.34
Season+Sex+Sex*Season+Year+Age	1080.75	2.073	0.033	0.355	21	1038.45
Season+Sex+Sex*Season+Year+Population	1080.80	2.119	0.032	0.347	21	1038.50
Season+Sex+Sex*Season+BreedingStatus	1081.16	2.477	0.027	0.290	15	1051.00
Season+Sex+Age+Age*Sex+Year+Sex*Season	1081.29	2.614	0.025	0.271	22	1036.97
Sex+Season+Sex*Season+Snow+Year+Age+BreedingStatus	1081.40	2.717	0.024	0.257	23	1035.04
Sex+Season+Sex*Season+Snow+Year+Population+BreedingStatus	1081.51	2.829	0.022	0.243	23	1035.15
Season+Sex+Sex*Season+Year+Age+Population+BreedingStatus	1081.52	2.836	0.022	0.242	23	1035.16
Season+Sex+Sex*Season	1081.68	3.001	0.020	0.223	14	1053.55
Sex+Season+Sex*Season+Snow+BreedingStatus	1081.72	3.036	0.020	0.219	16	1049.54
Season+Sex+Sex*Season+Year+Age+Population+BreedingStatus+Age*Sex	1081.96	3.276	0.018	0.194	24	1033.57
Sex+Season+Sex*Season+Snow+Year+Population	1081.96	3.279	0.018	0.194	22	1037.63
Sex+Season+Sex*Season+Snow+Year+Age	1082.10	3.423	0.017	0.181	22	1037.78
Sex+Age+Age*Sex+Season+Sex*Season+Snow+Year+BreedingStatus	1082.14	3.458	0.016	0.178	24	1033.75
Season+Sex+Sex*Season+Year+Age+Population	1082.16	3.475	0.016	0.176	22	1037.83
Sex+Season+Sex*Season+Snow	1082.26	3.578	0.015	0.167	15	1052.10
Season+Sex+Age+Age*Sex+Year+Population+Sex*Season	1082.47	3.789	0.014	0.150	23	1036.11
Year+Sex	1082.57	3.889	0.013	0.143	8	1066.52
Sex+Season+Sex*Season+Snow+Year+Age+Population+BreedingStatus	1082.69	4.011	0.012	0.135	24	1034.30
Season+Sex+Sex*Season+Age+BreedingStatus	1082.74	4.056	0.012	0.132	16	1050.56
Sex+Age+Age*Sex+Season+Sex*Season+Snow+Year	1082.74	4.058	0.012	0.131	23	1036.38

Snow+Year+Sex	1082.76	4.074	0.012	0.131	9	1064.70
Season+Sex+Sex*Season+Population+BreedingStatus	1083.17	4.492	0.010	0.106	16	1051.00
Sex+Age+Age*Sex+Season+Sex*Season+Snow+Year+Population+BreedingStatus	1083.21	4.525	0.010	0.104	25	1032.78

\* K is the number of parameters in the model

<sup>a</sup> ‘Season’ denotes the parameterization that allows for monthly variation in survival during the reproductive season (Mar-Sept) and a constant survival during the non-reproductive season (k=7)

<sup>b</sup> ‘Season\*Sex’ denotes the interaction of the ‘season’ parameterization with sex (k=7)

<sup>c</sup> ‘Year’ denotes a separate parameter for each year in the study allowing for annual variability (k=6)

<sup>d</sup> ‘BreedingStatus’ denotes a variable that is 1 if the hen is nesting during a particular month and 0 otherwise (k=1)

<sup>e</sup> ‘Snow’ is the linear parameter relating average monthly snow depth to survival (k=1)

<sup>f</sup> ‘Age’ represents yearlings when it is a 0 and adults when it is a 1 (k=1)

## **CHAPTER 4**

### **EVALUATING VIABILITY AND TRANSLOCATION STRATEGIES OF GUNNISON SAGE-GROUSE USING A POPULATION PROJECTION MODEL**

Gunnison Sage-grouse (*Centrocercus minimus*) are a candidate species under the U.S. Endangered Species Act. Species-specific vital rate information and analyses are important for implementing effective conservation and management actions and have been unavailable until now. I created a female-based, Leslie-type, post-birth pulse population model with three age classes (chicks, yearlings, and adults) to assess the viability of, and assess sensitivity of growth rates to vital rates in, two populations of Gunnison Sage-grouse; Gunnison Basin which comprises ~90% of the individuals in the species, and San Miguel which comprises ~3% of the species. I also evaluated translocation strategies from the larger Gunnison Basin population to the smaller San Miguel population. I found adult survival to be the most influential vital rate (based on sensitivity metrics) when the population is declining. Juvenile survival and nest success have the largest sensitivity proportional to their variation suggesting these rates might be ideal targets for management actions. Translocation strategies that move birds every five, or fewer, years result in an increase in population persistence. Moving more birds (e.g., > 400 over the course of 30 years) improves the expected population size, but does not improve the persistence probability as much as frequent translocation (e.g., moving birds every year or every other year).

## **INTRODUCTION**

Life-history theory and population modeling are useful methods for evaluating conservation and management targets for wildlife species (Wisdom et al. 2000) and vital rate analysis is important for understanding population dynamics (Pfister 1998). Conservation efforts are more often successful when they are focused on vital rates that are most influential on population growth (Wisdom et al. 2000, Morris

and Doak 2002, Reed et al. 2009) and effective management actions are particularly necessary for species that are rare or declining.

Gunnison Sage-grouse (GUSG, *Centrocercus minimus*) have declined substantially from their historic range (Schroeder et al. 2004) and are a candidate species under the US Endangered Species Act (ESA, United States Fish and Wildlife Service 2010). The status of GUSG highlights a need for effective management efforts. A paucity of species-specific information exists for GUSG and previous population modeling has had to rely on demographic information from the related Greater Sage-grouse (GRSG, *Centrocercus urophasianus*; Gunnison Sage-grouse Rangewide Steering Committee 2005). Concerns have been raised over using surrogate species information to make inference about species of concern (Caro et al. 2005). Therefore, a direct assessment of the population dynamics of GUSG is needed.

In addition to issues with the use of surrogate species, populations within the same species have required different conservation efforts due to variation in population dynamics among different populations (Johnson et al. 2010). GUSG are distributed into seven isolated populations. One population, Gunnison Basin (GB), comprises 85-90% of all GUSG and the other six populations are estimated to range in size from 20 to 170 individuals (Kathy Griffin, Colorado Parks and Wildlife [CPW], pers. comm.). Due to the inherent small sizes of these other populations and the fact they have been declining in recent years, the population dynamics of these small populations may be considerably different from the GB population.

Sage-grouse species are longer lived and have lower reproductive success than other upland game bird species (Larson et al. 2001, Schroeder and Baydack 2001, Schroeder et al. 2004). Vital rate analyses conducted on other galliforms has shown that juvenile recruitment and nesting success are the demographic rates that often drive upland game species population growth (Wisdom and Mills 1997, Peterson et al. 1998). However, GRSG sensitivity analyses suggest that they are more on the “survivor species” end of the spectrum for galliforms with adult survival and chick survival being the most

influential vital rates (Taylor et al. 2012). Identifying the important vital rates for GUSG is important for directing management of this species, including translocation.

Translocation is one of the primary management methods used for conservation of threatened wildlife species (Fischer and Lindenmayer 2000) and has been used for managing GUSG over the past decade, specifically the movement of individuals from the one large wild population (GB) to the smaller wild populations (Kathy Griffin, CPW, pers. comm.). The use of population projection models lends itself well to evaluating different translocation strategies. There are several factors thought to be related with the success of translocation: the number of individuals moved (Griffith et al. 1989, Wolf et al. 1996, Fischer and Lindenmayer 2000), the frequency of movement (Griffith et al. 1989, Stacey and Taper 1992, Lubow 1996), and the quality of habitat at the destination population (Griffith et al. 1989, Rout et al. 2007). In this study I focus on evaluating the influence of the number of females moved (females are the limiting factor in the population) and the frequency of movement.

The objectives of my study were to 1) develop a population matrix model for GUSG, 2) examine population projections under environmental and demographic stochasticity for two populations of GUSG, the large GB population and one of the small populations (San Miguel, SM), 3) evaluate the relative importance of vital rates under stochasticity, and 4) predict the effects of different translocation strategies on both the source and destination populations. My study provides a much needed species-specific population model for GUSG as well as evaluation that will help guide future conservation and management actions.

## **METHODS**

### **Study areas**

GUSG demographic rates were estimated for two of seven isolated populations: GB and SM (see chapters 1-3). Over 85% of the existing individuals are thought to be in the GB population in Gunnison and

Saguache County, Colorado, USA (Kathy Griffin, CPW, pers. comm., Figure 4.1). Gunnison Basin is a 2,000km<sup>2</sup> intermontane basin ranging in elevation from 2,300 to 2,900m (Hupp and Braun 1989, Gunnison Sage-grouse Rangewide Steering Committee 2005). The SM population is located in Montrose and San Miguel counties, Colorado, USA. The SM population is comprised of six, interconnected subpopulations over a 400km<sup>2</sup> area. The elevation of this area ranges from 1,900 to 2,800m (Gunnison Sage-grouse Rangewide Steering Committee 2005).

### **Matrix model**

I constructed a female-based, post-birth pulse, Leslie-type matrix model with three age classes: chicks, yearling, and adults (Figure 4.2A, Caswell 2001). The model is a discrete-time interval model with the time steps between each transition equaling one year. The transitions and corresponding matrix are shown in Figure 4.2B and the lower-level parameter components are detailed in Table 4.1. Matrix elements are calculated from age-specific vital rates means and process variance evaluated from six years of field data 2005-2010 (Chapters 1-3, Table 4.2). These arithmetic means were calculated from the six years of data and the process variances (Table 4.2) were calculated using the naïve estimator (Link and Nichols 1994):

$$\text{Process Variance} = \text{Total Variance} \left( \text{var}(\hat{\theta}) \right) - \text{Sampling Variance} \left( \overline{\text{var}(\hat{\theta})} \right).$$

I incorporated renesting attempts into my estimate of hen success (probability of a hen having a successful nest). Hen success was roughly 10% higher than individual nesting success for adult females; I had no records of yearlings renesting. Therefore, I increased the nest success rates for adult females by 10%.

The results from Chapters 1-3 suggest the only difference between the two populations examined (GB and SM) is in chick survival, with chick survival being nearly zero (0.03) in SM. Differences in other vital rates between the populations were not supported. The SM chick survival estimate is based on a sample size of only eight birds, and may not be representative of the population. The lack of any observed

survival of chicks in SM is the worst case scenario and would result in negative population growth. I focus on using estimates of chick survival from GB for my general matrix model and presenting those results. Results for the zero chick survival scenario can be found in Appendix 4.A.

Below I detail how I addressed environmental stochasticity (two methods), demographic stochasticity, data uncertainty, sensitivity analyses, and translocation methods.

### **Environmental stochasticity**

I used two methods to add environmental stochasticity to model projections. The first method of adding environmental stochasticity is to randomly select one complete set of demographic rates from the six available years of data (Table 4.2). These data represent actual realizations of annual variability. In order to randomly select a population matrix, I generated a random number from a uniform distribution between 0 and 1. I created six equal partitions from 0 to 1, and then I selected the corresponding matrix.

The second method of adding environmental stochasticity is based on simulating data (i.e., 10,000 sets of vital rates) from a distribution of possible values. I used the second method because it allows for sensitivity to be evaluated in situations outside of just the six years observed. I simulated vital rates both with and without correlations. Each of the vital rates described in Table 4.2 are bounded between zero and one except for the half clutch size. A beta distribution is well suited for simulating vital rate data because it is bounded between zero and one and is versatile in terms of the distribution shape (Morris and Doak 2002). I used a stretched beta distribution (Morris and Doak 2002) to simulate clutch size. The stretched beta distribution allows for the use of an upper and lower bound that are not bounded between zero and one but are bounded between the minimum and maximum values possible for the parameter of interest. I created correlations in the data by simulating data from a multivariate normal distribution. Using a logit transformation, I transformed data to be on the probability scale.

I calculated parameters for the beta distribution using the mean and process variance from the 2005-2010 data (Table 4.2, calculated from Chapters 1-3) and evaluated the minimum, maximum, mean, and

standard error of clutch size for the stretched beta distribution from six years of data. I calculated the covariance matrix (Table 4.3) using the six years of data, and this matrix was used in the multivariate normal distribution.

### **Demographic stochasticity**

I incorporated demographic stochasticity separately from environmental stochasticity. Using the mean vital rates across years I added demographic stochasticity by having each individual in the population either live or die, initiate a nest or not, and have a nest succeed or not, by randomly generating a number (from the uniform distribution between zero to one) and comparing it to the probability of each event (i.e., the vital rate, calculated from Chapters 1-3). I examined the relative range of population sizes at 30 years compared to the mean population size at 30 years to examine the effect of demographic stochasticity on the two populations (GB and SM).

### **Data uncertainty**

Because I only had a small segment of a time series (6 years), I also examined the possible effects of adding one year to the data series to better understand how sensitive my projection results were to my estimates in Chapters 1-3. I examined the effects of adding a good year (increasing growth rate), a neutral year (~constant growth rate), and a bad year (decreasing growth rate). I selected the additional year from the simulated vital rates. I used the vital rates that corresponded to the highest growth rates for the good year, the lowest growth rate for the bad year, and the growth rate that was closest to 1 (i.e., 0.99998) for the neutral year.

### **Sensitivity analyses**

In order to ensure reliable inference I conducted sensitivity analyses using the life-stage simulation analysis (LSA) framework (Wisdom et al. 2000) based on 10,000 simulated matrices. To evaluate how influential each vital rate is on the population growth rate ( $\lambda$ ) I used perturbation analysis to calculate the sensitivity, elasticity, and variance-stabilized sensitivity (VSS, Link and Doherty 2002) for each

simulated rate. Sensitivities represent an absolute change in  $\lambda$  based on an absolute change in a vital rate. The comparisons of sensitivities is complicated since they do not account for differences in scale (Link and Doherty 2002). Elasticities are the proportional change in  $\lambda$  based on a proportional change in a vital rate, calculated using a log-log transformation and is a commonly used measure to evaluate relative importance of vital rates in wildlife populations (Benton and Grant 1999). The VSS characterizes the scaled sensitivity based on a log transformation on  $\lambda$  and an arcsine-transformation on the vital rate. Some research suggests that VSS is a more appropriate method for examining the relative importance of vital rates that are bounded between zero and one (Link and Doherty 2002). Since the best method for comparing vital rates is debatable, I examined all three of the methods described above. To determine if a correlation between vital rate sensitivity and growth rate exists, I plotted the relationship between vital rate VSS and  $\lambda$  for each of the 10,000 simulations.

Some studies demonstrate that vital rates that are high in sensitivity metrics are not necessarily the most variable and suggest that the potential variability is important to account for in sensitivity analyses (Caswell 1989, 2010). I examined how the variability in each vital rate influences the variation in  $\lambda$  using a life-table response experiment (LTRE) analysis (Caswell 1989, 1996). I only focused on the vital rates that are bounded between zero and one as VSS is not calculated for other rates (i.e., clutch size).

### **Transient sensitivity**

The methods I have used here to explore the relative sensitivities of each vital rate are based on the effects of perturbation on the population growth rate calculated from the dominant eigenvalue of the Leslie matrix. Such eigenvalue sensitivities are calculations based on a stable-age distribution (Caswell 2001). Some researchers have suggested that sensitivities that are based on this stable-state are inappropriate for use with respect to management actions because the time scale that management would be effective is often considerably shorter and the dynamics of the population before it reaches its stable-state might be quite different (Koons et al. 2005, Buhnerkempe et al. 2011).

I used methods developed by Caswell (2007) to examine the sensitivity of vital rates at shorter time scales that might be more important for management actions. I evaluated the transient sensitivity of vital rates simulated with correlation at 1 and 5 year time frames. I compared these results to the sensitivity analyses performed using stable-state assumptions (described above).

### **Translocation methods**

I examined the effects of moving adult and yearling females from the large Gunnison Basin (GB) population to the smaller San Miguel (SM) population. The Colorado Division of Parks and Wildlife (CPW) have translocated 63 birds over the past 10 years from Gunnison Basin to the smaller populations. The fates of the translocated birds are either known alive, known dead, or unknown. Many of the unknown fates are of birds that did not remain in the destination population and therefore are failed translocations. I used raw estimates of apparent survival (number of birds known alive and in the population / total number of birds moved) at six months to account for a decreased survival initially after translocation. There are no estimates of reproductive success of translocated GUSG. Results from translocation studies on GRSG suggest that hens initiate nests and have similar nest success rates to resident birds (Baxter et al. 2009). I compared the results of no reduction, a 10% reduction, and a 50% reduction in hen success on the outcome of translocation strategies. To be conservative I used a 10% decrease in hen success for translocated birds for the population projections.

I simulated population projections for both GB and SM for 100 years with and without translocation. I used the 2010 estimates (GB=3659, SM=123, CPW unpublished data) for the initial population sizes assumed a ratio of 1.6 females/males (Stinson et al. 2004, Gunnison Sage-grouse Rangewide Steering Committee 2005). I used three age classes (chicks, yearlings, and adults) in my population model, but the above population estimates do not include chicks. Rather than starting my simulations with zero chicks, I estimated the number of chicks in the population based on the number that would be produced from the given number of yearling and adult females.

I was interested in evaluating two components of translocation that are in control of managers: the frequency of translocation and the number of birds moved. To evaluate the effects of translocation frequency, I fixed the number of birds moved and compared different frequencies (i.e., every frequency that is equally divisible into 30: every 1, 2, 3, 5, 6, 10, 15, and 30 years). I also examined the effect of moving different numbers of birds by fixing the translocation frequency and examined the effects of moving a total of 50 to 900 birds. I simulated each translocation option 1000 times.

In order to evaluate the effects of translocation on the source and destination populations I calculated several metrics. Since extinction probability is of particular interest to managers, I examined both the average extinction time and minimum extinction time for each translocation option. I also estimated the average population size at 30 years. I chose 30 years because it is long enough to be interesting to managers but not so long that considerable variation in the population projections would result.

The estimate of chick survival in the SM population is near zero. Introducing birds into a population that has no recruitment will eventually consist of only translocated birds; this is not desirable. Although the estimates of chick survival from GB are considerably higher than SM, they provide us with the ability to examine the effects of translocation in population that has some recruitment. I note that projections for the SM population are worse than those predicted from the simulation analysis.

## **RESULTS**

I created and simulated six deterministic population matrices (one for each year) for the GB and SM populations based on the 2005-2010 data (Table 4.2). The deterministic projections for GB show two years with increasing growth rates and four years with decreasing growth rates (Figure 4.3). The sole difference between GB and SM is the disparity in chick survival (Table 4.2). This divergence has a dramatic effect on the deterministic population projections (Appendix 4.A). For the four years where data were collected in both GB and SM (2007-2010) the  $\lambda$  values ranged from 0.65-0.91 in GB and 0.52-0.68

in SM. Using the method that randomly selects each of the six years of data to introduce environmental stochasticity, I plotted the 30-year projections from 1,000 simulations (Figure 4.4A) and the minimum extinction time is 31 years. The effect of adding one more year vary depending on if the year has an increasing growth rate (minimum extinction time 41 years, Figure 4.4B), constant growth rate (minimum extinction time 29 years, Figure 4.4C), or a decreasing growth rate (minimum extinction time 20 years, Figure 4.4D).

Demographic stochasticity has a proportionately larger effect on the SM population than the GB population with the ratio of the range over the mean (similar to a CV) equal to 0.12 in SM and 0.03 in GB (Figure 4.5). Additionally, the extinction risk (i.e., proportion of simulations that went extinct) was substantially larger for SM than for GB (0.53 for SM, 0 for GB).

I also simulated 10,000 sets of vital rates from estimates of means and process variances both with and without correlations (Tables 4.2 & 4.3). I compared the distribution of vital rates with and without correlation (Figure 4.6 A & B). The average clutch size did not vary across years in my study and thus simulating clutch size with correlation was the same as simulating clutch size without correlation (Appendix 4.B). The ranges of each vital rate are generally narrower when correlations are incorporated, suggesting that vital rates do not vary as much with correlation than without correlation. The range of corresponding growth rates from vital rates simulated with correlation is also narrower than those simulated without correlation (Appendix 4.C).

### **Sensitivity analysis**

The sensitivity analyses were conducted on the 10,000 simulations from both correlated and non-correlated data. The sensitivities, elasticities, and variance-stabilized sensitivities (VSS) all show similar patterns both with and without correlations. As a representative I show the VSS for data simulated with correlations (Figure 4.7; the other sensitivity metrics for data simulated with and without correlation are shown in Appendix 4.D). Adult survival is most influential on population growth (demonstrated by the

fact it is consistently the highest vital rate in VSS; Figure 4.7). Juvenile and chick survival are also very influential vital rates although typically less influential than adult survival. Adult nest success is consistently ranked fourth in importance. All vital rates associated with yearlings (yearling nest success, nest initiation, clutch size and survival) are consistently low in importance compared to all other vital rates (Figure 4.7). For comparison I examined the VSS based on the demographic rates from the SM population (Appendix 4.E). Adult survival is the most important vital rate, followed by chick survival, all other vital rates were less important.

To examine the relationship between variation in vital rate VSS and growth rate, for each simulation, I plotted the VSS by the corresponding growth rate ( $\lambda$ , Figure 4.8, based on data without correlation in Appendix 4.F). The relationship between vital rate VSS and lambda shows that adult survival is the most influential when the population is rapidly declining ( $\lambda < 0.84$ ). When the population is increasing or declining slowly ( $\lambda > 0.84$ ), juvenile survival is the most influential factor affecting population growth.

The transient sensitivity analyses for 1 and 5 year time frames showed a similar pattern to the stable-state analyses except for two key differences. Adult nest success and yearling survival were more important in the 1 and 5 year time frames than in the stable-state analysis (Appendix 4.G). Adult nest success was second in importance behind adult survival, and yearling survival was similarly influential to chick survival (Appendix 4.G). Juvenile survival was still relatively influential for both time frames.

Life-table Response Experiment (LTRE) simulations evaluate both the level of variability in each vital rate and how influential that vital rate is on the population growth rate. The results of my LTRE for GUSG suggest that juvenile survival is both influential to population growth and is highly variable (Figure 4.9). Juvenile survival was one of the top two parameters to which growth rate was most sensitive (Figure 4.7). However, the adult survival typically outranked juvenile survival in sensitivity analyses but is much less variable based on the LTRE, suggesting that adult survival does not fluctuate naturally as much as juvenile survival. Adult nest success was ranked the second highest in terms of

LTRE. Juvenile survival and adult nest success are the two vital rates that are likely to experience the largest year to year variation and also vary enough to be particularly influential.

## **Translocation results**

### *Destination population results*

All of the translocation methods examined showed an increase in average population size at 30 years, the mean extinction time, and the minimum extinction time for the destination population, SM (Figure 4.10). I examined the effects of translocating either all adults or all yearlings. The results shown in Figure 4.10 are from translocating only adult birds. The general patterns of the results were the same when only yearling birds were moved. However, moving yearling birds resulted in an increase (shifting of the planes in the 3D-plots) of 51% in the resulting population size, an 8% increase in mean extinction time, and an 11% increase in minimum extinction time based on the average difference across all options.

Moving birds more frequently had a slightly stronger effect than moving more total birds on the resulting population size (Figure 4.10). For example, moving 400 birds all at once does not have as good of an effect as moving just 50 birds at least every three years. Any translocation strategy had an increase in both mean and minimum extinction time by about 10 years. Similar to the results on the population size, more frequently translocating birds had a larger effect on the expected extinction time than the total number of birds moved (Figure 4.10). Moving 900 birds all at once had a similar effect on mean extinction time as moving 100 birds at least every six years. Moving birds every one, two, or three years improved the minimum extinction time by 20 years.

For the above results I used an estimated reduction in hen success of 10% for translocated birds. I evaluated the sensitivity of translocation results to changes in this reduction of hen success. The pattern with respect to number of birds moved and frequency of movement is the same when hen success is changed, the only effect is the magnitude of the results. If there is no reduction in hen success for

translocated birds the results would be increased by 3%. If there is as much as a 50% reduction in hen success for translocated birds the results would decrease by 13%.

*Source population results:*

Removing birds with any translocation strategy from GB had a negative effect on the resulting population size and the mean and minimum extinction time (Figure 4.10). The pattern was similar when yearlings were translocated (vs adults). When yearlings are removed an increase (positive shift in the planes for the 3D-plots in Figure 4.10) of 3% in resulting population size, 2% in mean extinction time, and 11% in minimum extinction time will occur.

In terms of extinction, removing birds all at once from GB had less of an effect than removing birds more frequently (Figure 4.10). Removing birds more frequently than every ten years substantially reduced the mean extinction time for the source population (at least a ten year reduction in extinction time). The minimum extinction time was also more sensitive to frequent translocations, removing birds every 15 years reduced the minimum extinction by 7 years as compared to removing birds only once.

## **DISCUSSION**

The U.S. Fish and Wildlife Service's classification of GUSG as warranted for listing under the ESA implies that the species is at risk of becoming extinct, and the deterministic population projections from the six years of data support this opinion. The growth rates experienced by GUSG during my study indicate declines occurred and that if these rates are indicative of the future, the GUSG will likely continue to decline (Figures 3 & 4A). Population indices of GUSG (lek counts, Walsh et al. 2004) during the same period (2005-2010) also show a declining trend (CPW unpublished data). However, the negative trends from my modeling, as well as the lek counts, suggest this may be a result of examining only a short segment of time (Brockwell and Davis 2002). For instance, lek count data are available

further back in time and although the current trend in the population indices suggests a decline over the past six years, previous index data suggest that the current index level is higher now than it was any time previous to 2005 (Chapter 5).

If my study had been conducted just a few years earlier (or later) I might have found a different trend across time. I examined the effects of adding one more year to the study where the year had and increasing (Figure 4.4B), constant (Figure 4.4C), and declining (Figure 4.4D) growth rate. If the next year the time series was a good year (the best year from my simulated data with a lambda of 1.27) the population projections change from obviously declining to widely variable. However, the addition of one year that is constant or declining results in population projections that are similarly negative as the six years observed. If the observed data are representative of the future, then this is evidence that intervention is needed to preserve this species. Alternatively, the probability that the next 30 years will be without a few years better than I observed, based on population indices may be viewed as unlikely.

Environmental stochasticity for the projections was based on selecting each of the six population matrices by chance. This method for adding environmental stochasticity reflects actual realizations in annual variability and inherent correlations in vital rates (Morris and Doak 2002). However, this method limits the values that each vital rate can take to values that have been observed in the past. The alternate method I used for adding environmental stochasticity is based on vital rate generation from a distribution (the beta distribution). This method allows for vital rates to vary assuming the vital rates observed are random realizations from a distribution of possible values. I simulated data both with and without correlation. Data simulated with correlation suggest a much tighter range of most vital rates (Figure 4.6) and thus of population growth rates than data simulated without correlation (Appendix 4.C). The maximum growth rate simulated from data with correlations is 1.27, whereas the maximum growth rate generated from data simulated without correlations is 1.65. Therefore if the correlation structure is as I have observed, and these data are representative of the future, then the population will most likely decline.

Population declines suggest a need for conservation and management actions to be employed. The best strategies for conservation are directed at the vital rate that is most influential on the population growth (Wisdom et al. 2000, Reed et al. 2009). I employed several methods in order to determine which vital rates might be most effective at influencing population growth rate. I considered standard sensitivity-type analyses: sensitivity, elasticity, and VSS; which indicate the relative change in growth rate per change in vital rate and are commonly used for evaluation of management targets (Heppell et al. 2000, Caswell 2001, Morris and Doak 2002). I plotted the VSS results under environmental stochasticity with the population growth rates to evaluate how sensitivity changes when the population experiences different growth rates. Some studies indicate that vital rates that are high in sensitivity metrics are not necessarily likely to vary much and thus potential variability is important to account for in such analyses (Caswell 1989, 2010). Therefore, I also conducted a life-table response experiment (LTRE). Each result contributes a slightly different aspect to understanding the relationship between growth rates and vital rate. Below I discuss the results of those analyses for the top four vital rates: adult survival, juvenile survival, chick survival, and adult nest success.

Based on the sensitivity-type analyses results, one conservation and management focus should be on improving GUSG adult survival (Figure 4.7, Appendix 4.G). This is consistent with life-history theory for longer-lived bird species (Saether and Bakke 2000). The process variance is low for adult survival (Table 4.2). Stearns and Kawecki (1994) observed that vital rates that have high sensitivity also have low variability, which they attribute to canalization of these rates through stabilizing selection pressures. In my case fluctuations in adult survival will likely have the largest effect on population growth; however adult survival is typically a very stable vital rate in nature (Table 4.2). Therefore adult survival is likely not the cause of current population declines. If management actions are able to increase adult survival past its typical bounds of natural variability then it might be a desirable target for management especially when populations are in steep decline (Figure 4.8).

Upland game birds are typically highly reproductive species with early maturity and larger clutch sizes (Wisdom and Mills 1997, Tirpak et al. 2006, Sandercock et al. 2008). Sage-grouse species are generally longer-lived, have higher adult survival, and have smaller clutch sizes than other upland game birds (Table 4.2, Taylor et al. 2012). Other galliforms species generally are highly sensitive to fluctuations in chick and juvenile survival. Chick and juvenile survival were consistently high in importance in the sensitivity analyses on GUSG but always lower than adult survival (Figure 4.7, Appendix 4.G). The importance of adult survival in the vital rate analyses suggests that GUSG are more on the “survivor species” end of the typically more “highly reproductive” spectrum of upland game birds (Wisdom and Mills 1997).

Juvenile survival is typically more influential than chick survival on GUSG population growth rates (Figures 7 & 8, Appendix 4.G) and juvenile survival appears to be the best management target when the population growth rate is slightly decreasing to increasing ( $\lambda > 0.8$ , Figure 4.8). Additionally, juvenile survival is more variable proportional to its sensitivity than chick survival (Figure 4.9). This indicates that there is more variability naturally in my data with respect to juvenile survival and thus potential management actions focused on juvenile survival may actually have a larger effect on the population growth rate than just the sensitivity analyses suggest. Since juvenile survival has shown a marked decrease during the six years of my study (Chapter 2), the importance of juvenile survival from the LTRE might be indicative that juvenile survival may be one primary cause for the decline in the population growth rate over the study.

A population model analysis conducted on the related GRSG (Taylor et al. 2012) suggests that nest success is one vital rate responsible for much of the variation in population growth. In my study adult nest success was one of the vital rates with the greatest sensitivity proportional to its variability for GUSG (Figure 4.9) and the transient sensitivity analysis suggests that nest success is much more important in the short term than the stable-state assumption (Appendix 4.G). Taylor et al. (2012) suggested that factors that vary annually such as vegetation characteristics (Holloran et al. 2005, Coates and Delehanty 2010,

Doherty et al. 2010), predator densities (Coates and Delehanty 2010), and weather events (Walker 2008) which impact nest success rates likely explain why nest success is so variable. The natural variability in nest success, coupled with its potential influence on population growth, suggests it might also make a good management target.

As with most systems in nature, GUSG population dynamics are complex and interrelated. It is reasonable to assume that each component of a grouse's life history plays a part in the current trajectory of the population. However, for management purposes, highlighting key aspects of a species' life history that will be most effective in improving population viability is necessary. Based on the above information, juvenile survival is both very important to GUSG population growth and highly variable making it a good target for conservation efforts. Additionally, declines in this vital rate may be causing the observed declines in the population (Chapter 2). Three other vital rates have shown merit as management targets based on the results described above: adult survival, chick survival, and adult nest success. As management actions are primarily implemented indirectly to affect management targets (e.g., habitat modification to improve nest success, predator control to improve survival) the potential for a management action to impact the vital rates should be a factor when selecting a target.

The population matrix data in my study come from the two populations I examined (GB and SM). For the sensitivity analyses I used the GB population matrices. The SM-specific population matrix only differs from the GB matrix in the chick survival parameters (Appendix 4.E). The sensitivity analyses on the SM population data are similar to the GB results: adult and chick survival were the most important vital rates. Chick survival was more important than juvenile survival in SM which is logical based on the almost complete lack of chick survival in SM. The population projections for this population are therefore worse than the estimates predicted for GB (Appendix 4.A). These results support the theory that different populations of the same species are under different ecological pressures and are likely to benefit from population-specific management actions (Johnson et al. 2010).

## **Translocation**

The overall results of the translocation analysis suggest that moving birds into the small SM population will improve the persistence of this declining population. Both the extinction time and resulting population size were improved for the destination population with some form of translocation compared to no translocation (Figure 4.10).

The destination population did not go extinct with methods that involved frequent translocations, while translocation was being conducted (population models projected out to 100 years but translocation methods desisted after 30 years). This demonstrates that if extinction time is the most important metric to be considered then moving birds into the population regularly will ensure the population does not go extinct. Previous research on optimal translocation strategies have found similar results that more frequent movement has a greater impact on improving population persistence (Stacey and Taper 1992, Lubow 1996). However, this may result in just maintaining a population of translocated birds (i.e., “keep filling a leaking bucket”) without addressing underlying causes of decline (e.g., not enough habitat, large predator populations). However, keeping a population viable until management actions can take place may be useful if establishing a population is considered more difficult than augmenting an existing population.

Moving more individuals is often associated with higher success of translocation studies (Griffith et al. 1989, Wolf et al. 1996, Fischer and Lindenmayer 2000). Moving more individuals predictably results in larger population sizes at 30 years (Figure 4.10). However, the impact on destination population persistence is not as dramatic as more frequent movements.

I also examined the effect of removing birds from the source population (GB) based on the same translocation strategies. Removing birds all at once had the least effect on the source population in terms of resulting population size and mean and minimum extinction time (Figure 4.10). The more frequent the

removal the more substantial the effect on the source population, this result was more pronounced when more than 400 birds were removed from the population.

Although translocation is generally shown to improve population persistence, several studies have shown that the site quality is more important than either number or timing of translocation in determining population persistence (Griffith et al. 1989, Fischer and Lindenmayer 2000, Rout et al. 2007). I observed no juvenile recruitment during my study in the destination population (Chapter 2). Regardless of how many birds are translocated, this population will not persist on its own unless the local vital rates are improved; which may suggest the quality of the location needs to be enhanced (e.g., habitat restoration, predator reduction, etc.).

Another result from the translocation simulation is that movement of yearling birds appears to result in larger population sizes on the destination population than movement of adults. Adult female sage-grouse are known to have high site fidelity both in breeding and wintering locations (CPW unpublished data, Gunnison Sage-grouse Rangewide Steering Committee 2005). Adult birds that are moved often disappear from the destination population (CPW unpublished data). The yearling females may not have established a movement pattern as strongly as adults and this may relate to their higher success rates in the destination population. No discernable difference in the effect on the source population size with respect to the age of the moved birds was observed (only a 3% increase in population size when yearlings are removed compared to adults). Yearling vital rates (survival, nest initiation, and nest success) are typically the lowest in importance based on the sensitivity analyses (Figure 4.7). This result may support the removal of yearlings from the source population as compared to removing adults.

A trade off exists in terms of costs and benefits to GUSG populations with respect to the different translocation strategies examined. Based on my analysis I would suggest moving a total of 300-500 birds over 30 years as it balances the impact on the source population and yet will still have considerable improvement on the destination population (Figure 4.10). I would suggest moving birds at a frequency of

every year or two to have the greatest impact on the destination population, but if the fate of the source population is in question than moving birds every five or six years will mitigate some of the effect of bird removals. The effects of translocations should be monitored for both populations and the method should be updated as more information is available. The translocation problem I describe lends itself well to adaptive management practices which facilitate learning through management practices by using modeling (Shenk and Franklin 2001). Adaptive management requires continual monitoring which would help improve the accuracy of survival and reproductive rates after translocation and learning would help improve the model projections.

**Table 4.1.** Matrix components and corresponding equations for a Gunnison Sage-grouse population model.

<b>Parameter</b>	<b>Equation</b>
F <sub>1</sub>	Juvenile recruitment * Yearling nest initiation rate * Yearling nest success rate * ½ Average clutch size
F <sub>2</sub>	Yearling survival * Adult nest initiation rate * Adult nest success rate * ½ Average clutch size
F <sub>3</sub>	Adult survival * Adult nest initiation rate * Adult nest success rate * ½ Average clutch size
P <sub>1</sub>	Chick survival * Juvenile survival
P <sub>2</sub>	Yearling survival
P <sub>3</sub>	Adult survival

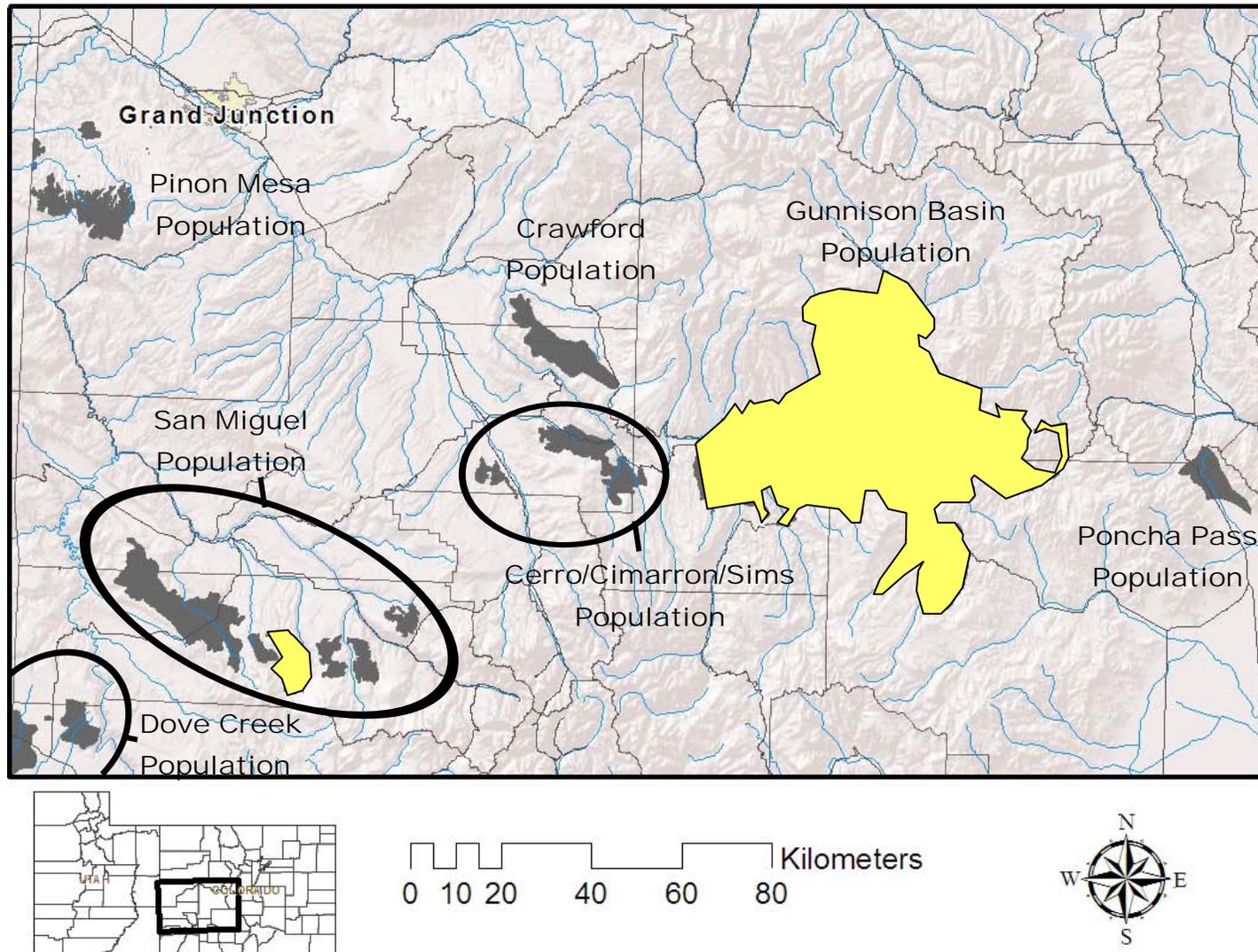
**Table 4.2.** Parameter estimates and standard errors for Gunnison Sage-grouse vital rates by year with vital rate means and process variance. Estimates are given by population only when a difference in populations was detected (i.e., chick survival).

Year	2005		2006		2007		2008		2009		2010		Vital Rate Mean	Process Variance
	$\theta$	SE												
Nest Initiation														
Yearling	1.000	0.000	0.930	0.060	0.810	0.030	0.870	0.040	0.850	0.050	0.860	0.100	0.887	0.0015
Nest Initiation Adult	1.000	0.000	0.910	0.067	0.840	0.034	0.960	0.009	0.970	0.052	0.920	0.024	0.933	0.0017
Hen Success Yearling	0.254	0.097	0.583	0.100	0.350	0.084	0.606	0.106	0.403	0.089	0.372	0.073	0.428	0.0106
Hen Success Adult	0.246	0.097	0.608	0.100	0.289	0.084	0.700	0.106	0.451	0.089	0.386	0.073	0.446	0.0233
Chick Survival (GB)	0.467	0.020	0.417	0.017	0.366	0.015	0.316	0.014	0.266	0.016	0.219	0.019	0.342	0.0084
(SM)	-	-	-	-	0.044	0.002	0.030	0.001	0.020	0.000	0.013	0.000	0.027	0.0002
Juvenile Survival	0.731	0.121	0.533	0.100	0.386	0.075	0.384	0.061	0.284	0.063	0.179	0.064	0.416	0.0307
Yearling Survival	0.745	0.108	0.613	0.110	0.559	0.112	0.560	0.115	0.718	0.089	0.610	0.106	0.634	0.0005
Adult Survival	0.705	0.116	0.561	0.113	0.502	0.108	0.504	0.109	0.675	0.088	0.557	0.099	0.584	0.0004
½ Clutch Size	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.0000

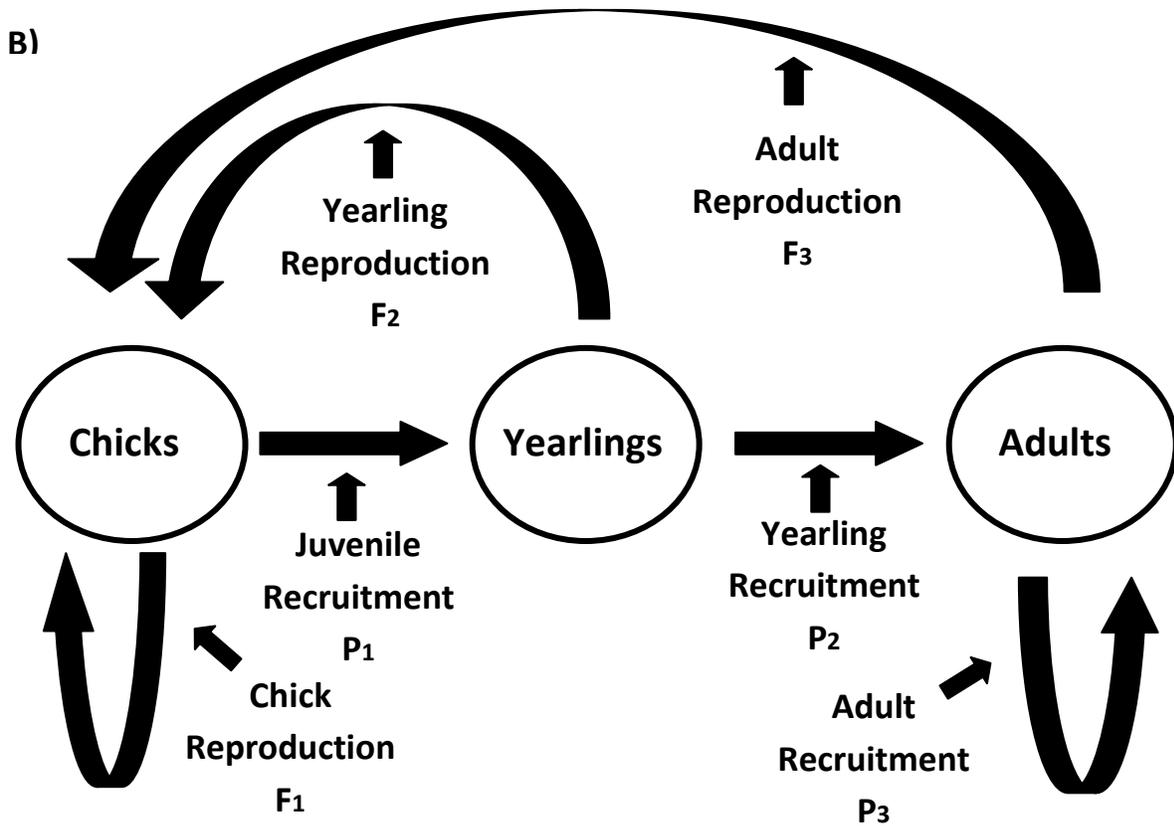
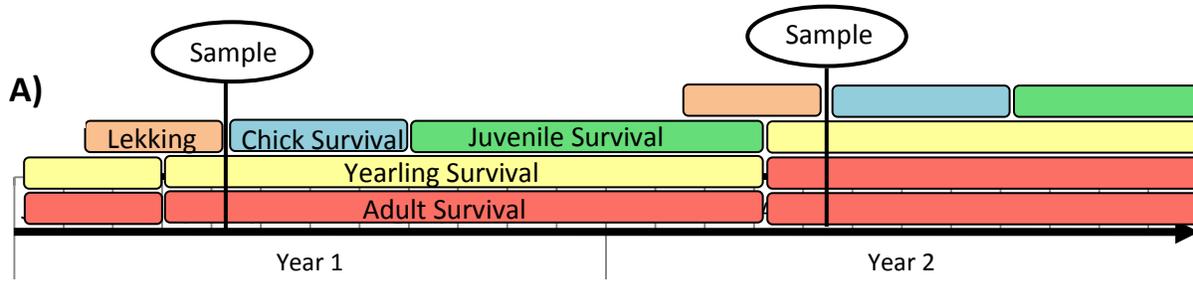
**Table 4.3.** Covariance matrix for Gunnison Sage-grouse vital rates calculated from six years of data.

	<b>Nest Initiation Yearling</b>	<b>Nest Initiation Adult</b>	<b>Hen Success Yearling</b>	<b>Hen Success Adult</b>	<b>Chick Survival</b>	<b>Juvenile Survival</b>	<b>Yearling Survival</b>	<b>Adult Survival</b>
<b>Nest Initiation</b>								
<b>Yearling</b>	0.004							
<b>Nest Initiation Adult</b>	0.002	0.003						
<b>Hen Success Yearling</b>	-0.001	-0.001	0.016					
<b>Hen Success Adult</b>	-0.001	0.001	0.020	0.027				
<b>Chick Survival</b>	0.004	0.000	-0.001	-0.003	0.007			
<b>Juvenile Survival</b>	0.009	0.003	-0.004	-0.006	0.015	0.031		
<b>Yearling Survival</b>	0.003	0.003	-0.005	-0.005	0.002	0.005	0.005	
<b>Adult Survival</b>	0.003	0.003	-0.006	-0.006	0.002	0.006	0.006	0.006

\*Clutch size was not calculated annually and thus is not included in the covariance matrix

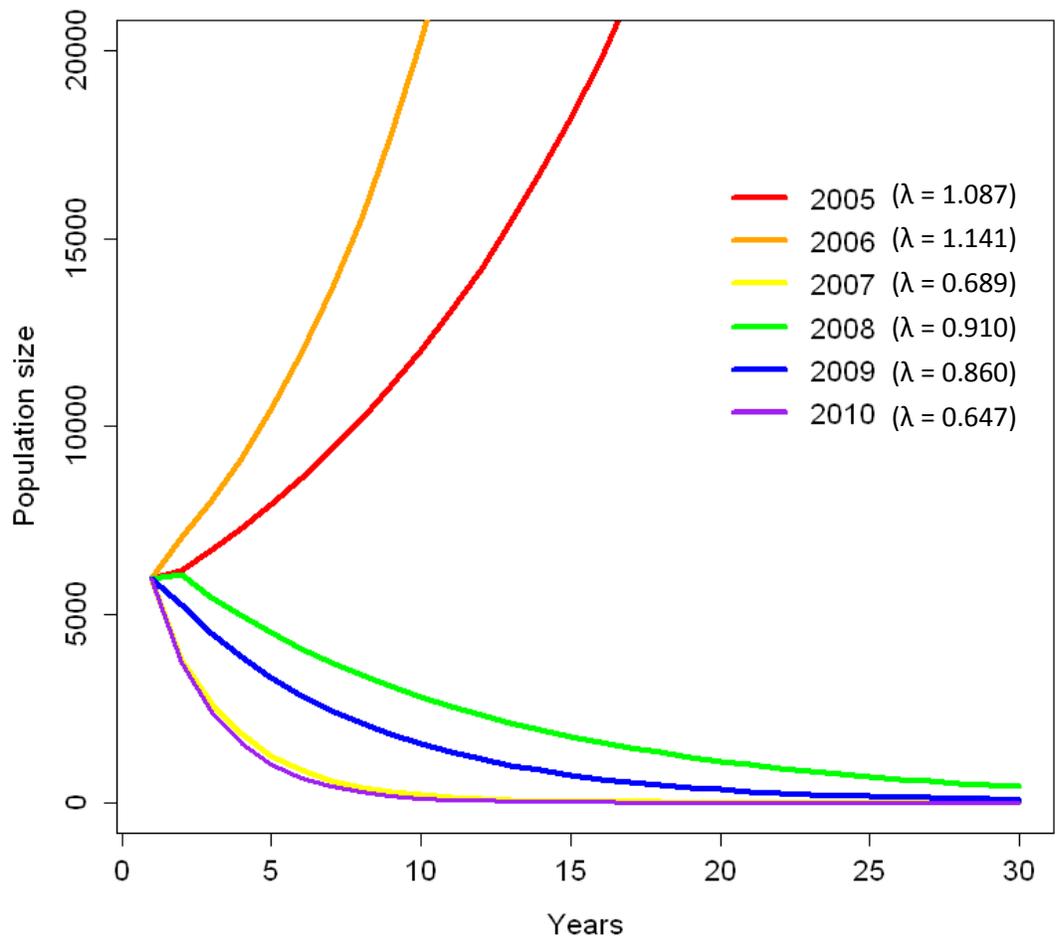


**Figure 4.1.** The names and location of the seven populations of Gunnison Sage-grouse. The two areas highlighted in yellow are the study areas.

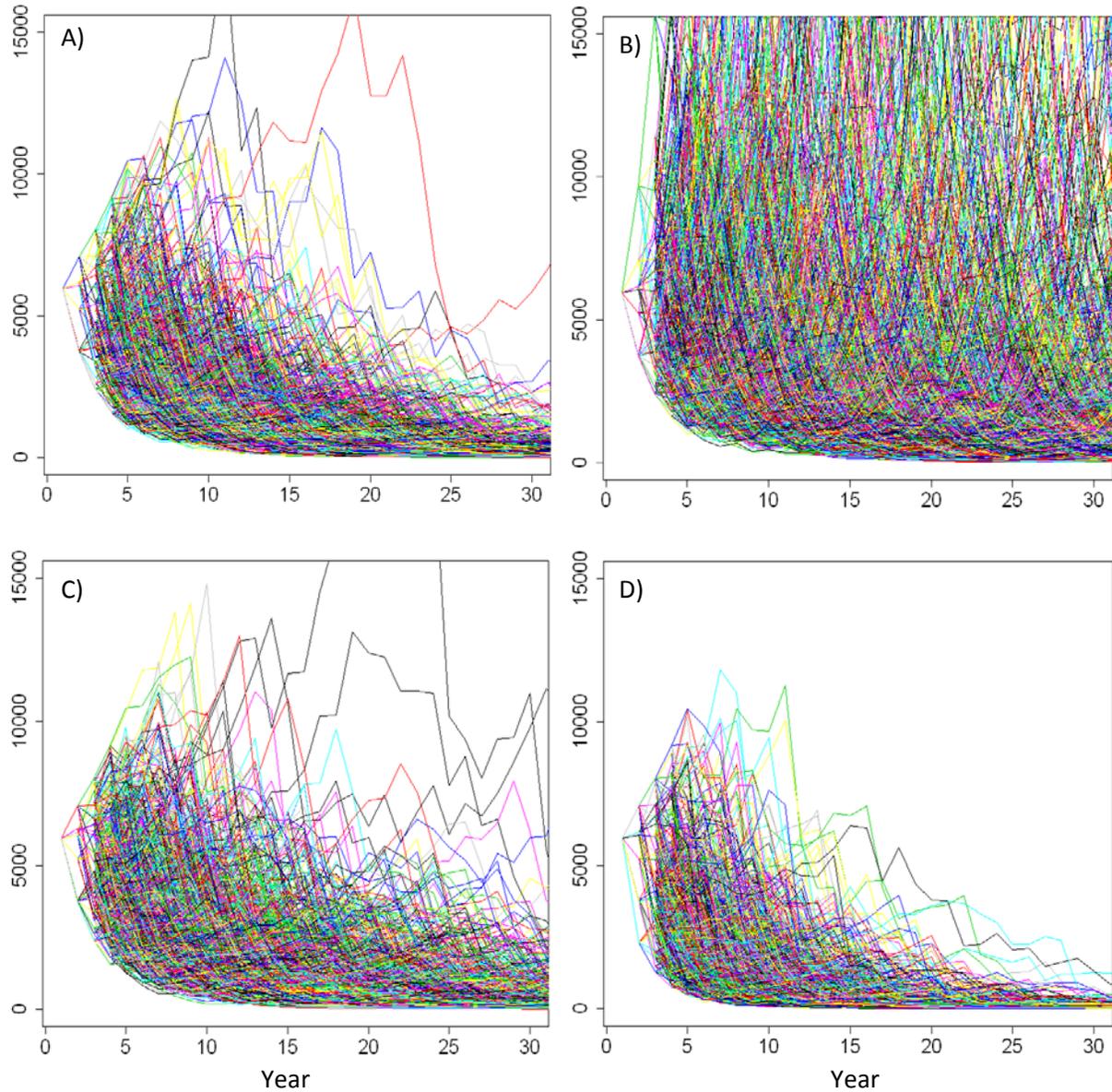


$$\begin{bmatrix} C_{t+1} \\ Y_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} \begin{bmatrix} C_t \\ Y_t \\ A_t \end{bmatrix}$$

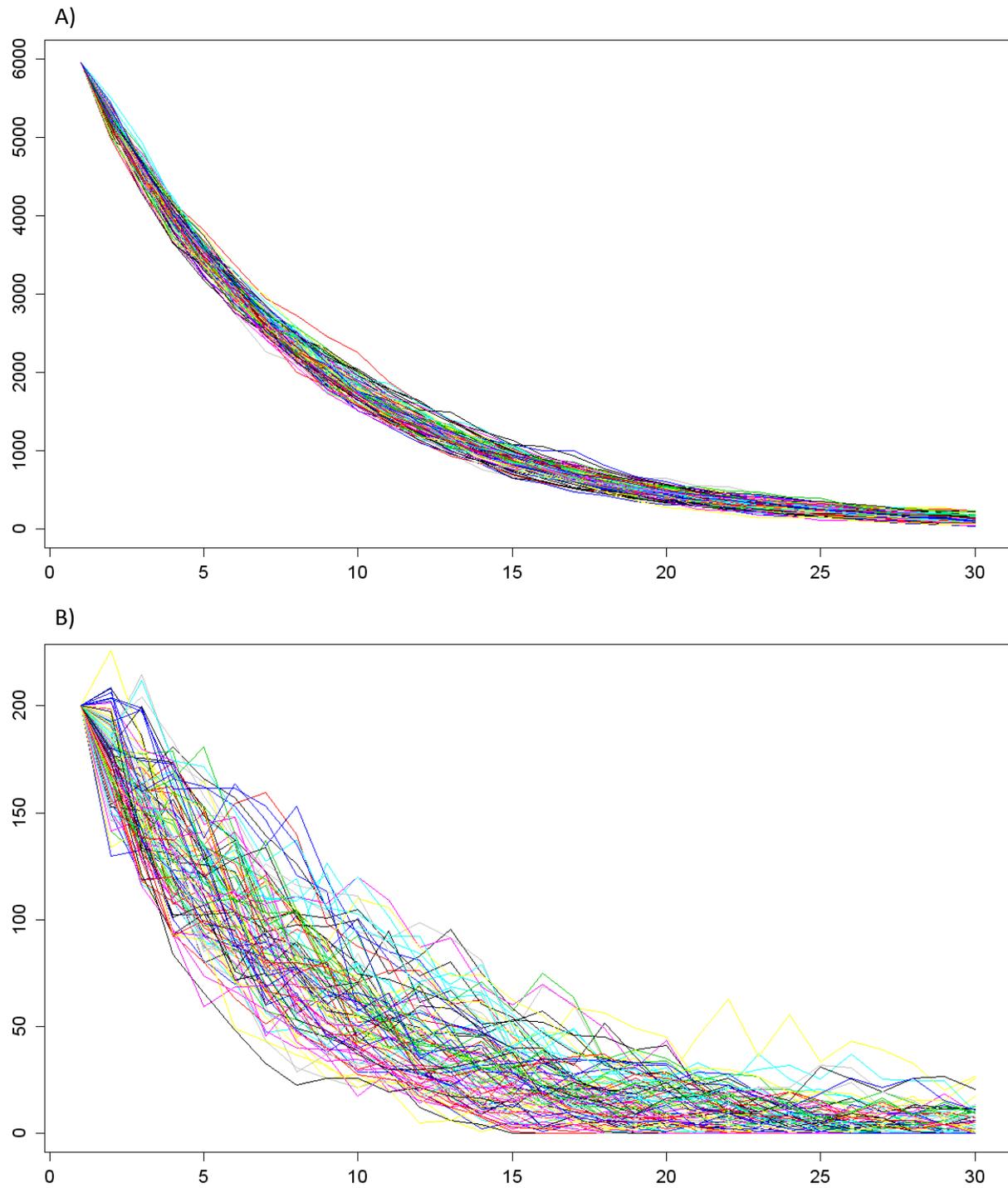
**Figure 4.2.** Life cycle and population matrix model for Gunnison Sage-grouse. Sampling is assumed to occur instantaneously after hatch in the post-birth pulse model. (A) shows the sampling time line including survival components. B) The age class transitions parameters shown both in the diagram and matrix.



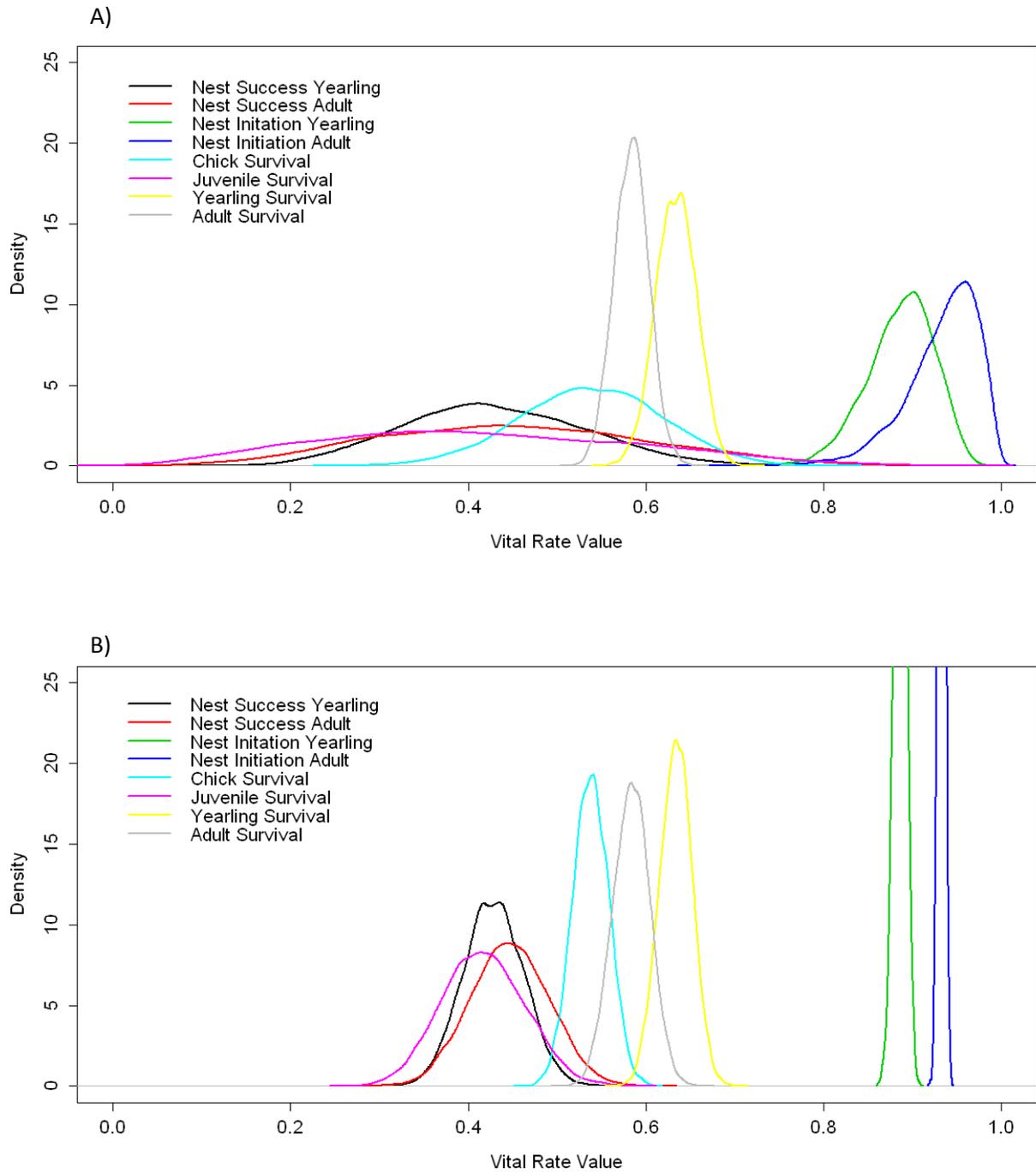
**Figure 4.3.** Deterministic Gunnison sage-grouse population projections and population growth rates ( $\lambda$ ) based on the vital rate matrices calculated from six years of data (2005-2010). Initial population size is based on the Gunnison Basin 2010 population estimate with expected number of chicks (1531 adults, 753 yearlings, and 3670 chicks).



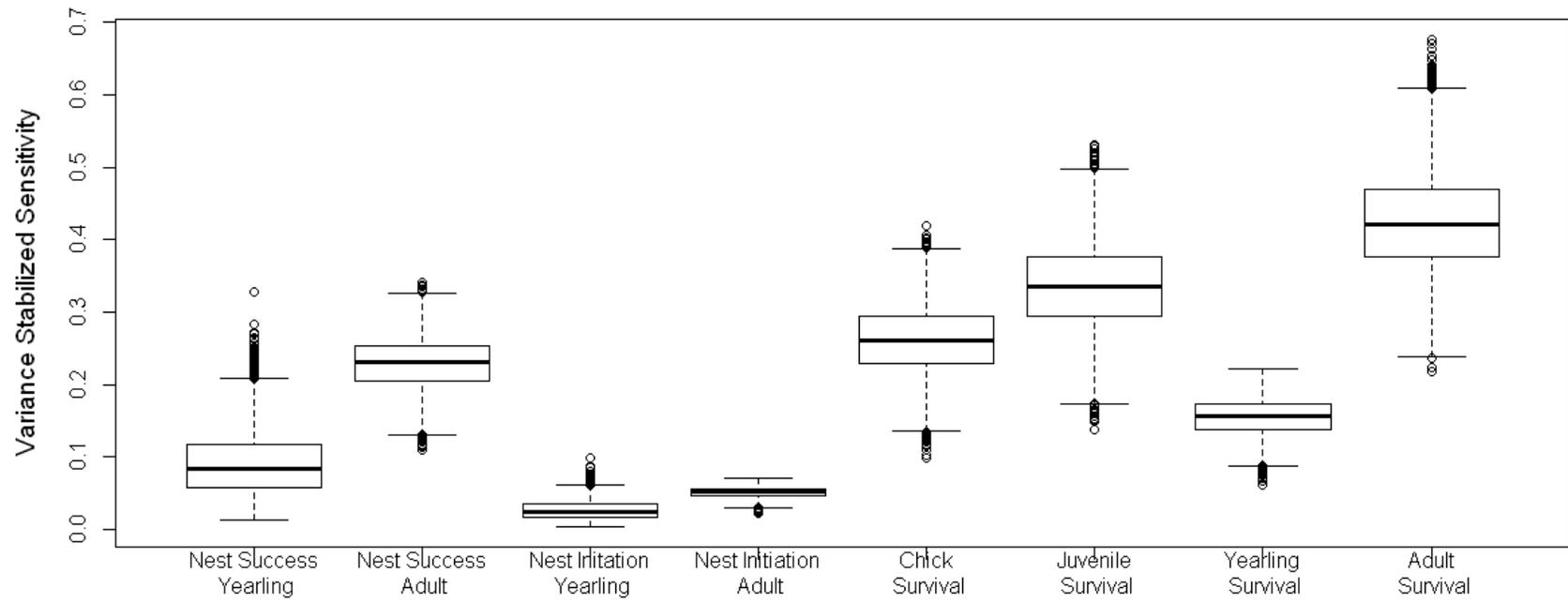
**Figure 4.4.** Gunnison Basin population projection of Gunnison Sage-grouse with environmental stochasticity for: A) projection based on the six years of data, B) projection with one additional year with a positive growth rate ( $\lambda = 1.27$ ), C) projection with one additional year with a constant growth rate ( $\lambda = 1.00$ ), D) projection with one additional year with a decreasing population growth rate ( $\lambda = 0.74$ ). Each line represents a simulation of one population projection.



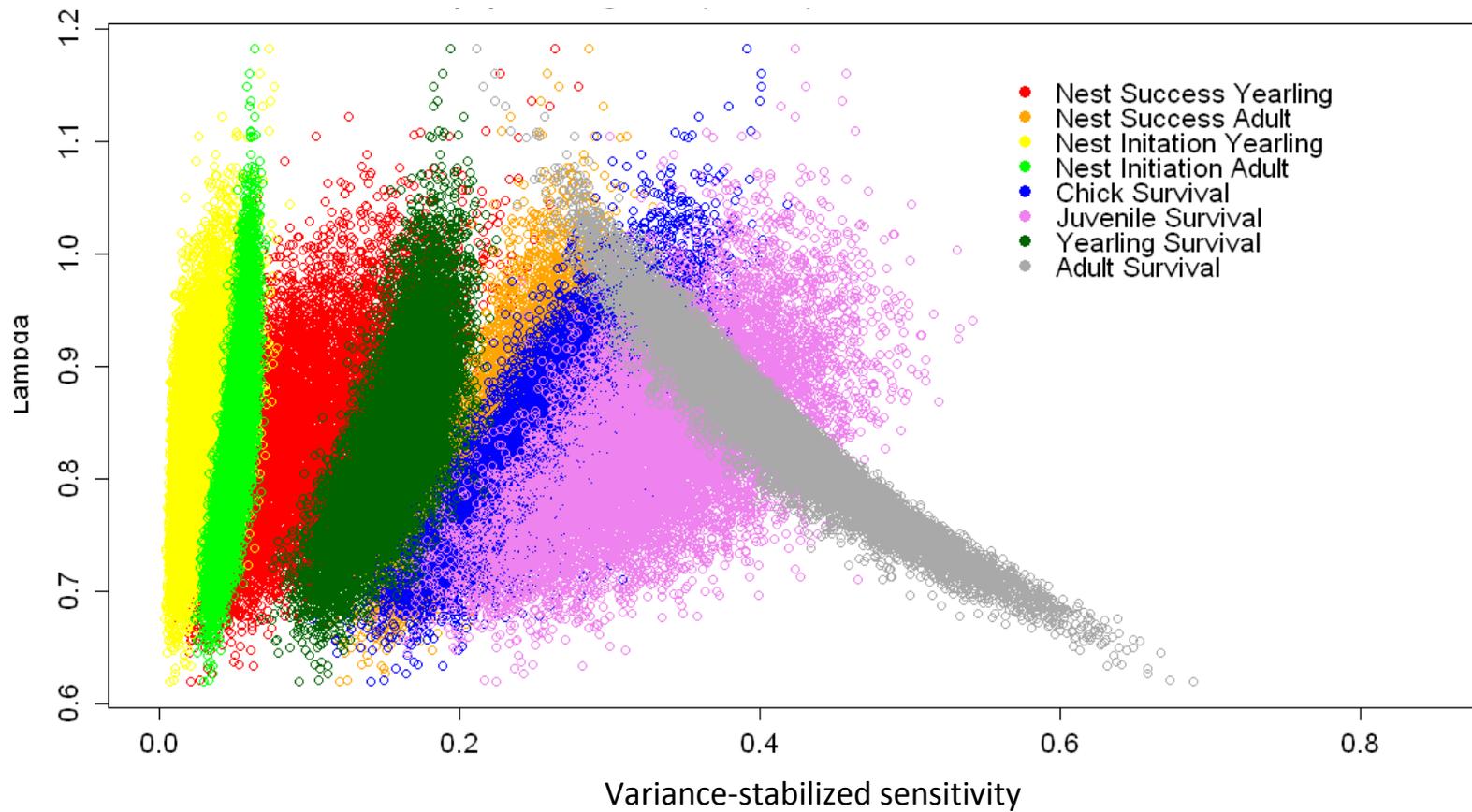
**Figure 4.5.** The effect of demographic stochasticity on population projections for the Gunnison sage-grouse in the Gunnison Basin (A) and San Miguel (B). Each line represents a single population projection. Although the simulations for Gunnison Basin are approaching extinction, none of the simulations went extinct in the 30 year time frame.



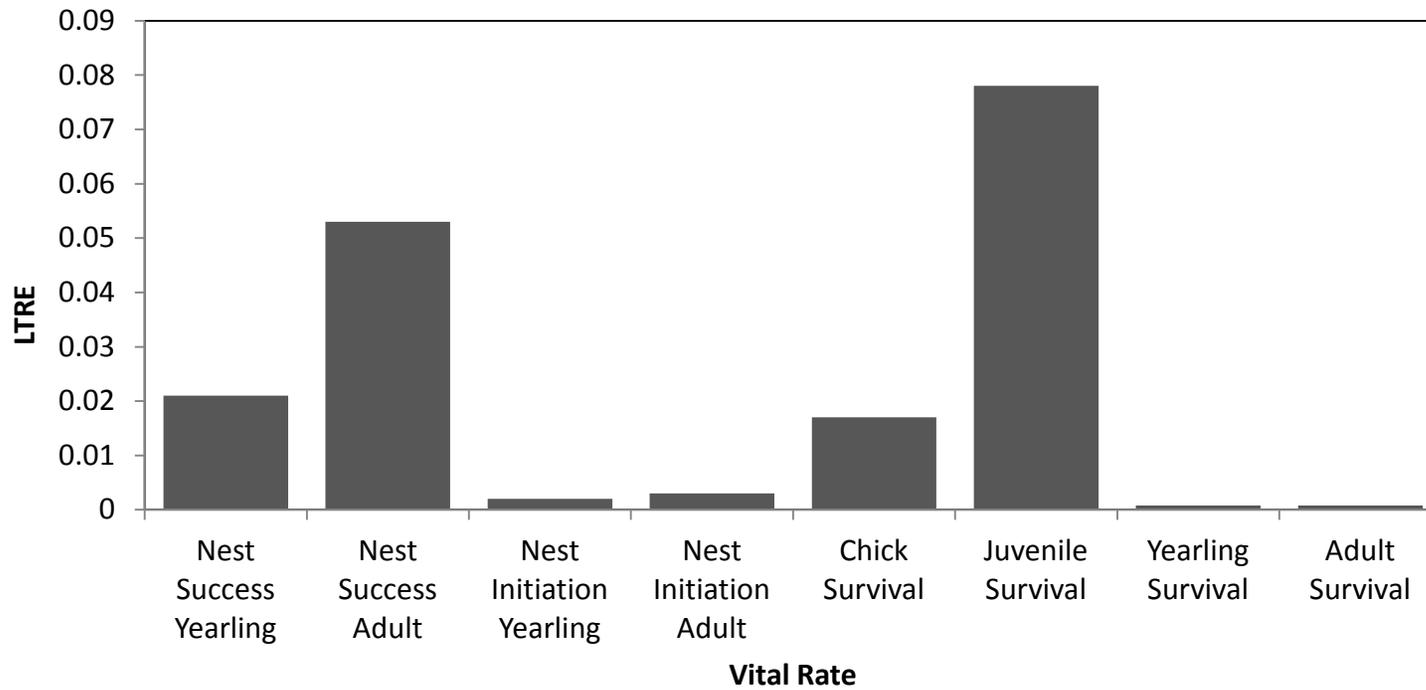
**Figure 4.6.** Plots of Gunnison sage-grouse vital rate distributions based on simulating data without (A) and with (B) correlation.



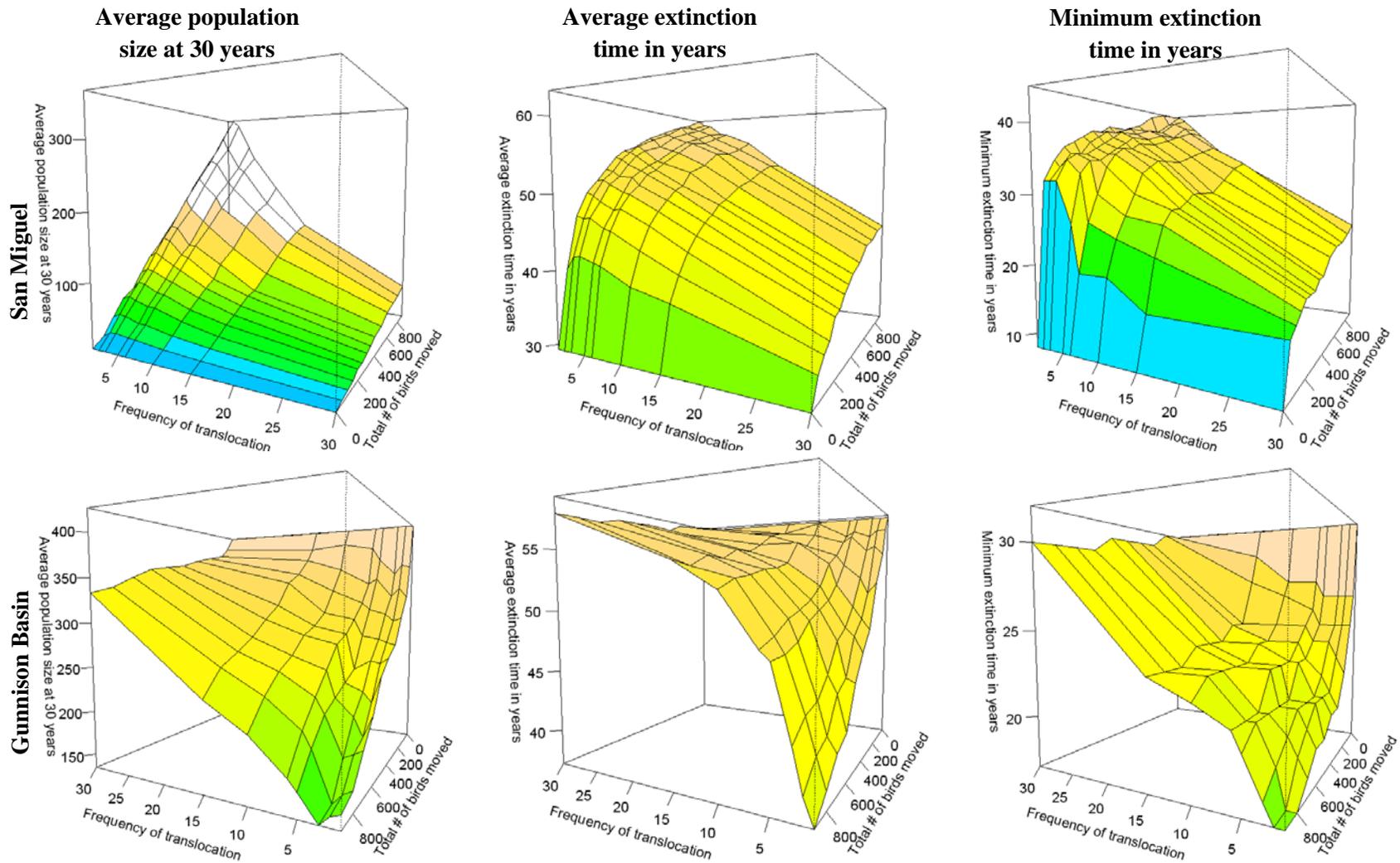
**Figure 4.7.** Box plots of variance-stabilized sensitivities (VSS) for Gunnison Sage-grouse vital rates based on 10,000 simulations with correlations.



**Figure 4.8.** Relationship between variance-stabilized sensitivity and population growth rate ( $\lambda$ ) by vital rate for simulated data with correlation for Gunnison Sage-grouse.



**Figure 4.9.** Life-table Response Experiment (LTRE) results by vital rate for Gunnison Sage-grouse. (LTRE = process variance \* variance-stabilized sensitivity)



**Figure 4.10.** Results of Gunnison Sage-grouse translocation events on the San Miguel (destination) and Gunnison Basin (source) populations. The results of average population size at 30 years, average extinction time, and minimum extinction time. Note that the axes are flipped for the SM plots vs. the GB plots to make the plots easier to read. Frequency of translocation axis should be interpreted as “birds are moved every x years”.

## LITERATURE CITED

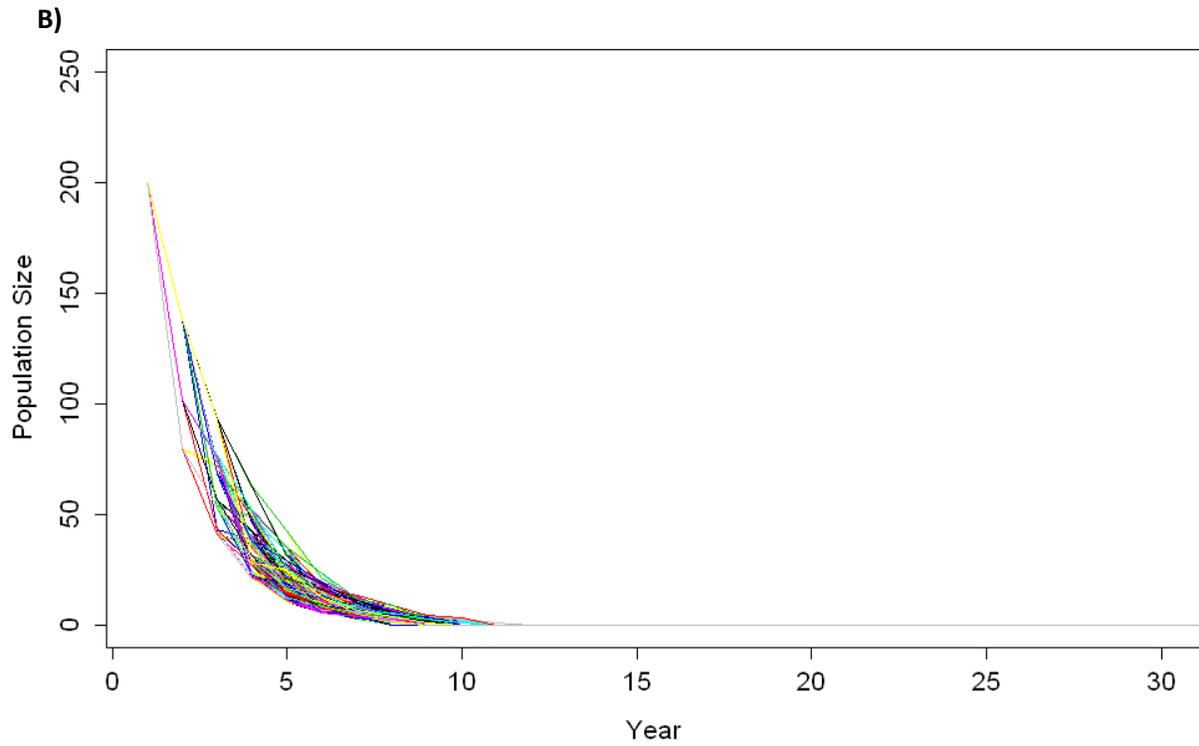
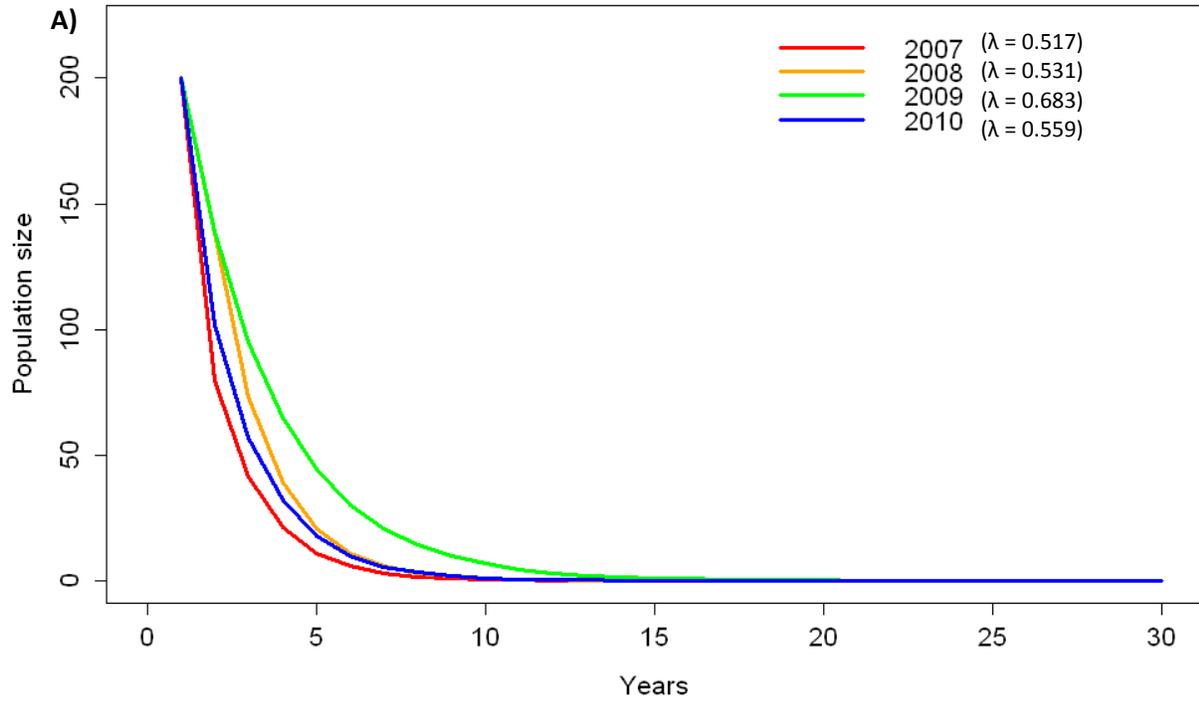
- Baxter, R. J., J. T. Flinders, D. G. Whiting, and D. L. Mitchell. 2009. Factors affecting nest-site selection and nest success of translocated greater sage grouse. *Wildlife Research* **36**:479-487.
- Benton, T. G. and A. Grant. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution* **14**:467-471.
- Brockwell, P. J. and R. A. Davis. 2002. *Introduction to Time Series and Forecasting*. 2nd edition. Springer-Verlag New York, Inc., New York, NY USA.
- Buhnerkempe, M. G., N. Burch, S. Hamilton, K. M. Byrne, E. Childers, K. A. Holfelder, L. N. McManus, M. I. Pyne, G. Schroeder, and P. F. Doherty. 2011. The utility of transient sensitivity for wildlife management and conservation: Bison as a case study. *Biological Conservation* **144**:1808-1815.
- Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. *Conservation Biology* **19**:1821-1826.
- Caswell, H. 1989. Analysis of Life Table Response Experiments. 1. Decomposition of Effects on Population-growth Rate. *Ecological Modelling* **46**:221-237.
- Caswell, H. 1996. Analysis of life table response experiments .2. Alternative parameterizations for size- and stage-structured models. *Ecological Modelling* **88**:73-82.
- Caswell, H. 2001. *Matrix Population Models*, 2nd ed. Sinauer Associates Inc, Sunderland, MA.
- Caswell, H. 2007. Sensitivity analysis of transient population dynamics. *Ecology Letters* **10**:1-15.
- Caswell, H. 2010. Life table response experiment analysis of the stochastic growth rate. *Journal of Ecology* **98**:324-333.
- Coates, P. S. and D. J. Delehanty. 2010. Nest Predation of Greater Sage-Grouse in Relation to Microhabitat Factors and Predators. *Journal of Wildlife Management* **74**:240-248.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater Sage-Grouse Nesting Habitat: The Importance of Managing at Multiple Scales. *Journal of Wildlife Management* **74**:1544-1553.
- Fischer, J. and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. *Biological Conservation* **96**:1-11.

- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a Species Conservation Tool - Status and Strategy. *Science* **245**:477-480.
- Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-Grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology* **81**:654-665.
- Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management* **69**:638-649.
- Hupp, J. W. and C. E. Braun. 1989. Topographic Distribution of Sage Grouse Foraging in Winter. *Journal of Wildlife Management* **53**:823-829.
- Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. *Ecological Applications* **20**:1753-1765.
- Koons, D. N., J. B. Grand, B. Zinner, and R. E. Rockwell. 2005. Transient population dynamics: Relations to life history and initial population state. *Ecological Modelling* **185**:283-297.
- Larson, M. A., M. E. Clark, and S. R. Winterstein. 2001. Survival of ruffed grouse chicks in northern Michigan. *Journal of Wildlife Management* **65**:880-886.
- Link, W. A. and P. F. Doherty. 2002. Scaling in sensitivity analysis. *Ecology* **83**:3299-3305.
- Link, W. A. and J. D. Nichols. 1994. On the Importance of Sampling Variance to Investigations of Temporal Variation in Animal Population-Size. *Oikos* **69**:539-544.
- Lubow, B. C. 1996. Optimal translocation strategies for enhancing stochastic metapopulation viability. *Ecological Applications* **6**:1268-1280.
- Morris, W. F. and D. F. Doak. 2002. *Quantitative Conservation Biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, Massachusetts, USA.

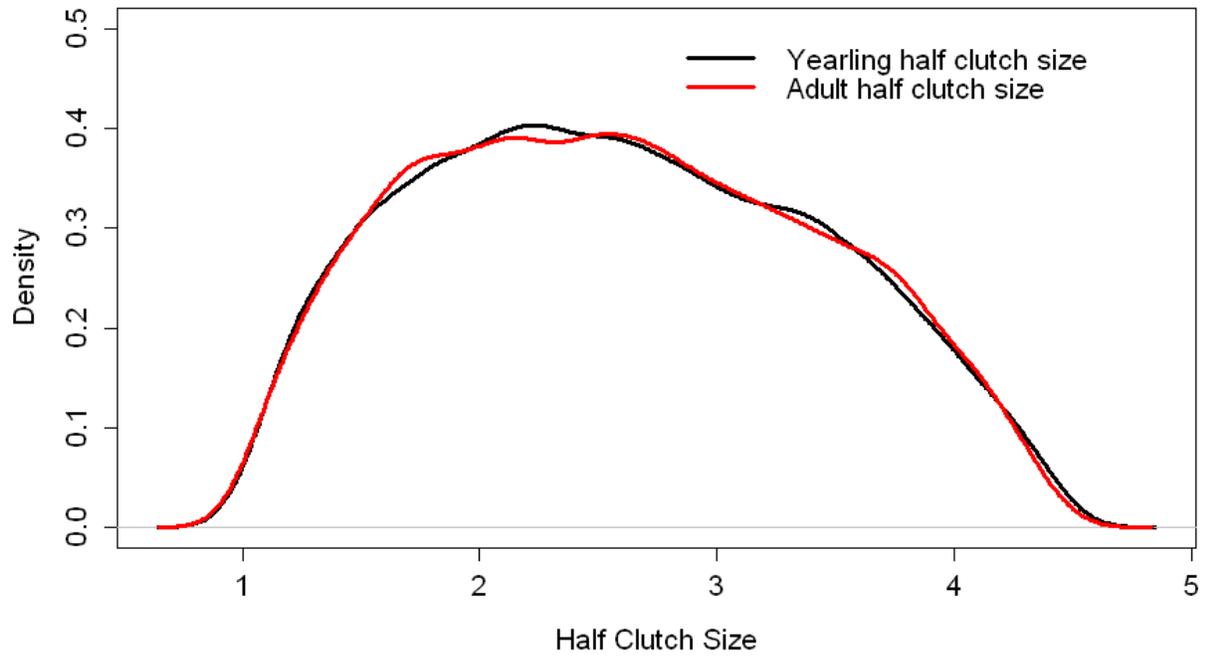
- Peterson, M. J., W. E. Grant, and N. J. Silvy. 1998. Simulation of reproductive stages limiting productivity of the endangered Attwater's prairie chicken. *Ecological Modelling* **111**:283-295.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America* **95**:213-218.
- Reed, J. M., N. Fefferman, and R. C. Averill-Murray. 2009. Vital Rate Sensitivity Analysis as a Tool for Assessing Management Actions for the Desert Tortoise. *Biological Conservation* **142**:2710-2717.
- Rout, T. M., C. E. Hauser, and H. P. Possingham. 2007. Minimise long-term loss or maximise short-term gain? Optimal translocation strategies for threatened species. *Ecological Modelling* **201**:67-74.
- Saether, B. E. and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642-653.
- Sandercock, B. K., W. E. Jensen, C. K. Williams, and R. D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. *Journal of Wildlife Management* **72**:970-982.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-Grouse in North America. *Condor* **106**:363-376.
- Schroeder, M. A. and R. K. Baydack. 2001. Predation and the management of prairie grouse. *Wildlife Society Bulletin* **29**:24-32.
- Shenk, T. and A. Franklin. 2001. *Modeling in Natural Resource Management: Development, Interpretation, and Application*. Island Press, Washington, D.C., USA.
- Stacey, P. B. and M. Taper. 1992. Environmental Variation and the Persistence of Small Populations. *Ecological Applications* **2**:18-29.
- Stearns, S. C. and T. J. Kawecki. 1994. FITNESS SENSITIVITY AND THE CANALIZATION OF LIFE-HISTORY TRAITS. *Evolution* **48**:1438-1450.

- Stinson, D. W., D. W. Hays, and M. A. Schroeder. 2004. Washington state recovery plan for the Greater Sage-grouse. . Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* **76**:336-347.
- Tirpak, J. M., W. M. Giuliano, C. A. Miller, T. J. Allen, S. Bittner, D. A. Buehler, J. W. Edwards, C. A. Harper, W. K. Igo, G. W. Normar, M. Seamster, and D. F. Stauffer. 2006. Ruffed grouse population dynamics in the central and southern Appalachians. *Biological Conservation* **133**:364-378.
- United States Fish and Wildlife Service, U. 2010. Determination of Gunnison Sage-grouse as a Threatened or Endangered Species. *in* D. o. t. Interior, editor. Federal Register
- Walker, B. L. 2008. Greater Sage-grouse Response to Coal-bed Natural Gas Development and West Nile Virus in the Powder River Basin, Montana and Wyoming, USA. University of Montana, Missoula, MT.
- Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Pages 56-68. *Wildlife Soc.*
- Wisdom, M. J. and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: Prairie-chickens as an example. *Journal of Wildlife Management* **61**:302-312.
- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. *Ecology* **81**:628-641.
- Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: Update and reanalysis of 1987 survey data. *Conservation Biology* **10**:1142-1154.

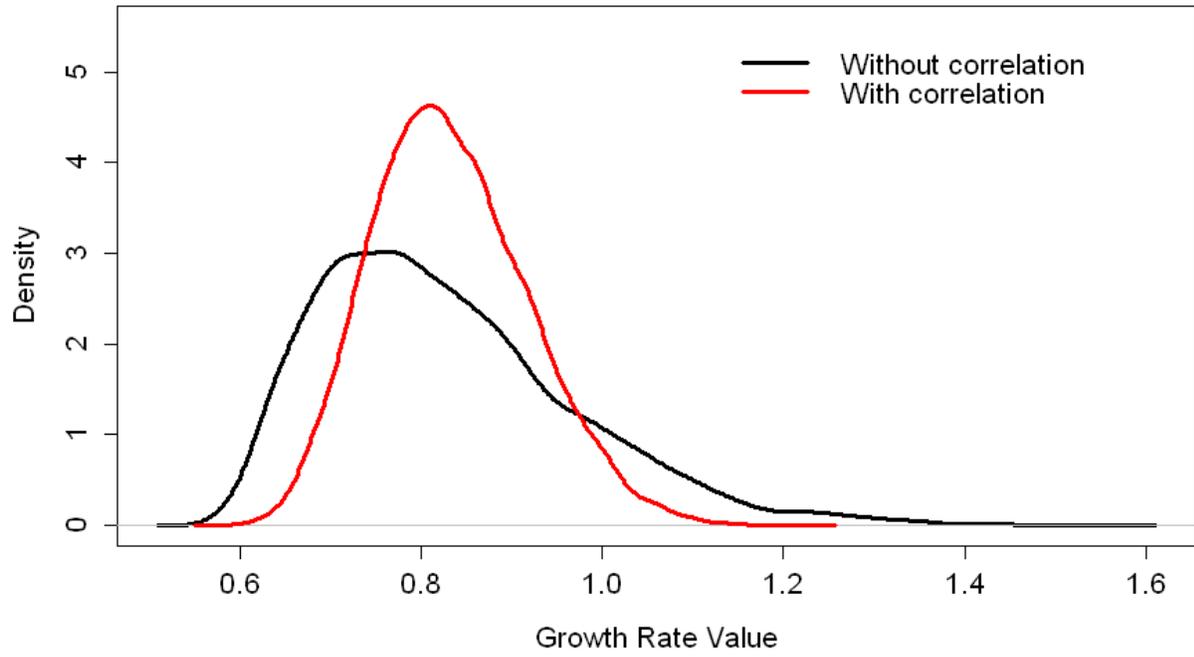
**APPENDIX 4.A.** Deterministic population projection (A) and projection with environmental stochasticity (B) for Gunnison sage-grouse in the San Miguel population.



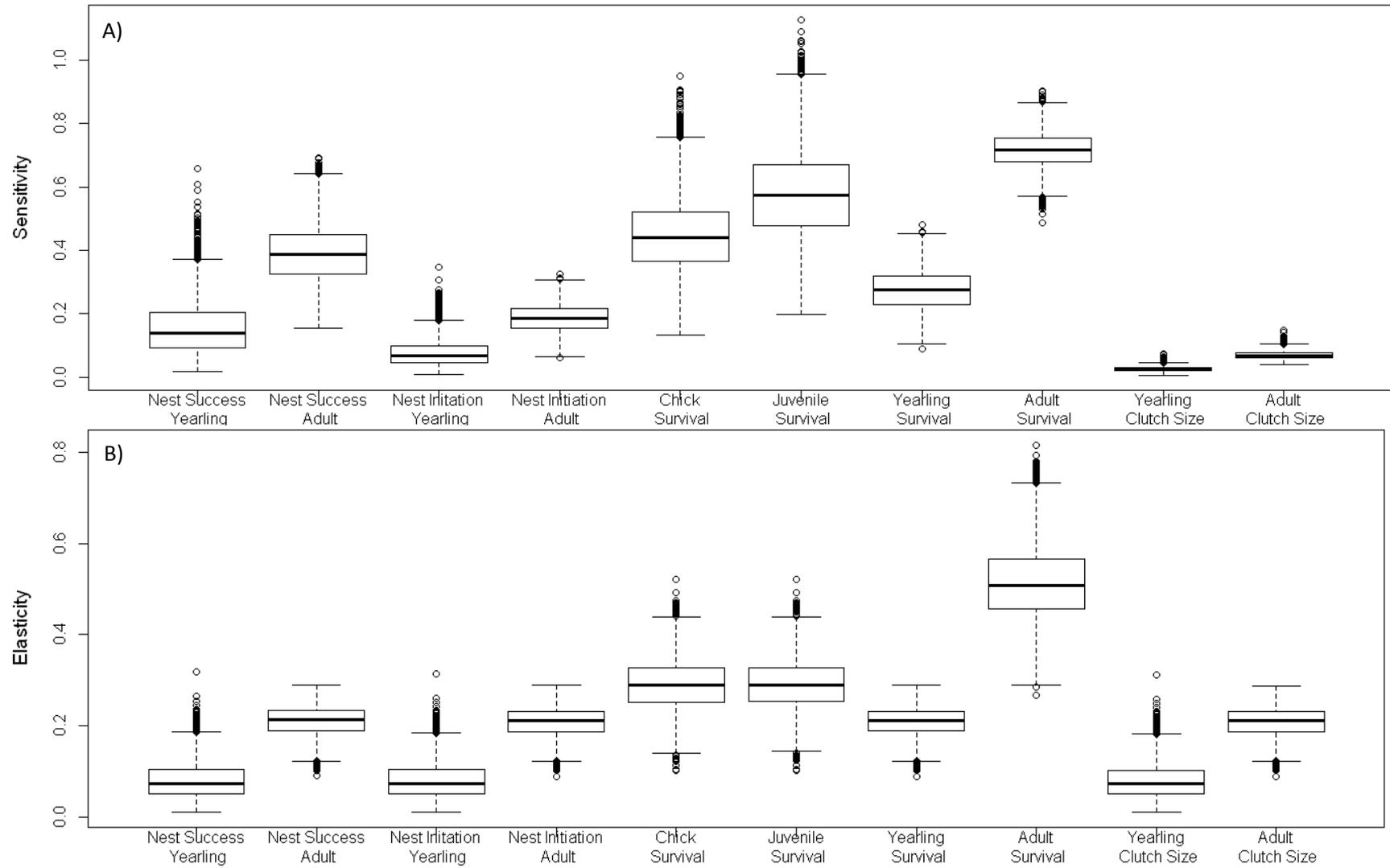
**APPENDIX 4.B.** Density plot of half clutch size parameters for Gunnison Sage-grouse based on simulating data without correlation (clutch size was not correlated with any other parameters).

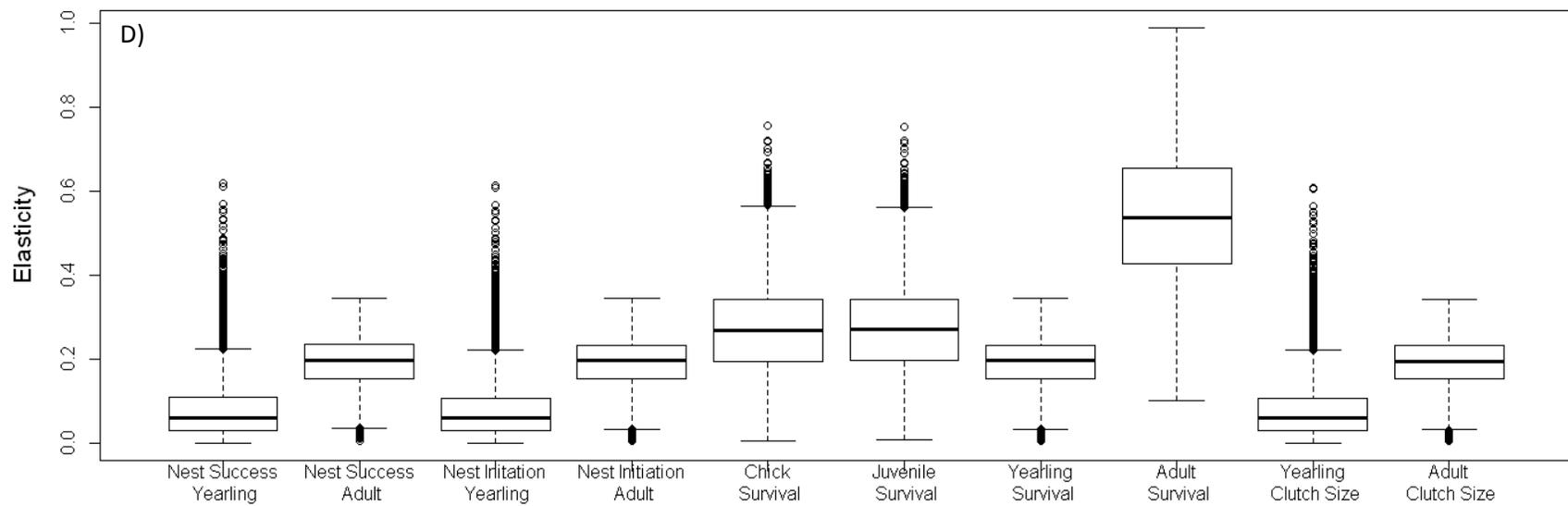
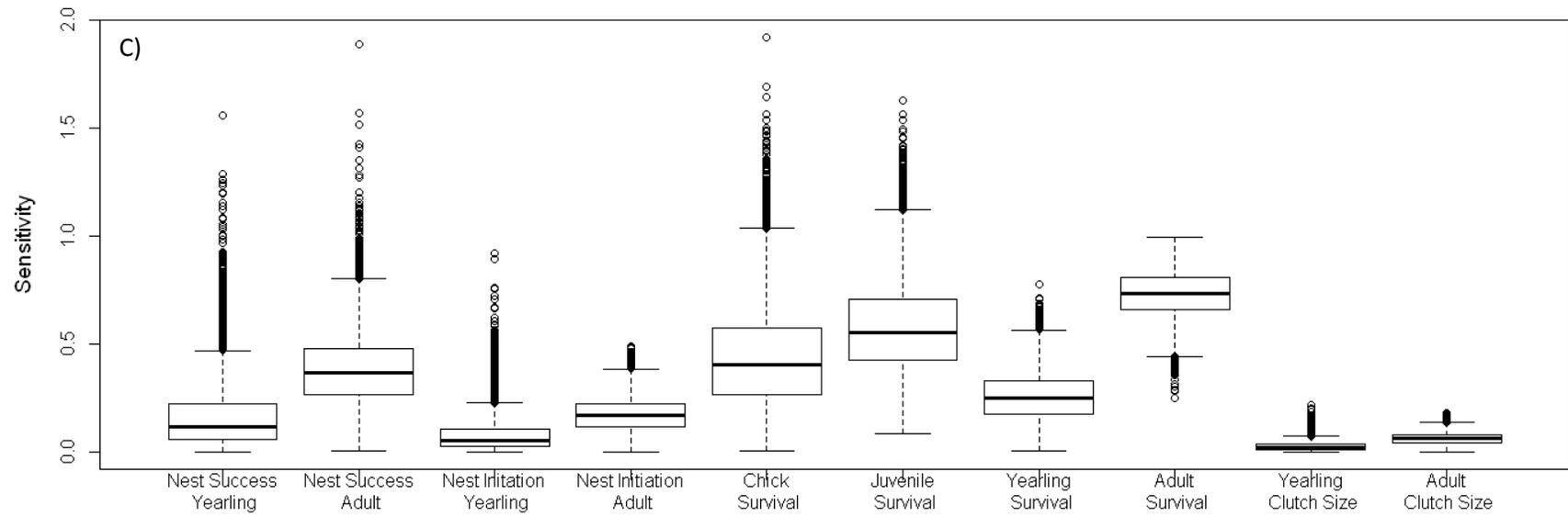


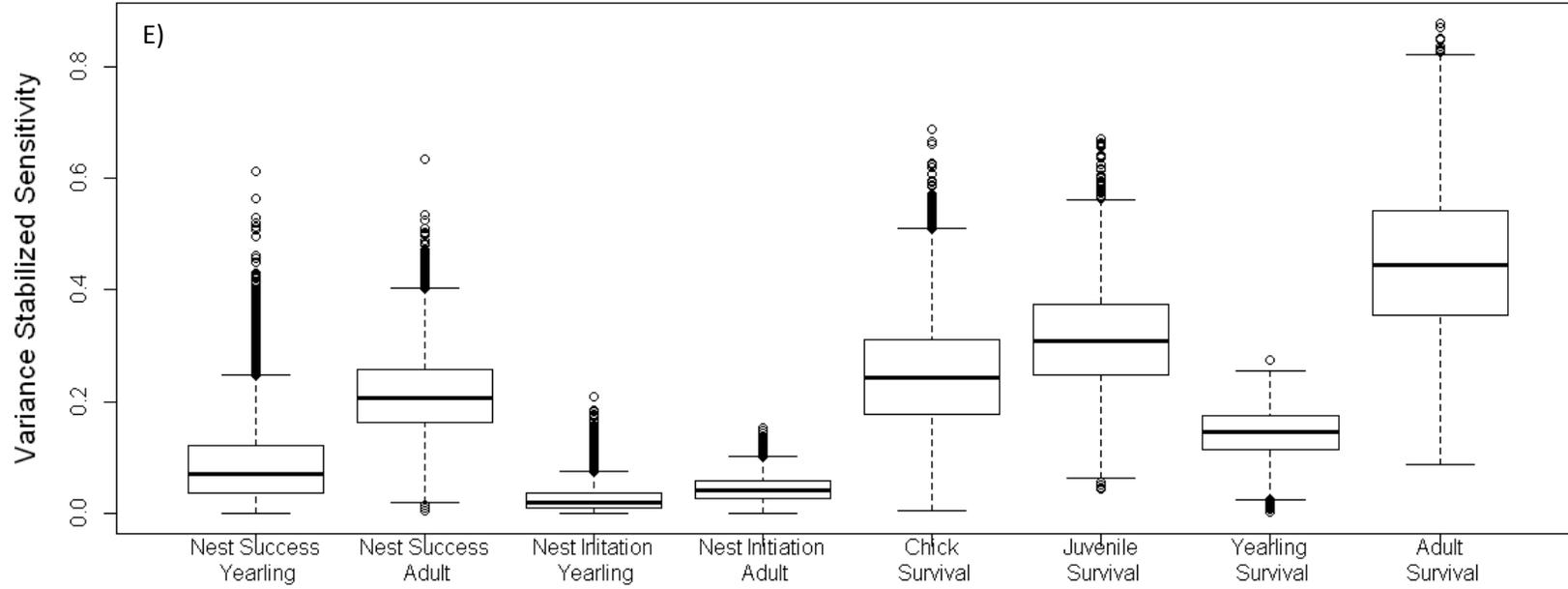
**APPENDIX 4.C.** Distribution of observed population growth rates (densities) for Gunnison Sage-grouse from vital rates simulated with and without correlation.



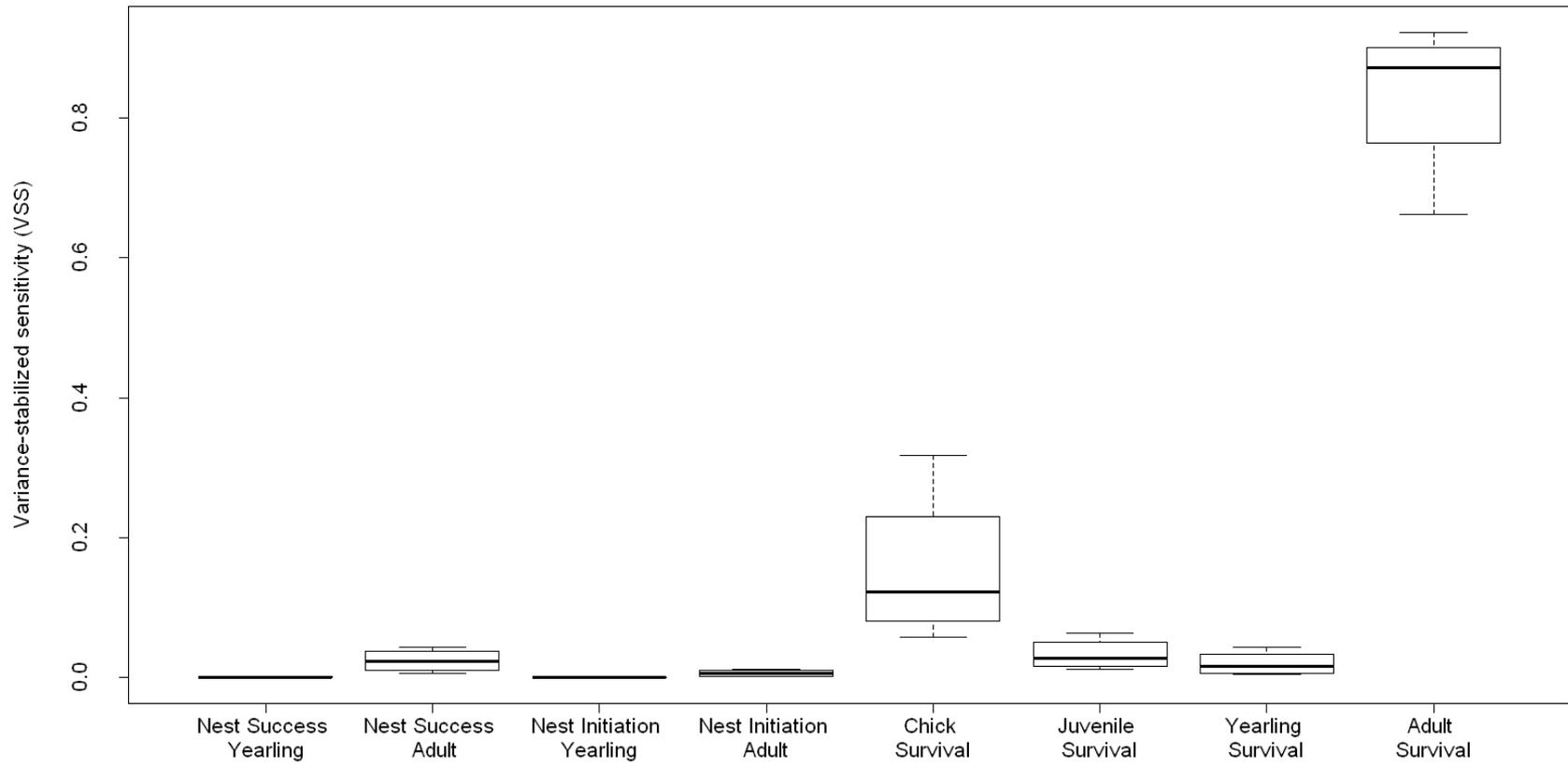
**APPENDIX 4.D.** Sensitivities (A) and elasticities (B) for simulated vital rates with correlations for Gunnison Sage-grouse, and sensitivity (C), elasticity (D), and variance-stabilized sensitivity (E) for vital rates simulated without correlation.



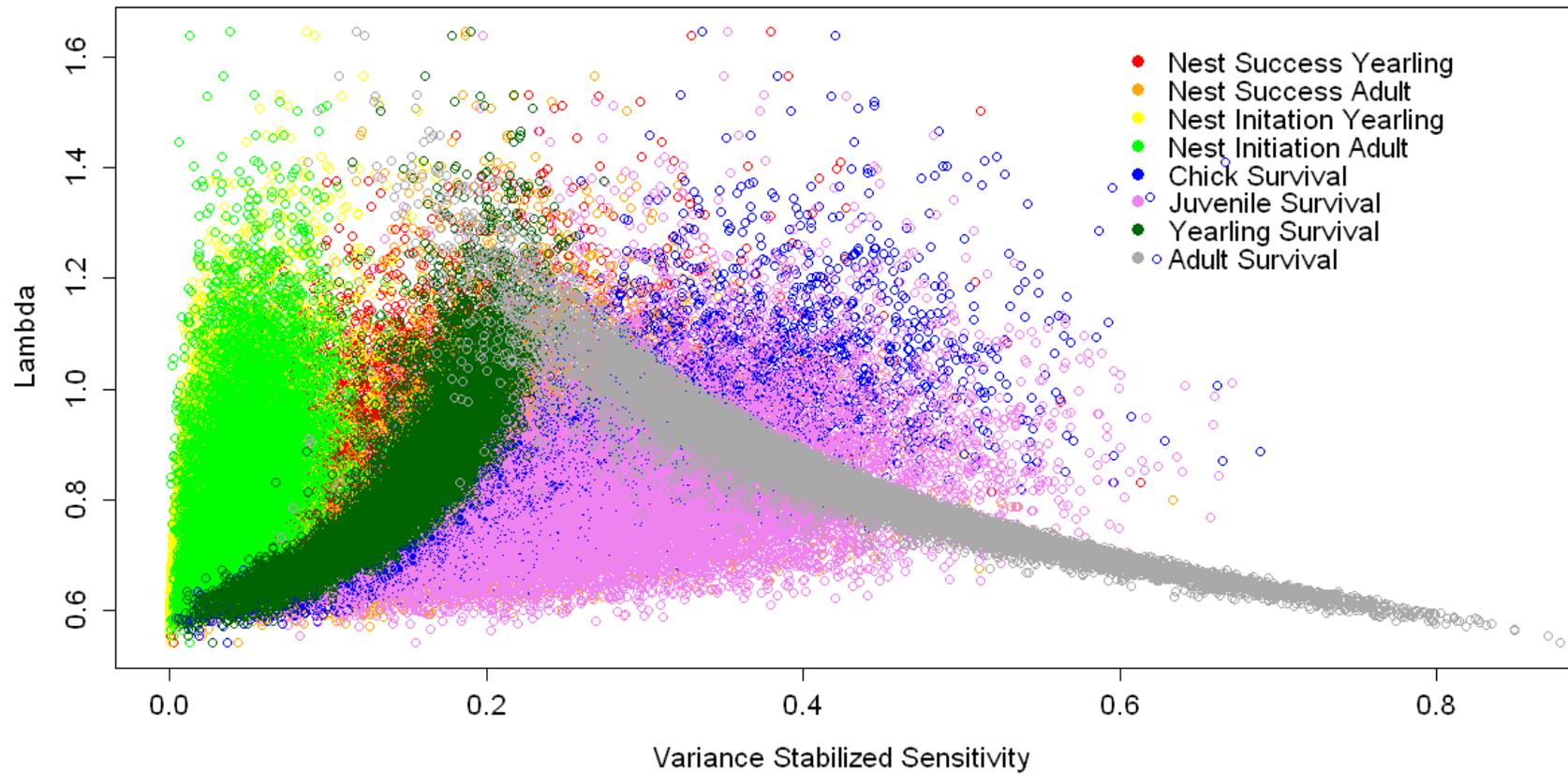




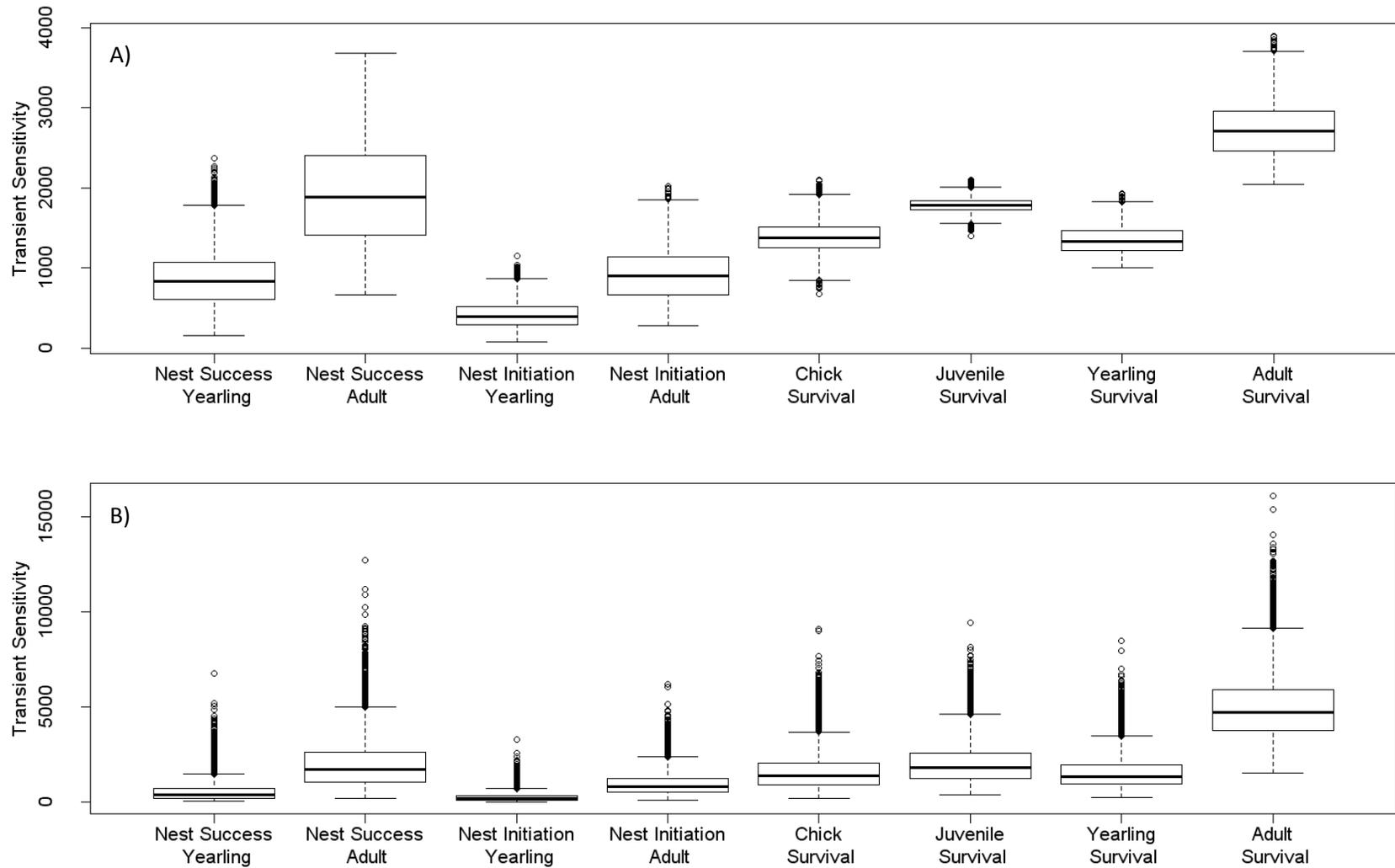
**APPENDIX 4.E.** Box plots of variance-stabilized sensitivities for each vital rate from the four years of data from the San Miguel population of the Gunnison Sage-grouse.



**APPENDIX 4.F.** Relationship between variance stabilized sensitivity and population growth rate by vital rate for simulated data without correlation for Gunnison Sage-grouse.



**APPENDIX 4.G.** Box plots of transient sensitivities for 10,000 simulations of Gunnison Sage-grouse vital rates for A) 1 year and B) 5 year time frames.



## CHAPTER 5

### AN INTEGRATED MODELING APPROACH TO ESTIMATING GUNNISON SAGE-GROUSE POPULATION DYNAMICS: COMBINING INDEX AND DEMOGRAPHIC DATA

Evaluation of population dynamics for rare and declining species is often limited to data that are sparse and/or of poor quality. Frequently the best data available for rare bird species are based on large-scale, population count data (e.g., Breeding Bird Survey, Christmas Bird Count, etc.). These data are commonly based on sampling methods that lack consistent sampling effort, do not accounting for detectability, and are complicated by observer bias. For some species short-term studies of demographic rates have been conducted as well, but the data from such studies are typically analyzed separately. To utilize the strengths, and minimize the weaknesses of these two data types, I developed a Bayesian integrated model that innovatively links population count data and population demographic data through population growth rate ( $\lambda$ ) for Gunnison Sage-grouse (*Centrocercus minimus*). The long-term population index data available for Gunnison Sage-grouse are annual (1953-2011) male lek counts. An intensive demographic study was also conducted from 2005-2010. I was able to reduce the variability in expected population growth rates across time, while correcting for potential small sample size bias in the demographic data. I found the population of Gunnison Sage-grouse to be slightly declining over the past 16 years ( $\lambda = 0.94$ , 95% CI 0.90,1.00). However, it is important to keep in mind that these results are preliminary as this methodology is novel and has not been fully vetted.

#### INTRODUCTION

Information is frequently sparse for rare and declining species (Beissinger and McCullough 2002) and is of poor quality or has little inferential value (Engler et al. 2004, McKelvey et al. 2008). For bird species many population survey methods exist that are wide ranging but their utility is disputed [e.g., Breeding Bird Survey (Sauer et al. 1994, Link and Sauer 1998), Christmas Bird Count (Link et al. 2006), aerial

surveys (Caughley 1974, Bromley et al. 1995), and lek counts (Walsh et al. 2004)]. However, for many species the most extensive information available is from these types of surveys (Sauer et al. 1994). Therefore a strong motivation to make the most of this type of data exists. However, short term demographic studies may also take place. These data are typically analyzed separately from long-term monitoring data, but uncertainty and possible bias can exist in these analyses especially if the sample size is small (Doak et al. 2005). Recent work has focused on using intensive, short-term demographic data to bolster information inherent in long-running, indices data (e.g., Catchpole et al. 1998, Abadi et al. 2010b). This integrated modeling approach has been used on many bird species (Catchpole et al. 1998, Besbeas et al. 2002, Brooks et al. 2004, Gauthier et al. 2007, Abadi et al. 2010b) and several mammal species including bats (Schaub et al. 2007), seals (Besbeas et al. 2005, Thomas et al. 2005), and kangaroos (Chee and Wintle 2010). Previous research focused on using different types of survey data in integrated models including: breeding bird surveys (Besbeas et al. 2002, Besbeas et al. 2003, Brooks et al. 2004), line transects (Chee and Wintle 2010), bat roost surveys (Schaub et al. 2007), and aerial surveys (Gauthier et al. 2007). Demographic data that have been combined with such survey data in integrated models include capture-recapture data (Gauthier et al. 2007, Schaub et al. 2007, Abadi et al. 2010a, Abadi et al. 2010b), ring-recovery data (Besbeas et al. 2002, Besbeas et al. 2003, Brooks et al. 2004), and reproductive success data (Schaub et al. 2007, Abadi et al. 2010b). Integrated modeling has been used to improve demographic and population parameter estimates (Brooks et al. 2004, Schaub et al. 2007, Abadi et al. 2010a), evaluate population projections (Besbeas et al. 2002, Besbeas et al. 2005), estimate immigration rates (Abadi et al. 2010b, Schaub et al. 2012), and evaluate the effects of culling on population size (Chee and Wintle 2010).

Improving population estimates and evaluating population projections are two primary motivations for applying integrated population modeling to Gunnison Sage-grouse (*Centrocercus minimus*, GUSG) data. GUSG were recognized as distinct from the Greater Sage-grouse (*Centrocercus urophasianus*, GRSG) in 2000 (American Ornithological Union 2000, Young et al. 2000a). GUSG have declined substantially

from their historic numbers and range (Schroeder et al. 2004) and are a candidate species under the U.S. Endangered Species Act (United States Fish and Wildlife Service 2010). I evaluated GUSG demographic rates using capture-recapture methods in Chapters 1-3. Population projections (Chapter 4) for this species suggest the population is currently declining; however the demographic data that produced this projection is based on a relatively small time frame of only six years.

Previous work on integrated modeling has combined data types similar to the data available for the GUSG (capture-recapture data and count data). However, the method that has so far been used for these analyses is to combine the matrix demographic data directly into a state space model that computes the population size at each time step. This method assumes a near one-to-one relationship between the data sources, but allows for estimation or sampling error between the projections. I developed a novel methodology that relaxes the relationship assumption by linking the two data sources through a derived parameter ( $\lambda$  – population growth). Additionally, I assume there is a relationship between the derived parameters but that the relationship is not necessarily one-to-one, and I am able to model that relationship; which adds flexibility to the technique.

Despite not being recognized as its own species until 2000, long-running population indices data (i.e., lek counts) have been collected on GUSG since 1953 (Colorado Division of Parks and Wildlife, CPW, unpublished data). Like many grouse species, the GUSG are a lekking species; males congregate on flat tracts of land to strut and display for breeding opportunities with females. Counting males on leks provides a reliable opportunity to survey this typically elusive species (Rogers 1964). Although over 60 years of lek count data are available on GUSG the utility of these data as a population indicator is questionable (Emmons and Braun 1984, Connelly 2003, Walsh et al. 2004). Some of the main concerns with lek count data come from the lack of standardization of protocol for many studies, lack of consistency between number of leks counted per year, the high level of within-year variation in lek count data (which may lead to large variance and potential bias), and the lack of accounting for detectability (Walsh et al. 2004).

The goal of my study is to, for GUSG, formally integrate the long-time series of index data (i.e., lek counts) with a short term, but statistically rigorous demographic data. I propose to integrate these two data types in a novel way by linking them through a common derived parameter (population growth rate,  $\lambda$ ). Through the use of this parameter I evaluate the relationship between these different types of data and I estimate patterns of population growth rate for this species of concern over time.

## **METHODS**

### **Data**

The two data types that have been collected on GUSG are population demographic data collected using mark-recapture and radio telemetry methods and population survey data on high male counts on leks. Demographic rates for GUSG were calculated from data collected in two of seven isolated populations: Gunnison Basin (GB) and San Miguel (SM) from 2005-2010. For this chapter I am only using the data specific to the GB population. Over 85% of the existing individuals are thought to be in the GB population in Gunnison and Sagauche Counties, Colorado, USA. Demographic estimates of reproduction for both yearling and adult females come from Chapter 1, and estimates of survival for both yearling and adult males and females are from Chapters 2&3 (Appendix 5.A). The mean and naïve estimates of process variance for each vital rate were calculated in Chapter 4. Covariance between the vital rates was also calculated in Chapter 4 (Appendix 5.B).

Population survey data used in this analysis come from lek counts in Gunnison Basin, Gunnison County, Colorado from 1953-2011 (Figure 5.1). Lek count data were missing for two years (1956 and 1975). For these years I used the average lek count (494) because missing data are not easily handled with these analysis methods and the average should be the least influential possible value. Most of the lek count data available are not by individual leks but by lek areas (a collection of leks in relatively close proximity to each other, the method of defining a lek area is subjective). The number of lek areas surveyed over

time has changed, generally increased (Figure 5.1). The protocol for conducting lek counts was standardized in 1996, before that there is considerable uncertainty about number of individual leks surveyed, how often leks were surveyed, when and how counts were conducted (Gunnison Sage-grouse Rangewide Steering Committee 2005), this is reflected in the variability in lek count data before 1996 (Figure 5.1). Therefore, I first ran the integrated model over the time period from 1996-2011. After fitting that model I fit the model to the entire data set (1953-2011) to evaluate the methodology under more, highly variable data.

### **Integrated population model**

The survival and reproduction data are population demographic data (Appendix 5.A). When the demographic data are arranged in a Leslie-type population matrix (equation 1), population projections can be evaluated and vital rate sensitivities can be calculated (Caswell 2000, 2001). The population growth rate is calculated as the dominant eigenvalue from Leslie matrices (Caswell 2001).

The index lek count data are an indicator of population size (Figure 5.1) and population growth rate can be estimated as  $M_{t+1}/M_t$ , (where  $M_t$  is the high male count at time  $t$ ). Thus, the population metric that both data types can estimate is the population growth rate ( $\lambda$ ). The relationships between the data types are shown in Figure 5.2.

The core of this integrated model is a Malthusian growth model on the lek count data ( $M_t$ , Malthus 1798, Savage et al. 2004). The Malthusian growth model estimates the rate of population change ( $\lambda$ ) based on the lek count data (equations 2, 3, and 4). The population growth rate ( $\lambda$ ) is assumed to be log-normally distributed (equations 4 and 5). I used the conjugate priors for the mean ( $\mu_r$ ) and variance ( $\sigma_r^2$ ) of the log normal distribution (equations 6 and 7). I related the growth rate values from the lek count data ( $\lambda_t^c$ ) to the growth rate data from the demographic data ( $\lambda_t^d$ ), through a normal distribution (equation 8 and 9), with a conjugate prior of Inverse Gamma on the variance ( $\sigma_\lambda^2$ , equation 10). I assumed a linear relationship between the two growth rates (equation 9). To account for a potential bias between the two

growth rates I modeled the intercept parameters in the linear equation ( $a_0$ ) as a normally distributed centered at zero (equation 11). The lek count data are male-based; the population matrix model is female-based. Therefore the growth rates may not be related directly in a one-to-one relationship. To estimate this possible difference I modeled the slope parameter in the linear equation with a normal distribution centered at 1 (equation 12). The benefit of this model formulation is that it directly relates the two data types in the one common parameter ( $\lambda$ ).

$$\begin{bmatrix} N_{yf} \\ N_{ym} \\ N_{af} \\ N_{am} \end{bmatrix}_t = \begin{bmatrix} F_y & 0 & F_a & 0 \\ F_y & 0 & F_a & 0 \\ P_{yf} & 0 & P_{af} & 0 \\ 0 & P_{ym} & 0 & P_{am} \end{bmatrix}_t * \begin{bmatrix} N_{yf} \\ N_{ym} \\ N_{af} \\ N_{am} \end{bmatrix}_{t-1} \quad (1)$$

Population survey data	Data	[	$M_t \sim \text{Poisson}(\varphi_t), \quad t = 2, \dots, T$	(2)
		]	$\log(\varphi_t) = \theta_t + \log(M_{t-1})$	(3)
			$\theta_t = \log(\lambda_t^c)$	(4)
	Process	[	$\theta_t \sim \text{Normal}(\mu_r, \sigma_r^2)$	(5)
		]	$\mu_r \sim \text{Normal}(\mu_\mu, \sigma_\mu^2)$	(6)
	Parameters	[	$\sigma_r^2 \sim \text{Inverse Gamma}(\gamma_1, \gamma_2)$	(7)
		]		

$$\begin{array}{l}
\text{Demographic data} \left\{ \begin{array}{l}
\text{Data} \quad \left[ \hat{\theta}_t = \log(\lambda_t^d) \right. \quad (8) \\
\text{Process} \left[ \hat{\theta}_t \sim \text{Normal}(a_0 + b_0 * \theta_t, \sigma_\lambda^2) \right. \quad (9) \\
\quad \quad \quad \sigma_\lambda^2 \sim \text{Inverse Gamma}(r, q) \quad (10) \\
\text{Parameters} \left\{ \begin{array}{l}
a_0 \sim \text{Normal}(0, \sigma_a^2) \quad (11) \\
b_0 \sim \text{Normal}(0, \sigma_b^2) \quad (12)
\end{array} \right.
\end{array} \right.
\end{array}$$

In order to obtain population estimates, I used a state-space model to calculate the population size at each time step, by using Leslie transition matrices (equation 13). However, I only had demographic data available from 2005-2010. Therefore in order to populate the state-space model for the rest of the timeline, I created 10,000 sets of simulated vital rates from a logit transformation of a multivariate normal distribution to allow for covariance between the vital rates (note that the clutch size is not bounded between zero and one and a stretched beta distribution was used for its simulation, methods described in Chapter 4). The corresponding growth rate ( $\lambda$ ) values were calculated for each set of simulated vital rates. I matched estimated  $\lambda$  values at each time step from the integrated model to  $\lambda$  values from simulated vital rate values. Thus, when demographic data were not available I selected the set of vital rates that most closely corresponded to the  $\lambda$  from the posterior distribution of the integrated model. The population projections rely on an initial population size ( $M_0$ , equation 14). I used a Poisson distribution for the prior of this parameter.

The six years of data upon which the demographic estimates are based was a period of decline (based on both the demographic estimates themselves and the lek count data, Figure 5.1). Based on the lek count data the range of growth rates is likely greater than that created from simulating data based on these six years of data (Figure 5.3). Therefore the  $\lambda$  matching strategy I used to calculate population sizes is likely to be biased low because the simulated vital rates do not experience growth rates as high as the lek count data suggest. In order to adjust for this, yet still maintain the correlation structure for the simulated vital rates, I multiplied the covariance structure by a constant to increase the range of growth rates that can be achieved by this simulation method. The covariance matrix needed to be multiplied by 50 in order to get close to the range of growth rates presented in the entire lek count data (Figure 5.3). This inflation factor is exceptionally large in part due to the fact the mean value for the growth rates based on the demographic data (0.89) is much lower than the mean value for the lek count data (1.11). The growth rates for the lek count from 1996-2011 are not as wide ranging but still needed an inflation factor of 20x the covariance structure to have the same range of growth rates.

Previous research on sage-grouse species has found that typically between 42% and 67% of males are on a lek at the high count (Walsh et al. 2004, Gunnison Sage-grouse Rangewide Steering Committee 2005). Additionally, studies suggest that there is a 1.6:1 female to male ratio for sage-grouse (CPW unpublished report, Gunnison Sage-grouse Rangewide Steering Committee 2005). For the model fit to the 1996-2011 data, I used the average lek count from 1996-2011 (725) multiplied by the population correction factor (2.96) to get an estimate of the mean for the Poisson distribution for the initial population size (2146). For the model fit to the entire data series, I used the average lek count (494) multiplied to the correction factor to get an estimate for the Poisson distribution of 1462.

$$\underline{N}_t = L_t * \underline{N}_t \quad (13)$$

$$M_o \sim \text{Poisson} (\beta_o) \quad (14)$$

The formulation of this model inherently puts more emphasis on the lek count growth rate data than the demographic data because it draws more information from the long time series. This results in possibly strong bias during the time period where demographic data are available. In order to find a balance between this bias and the variance estimated around the lek count growth rates, I ran the integrated model for different levels of variance around the demographic growth rate estimates ( $\sigma_\lambda^2$ ). I fixed this value between 0.005 (near zero) and 0.125 (near estimated  $\sigma_\lambda^2$  value, Table 5.1), running the model for 50 evenly spaced intervals in that range. I calculated the bias as the quantity of demographic data growth rates that were outside the 95% credible intervals. I plotted the bias versus the resulting variance around the lek count growth rates ( $\sigma_\lambda^2$ ) to determine the best balance between them. I used this balanced estimate to make inference about the pattern of growth rates for GUSG.

Since this is a new methodology and the posterior mean is sensitive to the choice of  $\sigma_\lambda^2$ , I plotted the posterior mean and 95% credible intervals for all values of  $\sigma_\lambda^2$  that I examined (ranging from 0.005 – 0.125). This allowed me to determine how influential the choice of  $\sigma_\lambda^2$  is on the posterior means.

The prior values I selected were chosen to be relatively flat and uninformative (Table 5.2). To calculate the posterior distributions of the parameters of interest, I ran the integrated model using a MCMC algorithm written in Program R (version 2.15, R Development Core Team 2012, code in Appendix 5.C). Diagnostic plots suggest that convergence occurred within 500 iterations for most parameters. I ran 20,000 iterations of the MCMC algorithm and discarded the first 2,000 iterations as burn in.

## **RESULTS**

The relationship between the growth rate from the demographic data and the lek count data was calculated by a linear relationship on the log of the growth rates (equation 9). The growth rates from the

demographic data are generally lower than those from the lek count data ( $a_0 = -0.51$ , 95% CI: -0.70, -0.25, Table 5.1). The slope parameter estimate of 0.03 suggests the growth rates are not identical (95% CI: -0.27, 0.30, Table 5.1 and Appendix 5.F). Additionally, the slope suggests that the higher the growth rate from the lek count data, the larger the disparity between the two. This relationship is supported by range of possible growth rates observed from simulation of vital rates.

The posterior estimates of the variance for the distribution that relates the lek count and demographic growth rates ( $\sigma_\lambda^2$ , equations 9 and 10) was 0.0121 (95% CI 0.041, 0.289, Table 5.1). This estimate is biased high based on the model formulation drawing more information from the lek count data than the demographic data. Therefore, I used it as the upper bound and a value near zero as the lower bound to evaluate the trade-off between bias and variance in the integrated model (Figure 5.4). The plot of this trade-off (Figure 5.5) shows a balance around 0.018.

I plotted the posterior mean and 95% credible intervals for all values of  $\sigma_\lambda^2$  that I examined (ranging from 0.005 – 0.125) in order to evaluate the sensitivity of the posterior to different values of  $\sigma_\lambda^2$ . The plot shows a curve that has a minimum around 0.018, the estimate that balances the variance and bias in the model (Figure 5.6). Therefore, the use of this estimate gives the lower bound for population growth. If I place the most confidence on the demographic data (fix  $\sigma_\lambda^2$  to 0.005) the estimate of population growth is 0.96 (95% CI 0.91, 1.02). If I place more confidence in the lek count data (fix  $\sigma_\lambda^2$  to 0.125) the estimate of population growth is 1.01 (95% CI 0.97, 1.05).

By fixing  $\sigma_\lambda^2$  at 0.018, I calculated that the posterior estimates for the annual population growth parameters varied between 0.83-1.04, with a mean of 0.94 (Figure 5.4) from the model on the 1996-2011 data. These estimates are shrunk considerably from the estimates of growth rate from the lek count data (0.79-1.92), and the average lek count growth rate is slightly positive (1.04). The posterior growth rates range is also narrower than the growth rates from the demographic data (0.65-1.14). The posterior mean

for  $\lambda$  is considerably higher than the mean from the demographic data (0.89). Diagnostic plots for a sample of growth rate values and prior parameters are shown in Appendices D, E, and F.

The lek count data are not only used as a population indicator, but also often used as a population estimator based on adjusting for the number of males assumed to be on leks and then adjusting based on the expected ratio of males to females. I compared the population projections based on the integrated model with the population estimation from the lek count data in Figure 5.7.

I ran the same integrated model on the entire time series (1953-2011) with the same prior values (Table 5.2). The estimated values for the parameters of the integrated model were similar in all cases between the partial data series (1996-2011) and the entire series (1953-2011) except for the variance of the growth rate parameter ( $s_{2,r}$  or  $\sigma_r^2$ , equation 5). The estimated variance is 10x larger for the entire data set (mean = 0.14, 95% CI: 0.10, 0.22). The estimated population growth rate values mimic the lek count growth rates nearly perfectly (Figure 5.8). This suggests the model is over fitting the data. There appears to be too much variability in the entire data set to be able to extract any meaningful results.

## **DISCUSSION**

A primary goal of my study was to evaluate the relationship between the two sources of data available for GUSG: demographic estimates of fecundity and survival, and population survey estimates from long-term lek count data. A unique challenge of this integration is that the two types of data are typically not used to estimate any parameters in common. The one parameter in common between the data types is an estimate of population growth. The dominant eigenvalue from Leslie matrices is generally considered to be an estimate of population growth (Caswell 2001). Additionally the rate of population change from one time step to another ( $M_{t+1}/M_t$ ) is another method that estimates population growth; this method is applicable to population count data like that of the lek counts from my study (Link and Sauer 2002, Sauer and Link 2002).

Although these different estimators of growth rate come from different techniques they are commonly accepted as estimating the population growth ( $\lambda$ ).  $\lambda$  from matrix calculations are generally thought to be asymptotic growth rates (the growth rate achieved when the population has reached a stable state, Caswell 2001). These are not exactly the same as the single time step growth rates ( $M_{t+1}/M_t$ ). However, the matrix growth rates are calculated every year. Therefore I am linking the expected asymptotic growth rate based on one year's data with the single time step growth rate for that same year. However, I recognize that the growth rates may not be directly related, especially given that the demographic data are based on a female driven model and the population count data is only of males. Therefore, I estimated a linear relationship between the log of the growth rates (equation 9). This evaluation, based on the more reliable 1996-2011 time series, suggests that lek count estimates of population growth are typically biased high and exhibit extreme high values that are not realistic based on demographic analysis. Dahlgren (2009) similarly found that lek count estimates of population growth are routinely higher than estimates from population modeling.

Each of the types of data available for GUSG has their strengths and weaknesses. The lek count data are long running and relatively inexpensive to collect as they depend heavily on volunteer support, which also leads to community involvement and awareness (Bell et al. 2008). However, long term data and volunteer collected data come with numerous drawbacks. Long-term data can be difficult to manage over time, especially with frequent turnover of people in charge of the data set and transitions from different data management techniques over the past 60 years (comments from people in charge of lek count data at CPW). Additionally there are drawbacks of using volunteers to collect data as observers vary greatly in their ability to detect birds (Sauer et al. 1994). These problems lead to large variability and high uncertainty in the data.

The population growth rates exhibited by the lek count data varied wildly (max  $\lambda$  near 2), and the range was much greater than is typically seen in growth rate estimations from Leslie matrix calculations for sage-grouse species (Dahlgren 2009, Taylor et al. 2012). Lek count information is known to be variable

and its utility has been questioned based on the fact that lek counts are known to vary considerably within a year (Colorado Sage Grouse Working Group 1997, Connelly 2003, Walsh et al. 2004), detectability is not accounted for (Walsh et al. 2004, Walsh et al. 2010), potential problems with observer bias may exist (Walsh et al. 2004), survey effort may not be consistent among years and/or spatial variability may be present (Connelly 2003, Broms et al. 2010). The lek count data have potential as a population indicator but the extreme values and high variability suggest that caution should be used when drawing conclusions solely from this data. Through the use of this integrated model, the estimated population growth rates should be less extreme and converge closer to the mean for the growth rates (equation 5). My study shows the ability for this type of modeling to achieve more precise estimates by combining the data sources (Figure 5.4).

The demographic data (Chapters 1-3), are intensive and statistically rigorous, but only span a small time series (2005-2011). Therefore, there is a potential for bias in estimations of population viability that are based on a small sample size (Doak et al. 2005). Population projection models based on these demographic data (Chapter 4) suggest that the GUSG are declining, and are declining rapidly (expected extinction time of 58 years, Chapter 4). Both the demographic data and the lek count data suggest the grouse are experiencing a decline in the Gunnison Basin over the 6 years of the demographic study (Figure 5.1). However, lek count data extend farther back in time than the demographic estimates and show that the population exhibited a considerable increase just prior to the demographic study being initiated (Figure 5.1). The integrated model should enable the evaluation of population growth based on a larger time series to help avoid misleading results from the small time series. My study shows a decreasing population growth for GUSG ( $\bar{\lambda} = 0.94$ , 95% CI 0.90,1.00) based on the past 16 years of data. Additionally, the 6 years of the demographic study are lower, on average, than the rest of the 16 year time series (Figure 5.4). This may support the theory that the population is in a declining trend that is more pronounced than in the rest of the time series.

The posterior growth rate estimate of 0.94 is derived from fixing  $\sigma_\lambda^2$  in order to balance the bias and variance ( $\sigma_r^2$ ) in the integrated model. I am aware that the posterior estimate is sensitive to the choice of this fixed value. Therefore I compared how the posterior growth rate changed as  $\sigma_\lambda^2$  changed (Figure 5.6). Unless I am willing to except a high level of bias (Figure 5.5), the estimate shows the population has declined ( $\lambda < 1$ , Figure 5.6). Since the demographic data are more rigorously collected than the lek count data, a high level of bias is probably not defensible.

Another objective of my study was to evaluate the population size estimates and projections over time under the integrated modeling approach. According to the evaluation of the population growth rate over the past 16 years one would expect a population that declines slightly over time. The projections show a population that fluctuates over time, and shows the most recent 6 years are exhibiting a decline in the population (Figure 5.7). This is contrary to the projections based solely on the demographic data (Chapter 4). A key aspect to this analysis was to help eliminate potential bias in the shorter time series. These results suggest that the population, on average, is relatively stable over the past 16 years, but the end of the time series shows a slight decline. I note that I did not include a parameter that could include a time trend in population growth. The method, as I applied it, seeks to find a mean and variance from which population growth rates are realized. Forcing this average to be stable over time might be shrinking the growth rates too much towards the mean to prevent a trend from being detected. However, in the framework I chose, by fixing the variance for equation 9, I was able to detect a change in population growth in the time series, which is a primary goal of this study. I do feel that the inclusion of a trend parameter on population growth would be beneficial and is recommended for future work.

I attempted to fit the model to the entire time series (1953-2011). However, the high level of variability in the data prevented the model from converging to a single population growth rate. The posterior growth rate estimates match the lek count growth rates almost exactly (Figure 5.8). There are many factors that contribute to this variability (described above). An additional source of variation in the entire time series that is minimized in the 1996-2011 time series is the number of leks (more specifically lek areas) counted

per year. The total number of leks counted each year has not been consistently recorded for Gunnison Basin. Instead the number of lek areas has been counted, this involves grouping individual leks that are in close proximity to each other (Colorado Sage Grouse Working Group 1997). There was a sharp increase in lek areas counted in 1996, when the protocol for lek counts was standardized in the Gunnison Basin (Colorado Sage Grouse Working Group 1997, Gunnison Sage-grouse Rangewide Steering Committee 2005). Therefore the variation in the lek counts might reflect a change in survey effort and not a change in population size. Although this integrated modeling technique shows promise to make use of statistically weak count data, it is not capable of making bad data good. When the data have as many issues as the historic lek count data do, no statistical method is going to fix them. All attempts should be made to standardize these data (e.g., with respect to sampling effort) before any conclusions can be drawn.

Integrated modeling is a powerful and flexible statistical tool that can be adapted to many different scenarios. The advantage of integrated modeling for many wildlife studies is that it allows for the combination of different data types; by drawing strength from more rigorous studies and adding longevity to sparse data (Besbeas et al. 2002). This is particularly advantageous for rare or declining species in which there is often a paucity of data. My study demonstrates a novel method that allows for two data types to be formally linked through a derived parameter in a statistically rigorous manner. This is an increase in the flexibility currently demonstrated in the literature for Bayesian integrated population models. Additionally, being able to estimate the relationship between these parameters directly in the integrated model adds versatility that could have wide applications in wildlife data analysis. My integrated model draws from the strengths of two different data sets to help estimate population growth for GUSG. These estimates are a reduction in the high variability present in the count data and corrected for potential small sample size bias in the demographic data (Figure 5.4) and is an improvement over the independent analysis of each data set. However, it is important to note that these are novel methods and

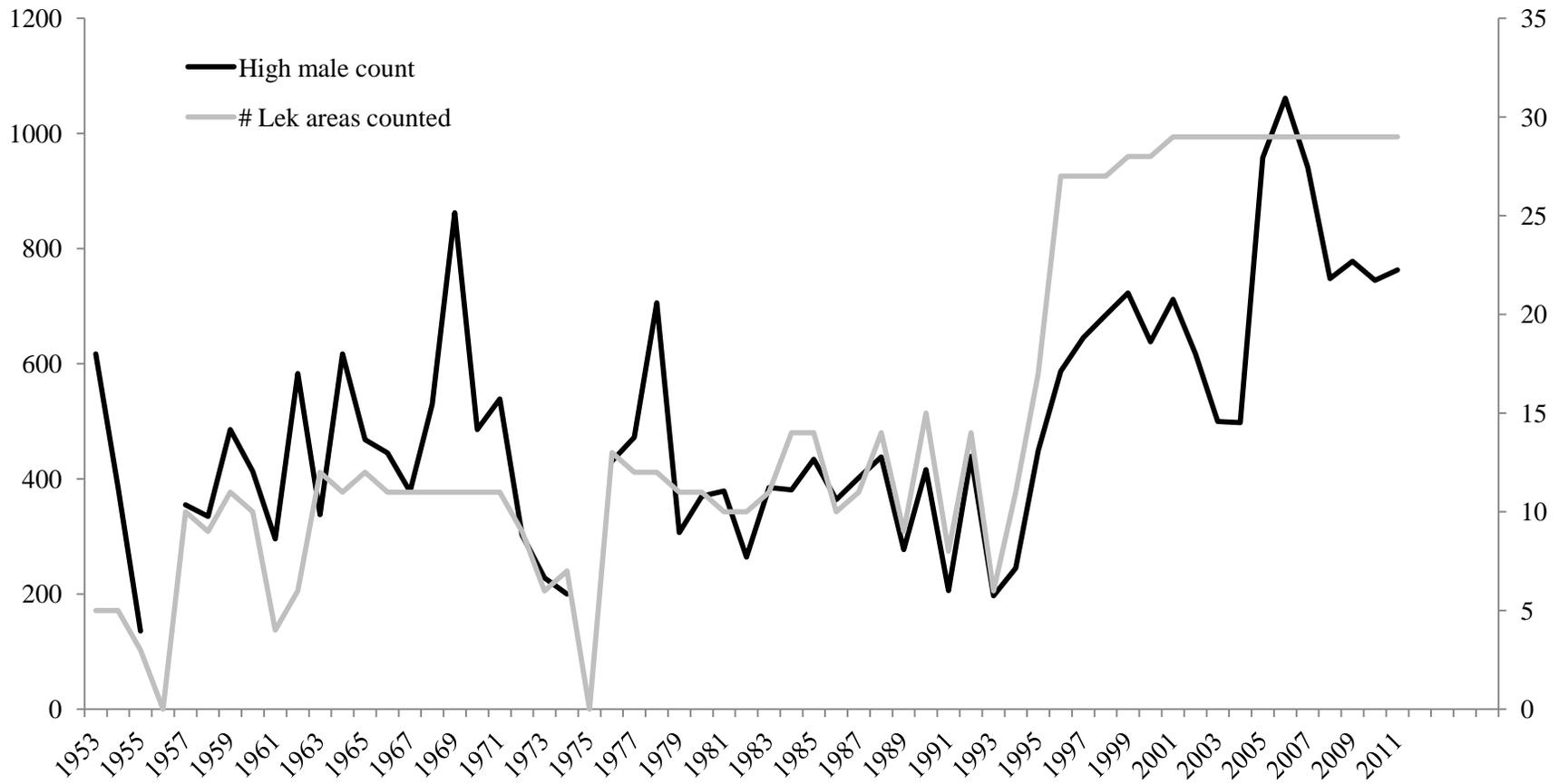
they have yet to been fully vetted. The methodology shows promise, but until more work is done it is important to view these results as preliminary.

**Table 5.1.** Posterior means and 95% credible intervals for parameter values from the integrated model for Gunnison Sage-grouse in Gunnison Basin, Colorado.

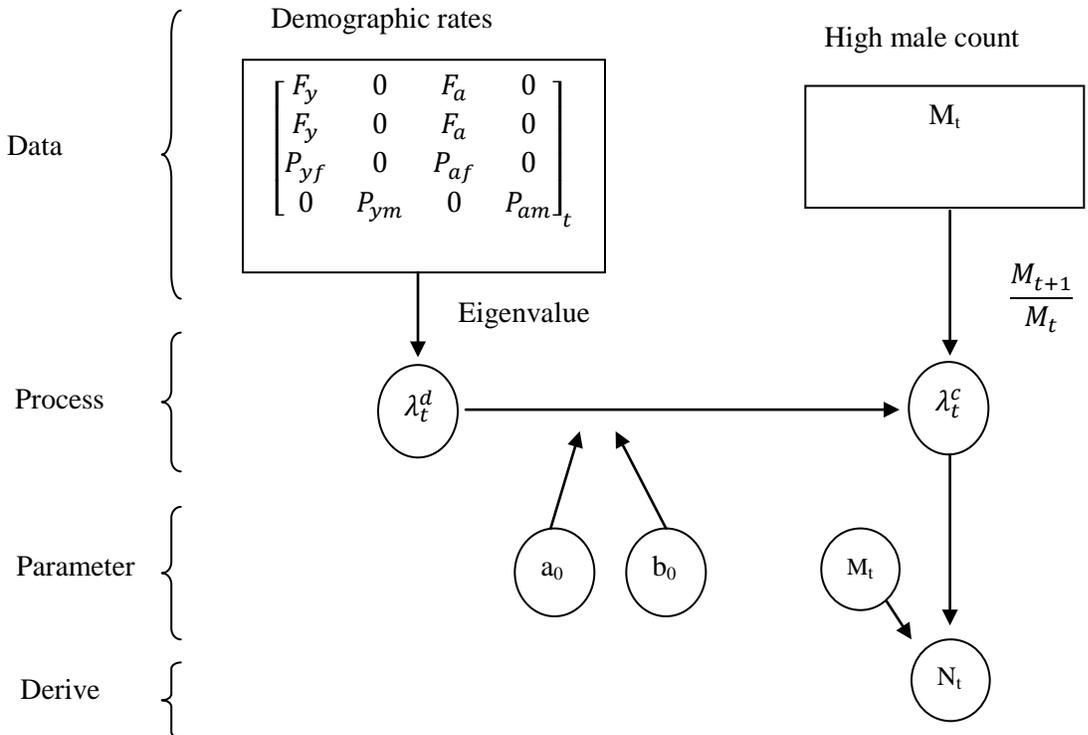
Parameter	Description	Posterior Mean	Posterior 95% Credible Interval	
			Lower	Upper
$\mu_r$	Mean parameter for the $\lambda$ from the lek count data	0.018	-0.007	0.044
$\sigma_r^2$	Variance parameter of the $\lambda$ values from the lek count data	0.013	0.006	0.025
$\sigma_\lambda^2$	Variance parameter of the $\lambda$ values from the demographic data	0.121	0.041	0.289
$a_0$	Log difference between $\lambda$ from lek count data and $\lambda$ from demographic data	-0.51	-0.702	-0.247
$b_0$	Log of the slope of the difference between $\lambda$ from lek count data and $\lambda$ from demographic data	0.029	-0.268	0.302

**Table 5.2.** Prior values used in the integrated model on Gunnison Sage-grouse.

<b>Prior is for the distribution of:</b>	<b>Prior parameter</b>	<b>Value used for 1996-2011 data set</b>	<b>Description</b>
$\mu_r$	$\mu_\mu$	0.02	Mean for the mean distribution of $\log(\lambda)$
	$\sigma_\mu^2$	0.50	Variance for the mean distribution of $\log(\lambda)$
$\sigma_r^2$	$\gamma_1$	9.90	Shape parameter for the distribution of the variance of $\log(\lambda)$
	$\gamma_2$	2.01	Scale parameter for the distribution of the variance of $\log(\lambda)$
$\sigma_\lambda^2$	r	5.00	Shape parameter for the variance between the two $\lambda$ s
	q	5.00	Scale parameter for the variance between the two $\lambda$ s
$a_0$	$\sigma_a^2$	10	Variance for the intercept parameter relating the two $\lambda$ s
$b_0$	$\sigma_b^2$	10	Variance for the slope parameter relating the two $\lambda$ s

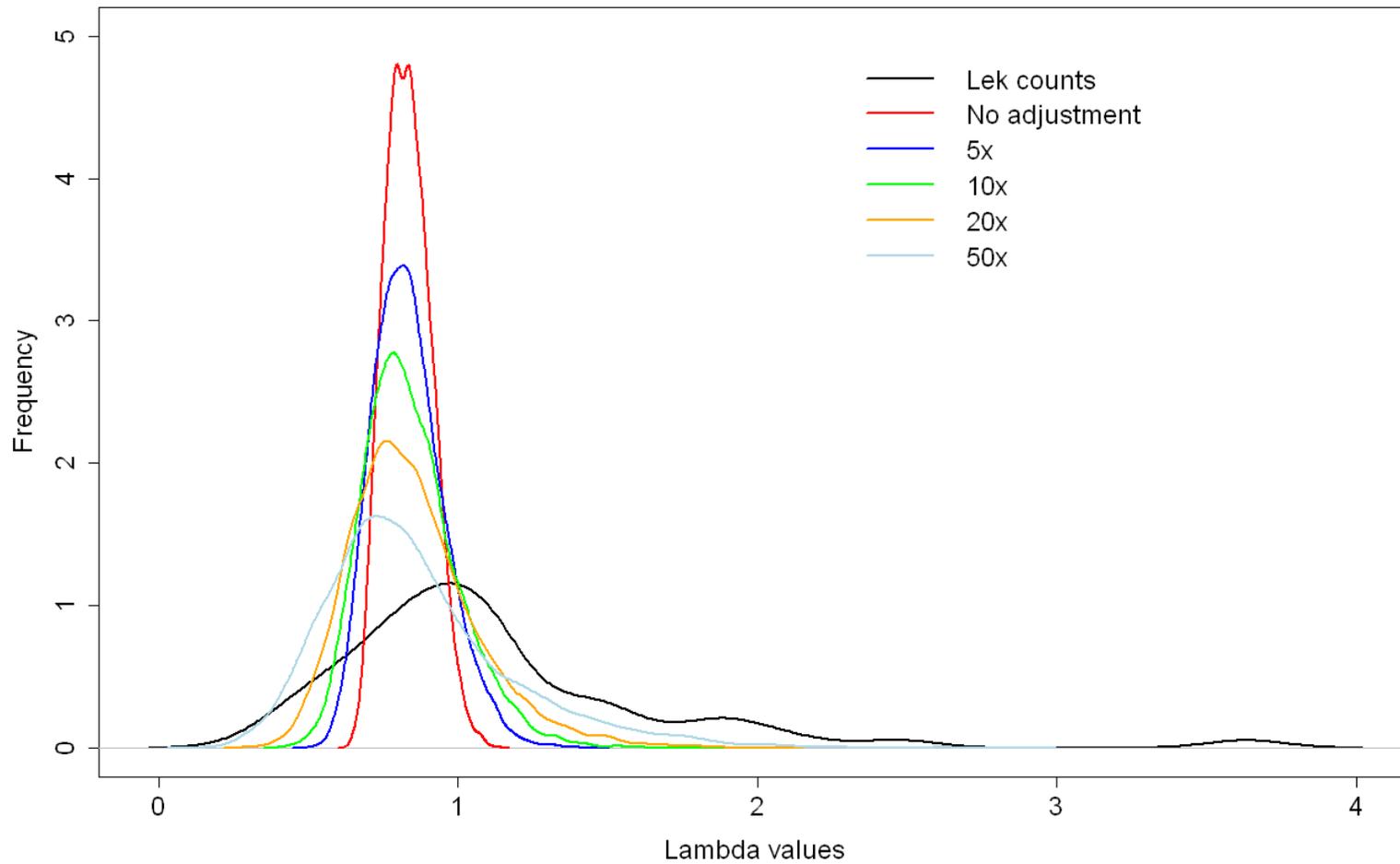


**Figure 5.1.** Plot of high male lek counts by year (with corresponding axis on the left) and number of lek areas counted over time (corresponding axis on the right) for Gunnison Sage-grouse in Gunnison Basin, Colorado, USA.

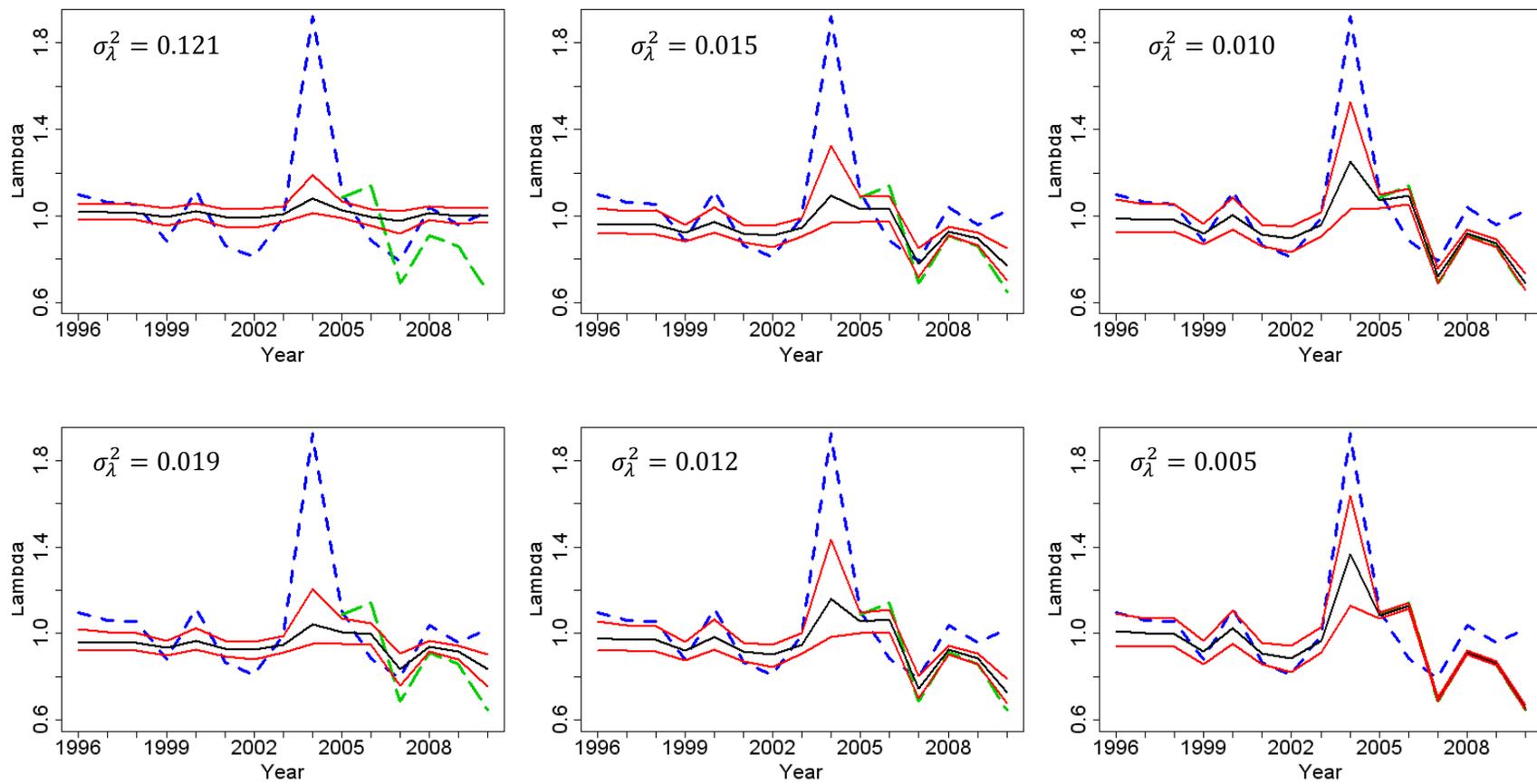


Parameter	Description
$F_y$	Yearling nest initiation rate ( $NI_Y$ ) * Yearling nest success rate ( $NS_Y$ ) * $\frac{1}{2}$ Average clutch size ( $C_Y$ ) * Juvenile recruitment ( $S_C * S_J$ )
$F_a$	Adult nest initiation rate ( $NI_A$ ) * Adult nest success rate ( $NS_A$ ) * $\frac{1}{2}$ Average clutch size ( $C_A$ ) * Juvenile recruitment ( $S_C * S_J$ )
$P_{yf}$	Yearling female survival ( $S_{YF}$ )
$P_{ym}$	Yearling male survival ( $S_{YM}$ )
$P_{af}$	Adult female survival ( $S_{AF}$ )
$P_{am}$	Adult male survival ( $S_{AM}$ )
$\lambda_t^c$	Population growth rate being estimated
$\lambda_t^d$	Population growth rate from demographic data
$M_t$	High male lek count data
$M_0$	Initial population size
$N_t$	Population size
$a_0$	Intercept parameter that relates the $\log(\lambda)$ s
$b_0$	Slope parameter that relates the $\log(\lambda)$ s

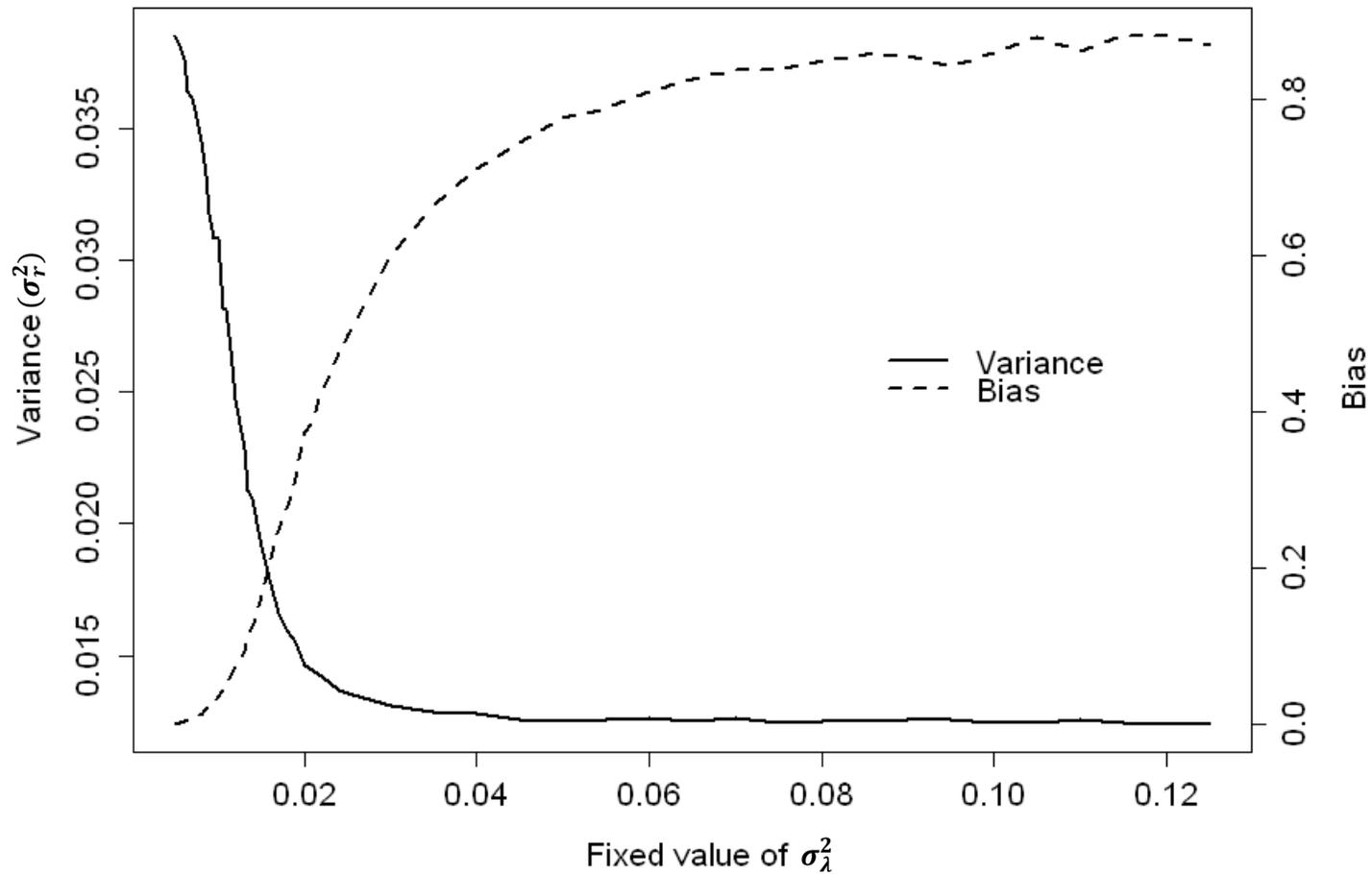
**Figure 5.2.** Directed acyclic graph of the structure of the integrated population model for Gunnison Sage-grouse. Estimated parameters are represented by circles and data are represented by squares



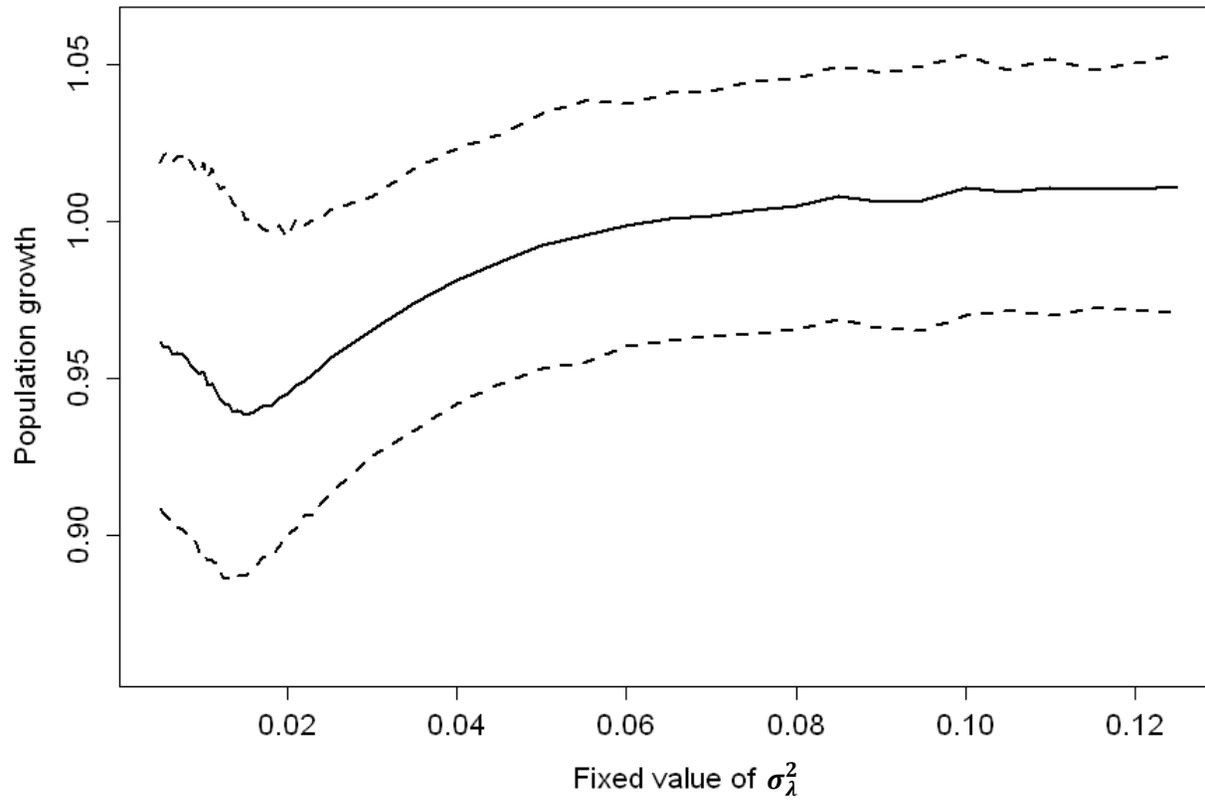
**Figure 5.3.** Plot of distribution of population growth rate ( $\lambda$ ) values for the lek count data (in black) compared to the growth rates created from simulated vital rate data with different adjustments to the covariance matrix.



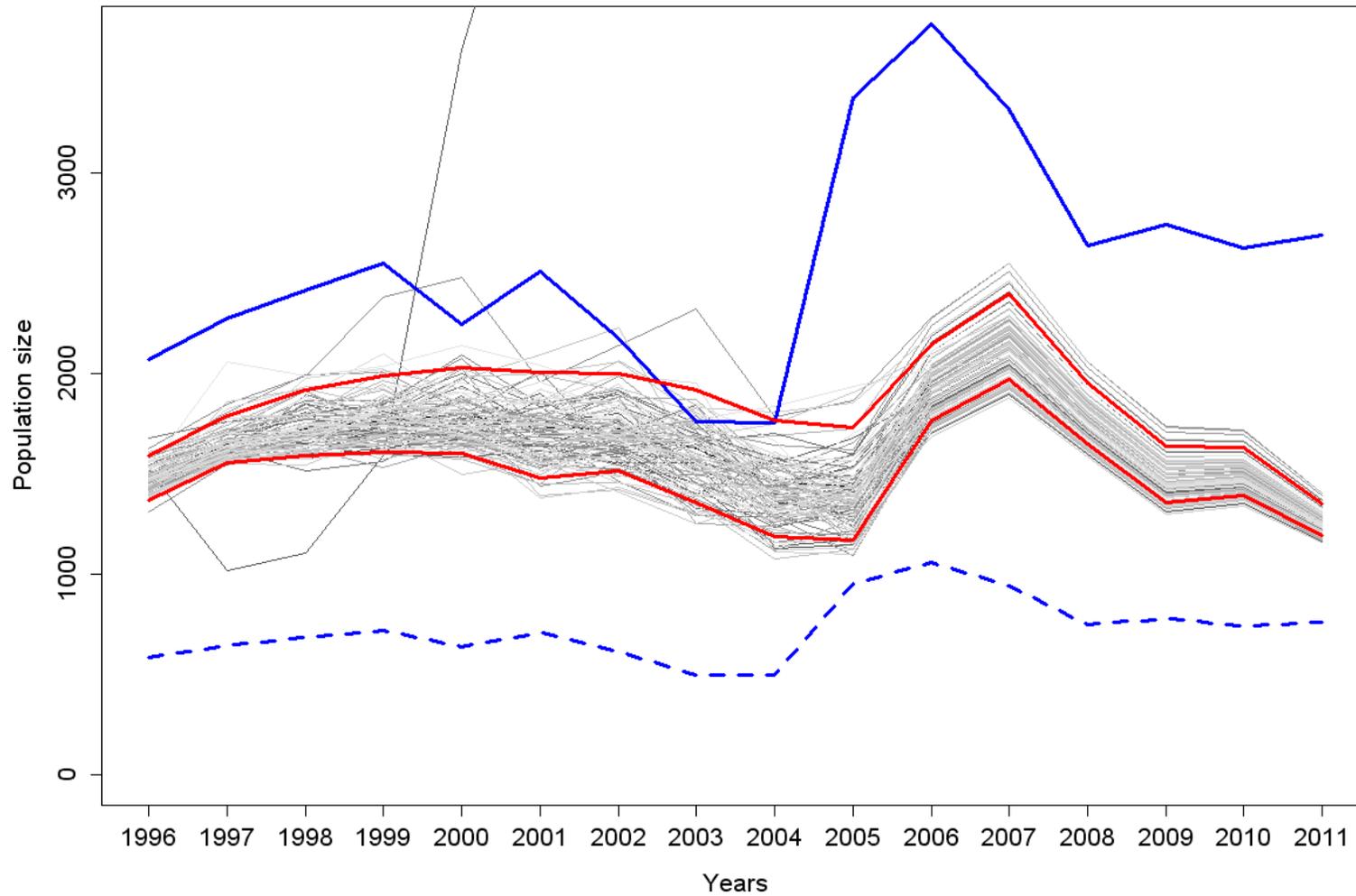
**Figure 5.4.** Plot of posterior means for the population growth rate ( $\lambda$ ) values (black line), with 95% credible intervals (red lines). The growth rates calculated from the lek count data (blue dashed line) and demographic data (green dashed line) are shown for comparison. The top left plot shows the posterior estimates where  $\sigma_\lambda^2$  is estimated from the integrated model. The remaining plots are a sample of fixed values for  $\sigma_\lambda^2$  showing how the posterior means change as  $\sigma_\lambda^2$  decreases.



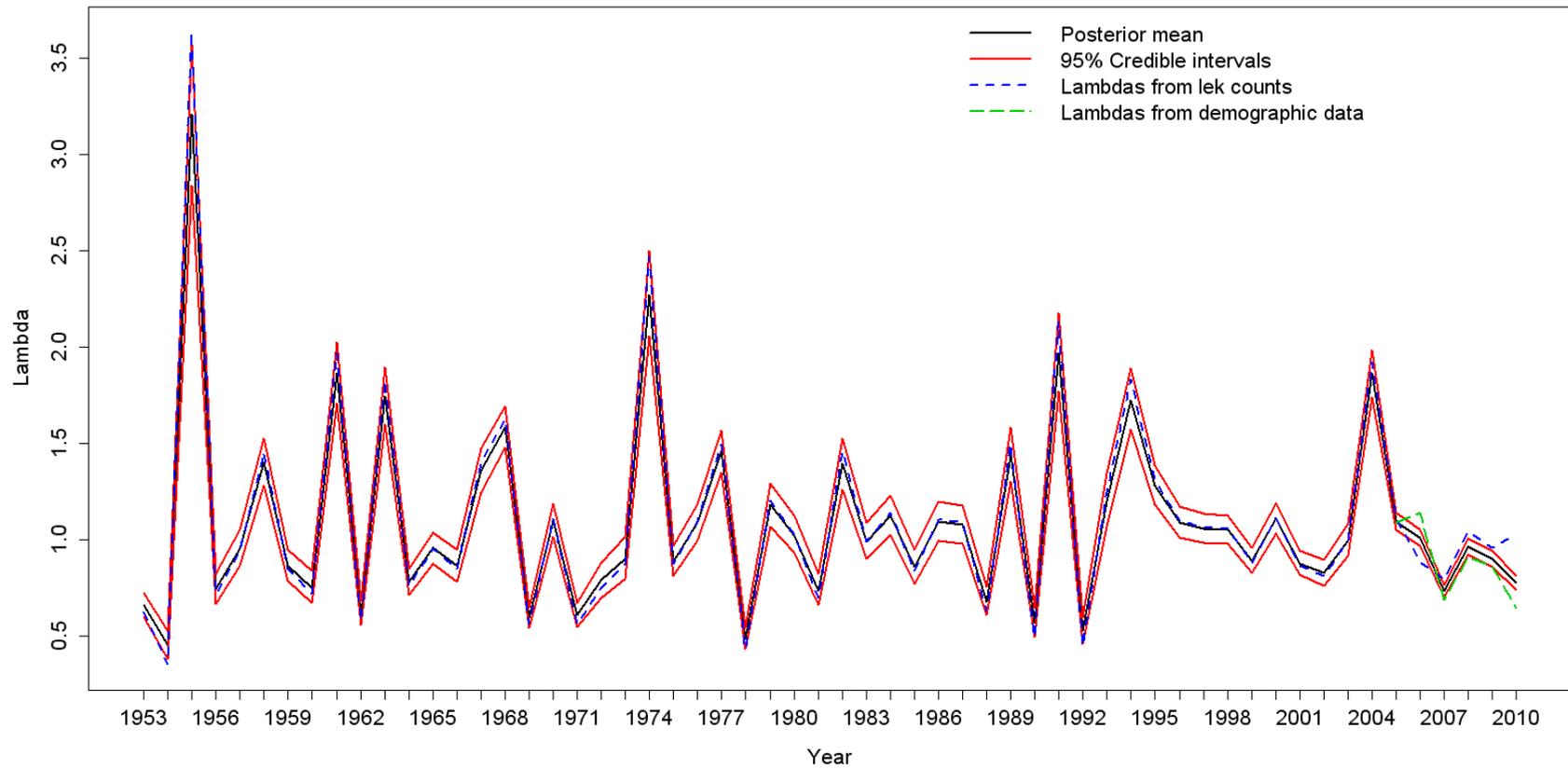
**Figure 5.5.** Plot of bias vs variance for different values of the variance from the distribution of growth rates from the demographic data ( $\sigma_\lambda^2$ ) for Gunnison Sage-grouse. Bias is measured by the sum of growth rate values that were outside the credible intervals. Bias is balanced by the variance from the distribution of growth rates for the lek count data  $\sigma_r^2$ .



**Figure 5.6.** Posterior means and 95% credible intervals of population growth rate for fixed values of the variance parameter that relates the demographic and lek count data ( $\sigma_\lambda^2$ ) for Gunnison Sage-grouse.



**Figure 5.7.** Population projections from the integrated model on Gunnison Sage-grouse in Gunnison Basin, Colorado. Gray lines are realizations of iterations of the MCMC algorithm. The red lines are the 90% credible intervals for the population size at each time. The blue dashed line is the high male lek count (the logical lower bound for the population). The solid blue line is the projected population size based on the direct calculation from the lek count data ( $\times 2.96$ ).



**Figure 5.8.** Plot of posterior means for the population growth rate ( $\lambda$ ) values, with 95% credible intervals. The growth rates calculated from the lek count data and demographic data are shown for comparison.

## LITERATURE CITED

- Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010a. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* **91**:7-14.
- Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub. 2010b. Estimation of immigration rate using integrated population models. *Journal of Applied Ecology* **47**:393-400.
- American Ornithological Union, A. 2000. Forty-Second supplement to the American Ornithologists Union Check-list for North American Birds. *The Auk* **117**:847-858.
- Beissinger, S. R. and D. R. McCullough. 2002. Population viability analysis. University of Chicago Press, Chicago, IL.
- Bell, S., M. Marzano, J. Cent, H. Kobierska, D. Podjed, D. Vandzinskaite, H. Reinert, A. Armaitiene, M. Grodzinska-Jurczak, and R. Mursic. 2008. What counts? Volunteers and their organisations in the recording and monitoring of biodiversity. *Biodiversity and Conservation* **17**:3443-3454.
- Besbeas, P., S. N. Freeman, and B. J. T. Morgan. 2005. The potential of integrated population modelling. Pages 35-48. Blackwell Publ Ltd.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* **58**:540-547.
- Besbeas, P., J. D. Lebreton, and B. J. T. Morgan. 2003. The efficient integration of abundance and demographic data. *Journal of the Royal Statistical Society Series C-Applied Statistics* **52**:95-102.
- Bromley, R. G., D. C. Heard, and B. Croft. 1995. VISIBILITY BIAS IN AERIAL SURVEYS RELATING TO NEST SUCCESS OF ARCTIC GEESE. *Journal of Wildlife Management* **59**:364-371.
- Broms, K., J. R. Skalski, J. J. Millspaugh, C. A. Hagen, and J. H. Schulz. 2010. Using Statistical Population Reconstruction to Estimate Demographic Trends in Small Game Populations. *Journal of Wildlife Management* **74**:310-317.

- Brooks, S. P., R. King, and B. J. T. Morgan. 2004. A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* **27**:515-529.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology* **81**:619-627.
- Caswell, H. 2001. *Matrix Population Models*, 2nd ed. Sinauer Associates Inc, Sunderland, MA.
- Catchpole, E. A., S. N. Freeman, B. J. T. Morgan, and M. P. Harris. 1998. Integrated recovery/recapture data analysis. *Biometrics* **54**:33-46.
- Caughley, G. 1974. Bias in Aerial Survey. *Journal of Wildlife Management* **38**:921-933.
- Chee, Y. E. and B. A. Wintle. 2010. Linking modelling, monitoring and management: an integrated approach to controlling overabundant wildlife. *Journal of Applied Ecology* **47**:1169-1178.
- Colorado Sage Grouse Working Group. 1997. *Gunnison Sage-grouse Conservation Plan*, Gunnison Basin, Colorado. Colorado Division of Wildlife.
- Connelly, J. W., Reese, K.P., and Schroeder, M.A. 2003. *Monitoring of Greater Sage-Grouse Habitats and Populations*. University of Idaho, Moscow, Idaho.
- Dahlgren, D. K. 2009. *Greater Sage-grouse Ecology, Chick Survival, and Population Dynamics*, Parker Mountain, Utah. Utah State University.
- Doak, D. F., W. F. Morris, C. Pfister, B. E. Kendall, and E. M. Bruna. 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. *American Naturalist* **166**:E14-E21.
- Emmons, S. R. and C. E. Braun. 1984. Lek Attendance of Male Sage Grouse. *The Journal of Wildlife Management* **48**:1023-1028.
- Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* **41**:263-274.
- Gauthier, G., P. Besbeas, J. D. Lebreton, and B. J. T. Morgan. 2007. Population growth in snow geese: A modeling approach integrating demographic and survey information. *Ecology* **88**:1420-1429.

- Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-Grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Link, W. A. and J. R. Sauer. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. *Ecological Applications* **8**:258-268.
- Link, W. A. and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology* **83**:2832-2840.
- Link, W. A., J. R. Sauer, and D. K. Niven. 2006. A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. *Condor* **108**:13-24.
- Malthus, T. 1798. *An Essay on the Principle of Population*. Electronic Scholarly Publishing Project, London, UK.
- McKelvey, K. S., K. B. Aubry, and M. K. Schwartz. 2008. Using anecdotal occurrence data for rare or elusive species: The illusion of reality and a call for evidentiary standards. *Bioscience* **58**:549-555.
- R Development Core Team. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rogers, G. E. 1964. *Sage grouse investigations in Colorado*. Colorado Game, Fish and Parks Department.
- Sauer, J. R. and W. A. Link. 2002. Hierarchical modeling of population stability and species group attributes from survey data. *Ecology* **83**:1743-1751.
- Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer Difference in the North American Breeding Bird Survey. *Auk* **111**:50-62.
- Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. *American Naturalist* **163**:429-441.
- Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conservation Biology* **21**:945-955.

- Schaub, M., T. S. Reichlin, F. Abadi, M. Kery, L. Jenni, and R. Arlettaz. 2012. The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia* **168**:97-108.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-Grouse in North America. *Condor* **106**:363-376.
- Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* **76**:336-347.
- Thomas, L., S. T. Buckland, K. B. Newman, and J. Harwood. 2005. A unified framework for modelling wildlife population dynamics. *Australian & New Zealand Journal of Statistics* **47**:19-34.
- United States Fish and Wildlife Service, U. 2010. Determination of Gunnison Sage-grouse as a Threatened or Endangered Species. *in* D. o. t. Interior, editor. Federal Register
- Walsh, D. P., J. R. Stiver, G. C. White, T. E. Remington, and A. D. Apa. 2010. Population Estimation Techniques for Lekking Species. *Journal of Wildlife Management* **74**:1607-1613.
- Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Pages 56-68. Wildlife Soc.
- Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000. A new species of sage-grouse (Phasianidae : *Centrocercus*) from southwestern Colorado. *Wilson Bulletin* **112**:445-453.

**APPENDIX 5.A.** Parameter estimates and standard errors for Gunnison Sage-grouse vital rates by year with vital rate means and process variance.

Year	2005		2006		2007		2008		2009		2010		Vital Rate Mean	Process Variance
	$\theta$	SE												
Nest Initiation Yearling	1.000	0.000	0.930	0.060	0.810	0.030	0.870	0.040	0.850	0.050	0.860	0.100	0.887	0.0015
Nest Initiation Adult	1.000	0.000	0.910	0.067	0.840	0.034	0.960	0.009	0.970	0.052	0.920	0.024	0.933	0.0017
Hen Success Yearling	0.254	0.097	0.583	0.100	0.350	0.084	0.606	0.106	0.403	0.089	0.372	0.073	0.428	0.0106
Hen Success Adult	0.246	0.097	0.608	0.100	0.289	0.084	0.700	0.106	0.451	0.089	0.386	0.073	0.446	0.0233
Chick Survival (GB)	0.467	0.020	0.417	0.017	0.366	0.015	0.316	0.014	0.266	0.016	0.219	0.019	0.342	0.0084
Juvenile Survival	0.731	0.121	0.533	0.100	0.386	0.075	0.384	0.061	0.284	0.063	0.179	0.064	0.416	0.0307
Yearling Female Survival	0.745	0.108	0.613	0.110	0.559	0.112	0.560	0.115	0.718	0.089	0.610	0.106	0.634	0.0005
Yearling Male Survival	0.729	0.178	0.560	0.213	0.523	0.229	0.518	0.231	0.678	0.183	0.572	0.220	0.597	0.0037
Adult Female Survival	0.705	0.116	0.561	0.113	0.502	0.108	0.504	0.109	0.675	0.088	0.557	0.099	0.584	0.0004
Adult Male Survival	0.523	0.188	0.312	0.175	0.274	0.163	0.268	0.167	0.453	0.179	0.325	0.172	0.359	0.0019
½ Clutch Size	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.000	3.486	0.0000

**APPENDIX 5.B.** Covariance matrix for Gunnison Sage-grouse vital rates calculated from six years of data.

	Nest Initiation Yearling	Nest initiation Adults	Hen Success Yearling	Hen Success Adult	Chick Survival	Juvenile Survival	Yearling Female Survival	Yearlin g Male Survival	Adult Female Survival	Adult Male Survival
Nest Initiation Yearling	0.004									
Nest initiation Adults	0.002	0.003								
Hen Success Yearling	-0.001	-0.001	0.016							
Hen Success Adult	-0.001	0.001	0.020	0.027						
Chick Survival	0.003	0.000	-0.001	-0.002	0.006					
Juvenile Survival	0.008	0.001	-0.003	-0.006	0.013	0.029				
Yearling Female Survival	0.003	0.003	-0.005	-0.005	0.001	0.003	0.005			
Yearling Male Survival	0.003	0.003	-0.006	-0.007	0.001	0.004	0.006	0.006		
Adult Female Survival	0.003	0.003	-0.006	-0.006	0.001	0.003	0.006	0.006	0.006	
Adult Male Survival	0.004	0.004	-0.008	-0.008	0.002	0.005	0.007	0.008	0.007	0.009

\*Clutch size was not calculated annually and thus is not included in the covariance matrix

## APPENDIX 5.C. R code used to run integrated MCMC algorithm.

```
for(k in 1:n.gibbs){
  cat(k, " ");flush.console()

  ### Sample from theta using Metropolis-Hastings
  ###
  thetastar=rnorm(t-1,theta,1.tune)
  gstar=exp(thetastar + y[1:t-1])      ### get to the Poisson parameter
  g = exp(theta + y[1:(t-1)])
  mh1a=dnorm(thetahat,(a+b*thetastar),s2.1,log=TRUE)
  mh1a[is.na(mh1a)]<-0                ### Account for these values only occuring when t is in tao
(2005-2010)
  mh2a=(dnorm(thetahat,(a+b*theta),s2.1,log=TRUE))
  mh2a[is.na(mh2a)]<-0                ### Account for these values only occuring when t is in tao
(2005-2010)
  mh1=(dpois(m[2:t],gstar,log=TRUE))+dnorm(thetastar,mu.r,s2.r,log=TRUE))+mh1a
  mh2=(dpois(m[2:t],g,log=TRUE))+dnorm(theta,mu.r,s2.r,log=TRUE))+mh2a
  mhratio=exp(mh1-mh2)
  tmp.keep=mhratio>runif(t-1)
  theta[tmp.keep]=thetastar[tmp.keep]

  ### Sample from mu.r (the mean parameter for the theta distribution)
  ###
  tmpmu<-((mumu/s2mu+sum(theta)/s2.r)*(1/(((t-1)/s2.r)+(1/s2mu))))
  tmps2<-(1/(((t-1)/s2.r)+(1/s2mu)))
  mu.r<-rnorm(1,tmpmu,tmps2)

  ### Sample from s2.r (the variance parameter for the theta distribution)
  ###
  tmpr=1/((sum((theta-mu.r)^2)/2)+1/r1)  ### Creating the 'r' parameter for the IG
  tmpq=(t-1)/2+q1                      ### Creating the 'q' parameter for the IG
  s2.r=1/rgamma(1,tmpq,.,tmpr)         ### Sampling from the IG with the 'r' and 'q' from above

  ### Sample from s2.1 (the variance parameter for the thetihat distribution)
  ###
  tdiff=thetahat-(a+b*theta)
  tdiff[is.na(tdiff)]<-0
  tmpr2=1/((sum((tdiff)^2)/2)+1/r2)     ### Creating the 'r' parameter for the IG
  tmpq2=(6-1)/2+q2                    ### Creating the 'q' parameter for the IG
  s2.1=1/rgamma(1,tmpq2,.,tmpr2)      ### Sampling from the IG with the 'r' and 'q' from above

  ### Sample from a (the intercept parameter for the difference in thetas)
  ###
  tmpmua<-((sum(thetahat[(t-6):(t-1)]-b*theta[(t-6):(t-1)])/s2.1)*(1/((6/s2.a)+(1/s2.1))))
  tmps2a<-(1/((6/s2.a)+(1/s2.1)))
  a<-rnorm(1,tmpmua,tmps2a)
```

```

### Sample from b (the slope parameter for the difference in thetas)
###
tmpmub<-(((1/s2.b)+sum(theta[(t-6):(t-1)]*(thetahat[(t-6):(t-1)]-a))/s2.l)*(1/(((6/s2.b)+(1/s2.l))))
tmps2b<-(1/(((6/s2.b)+(1/s2.l)))
b<-rnorm(1,tmpmub,tmps2b)

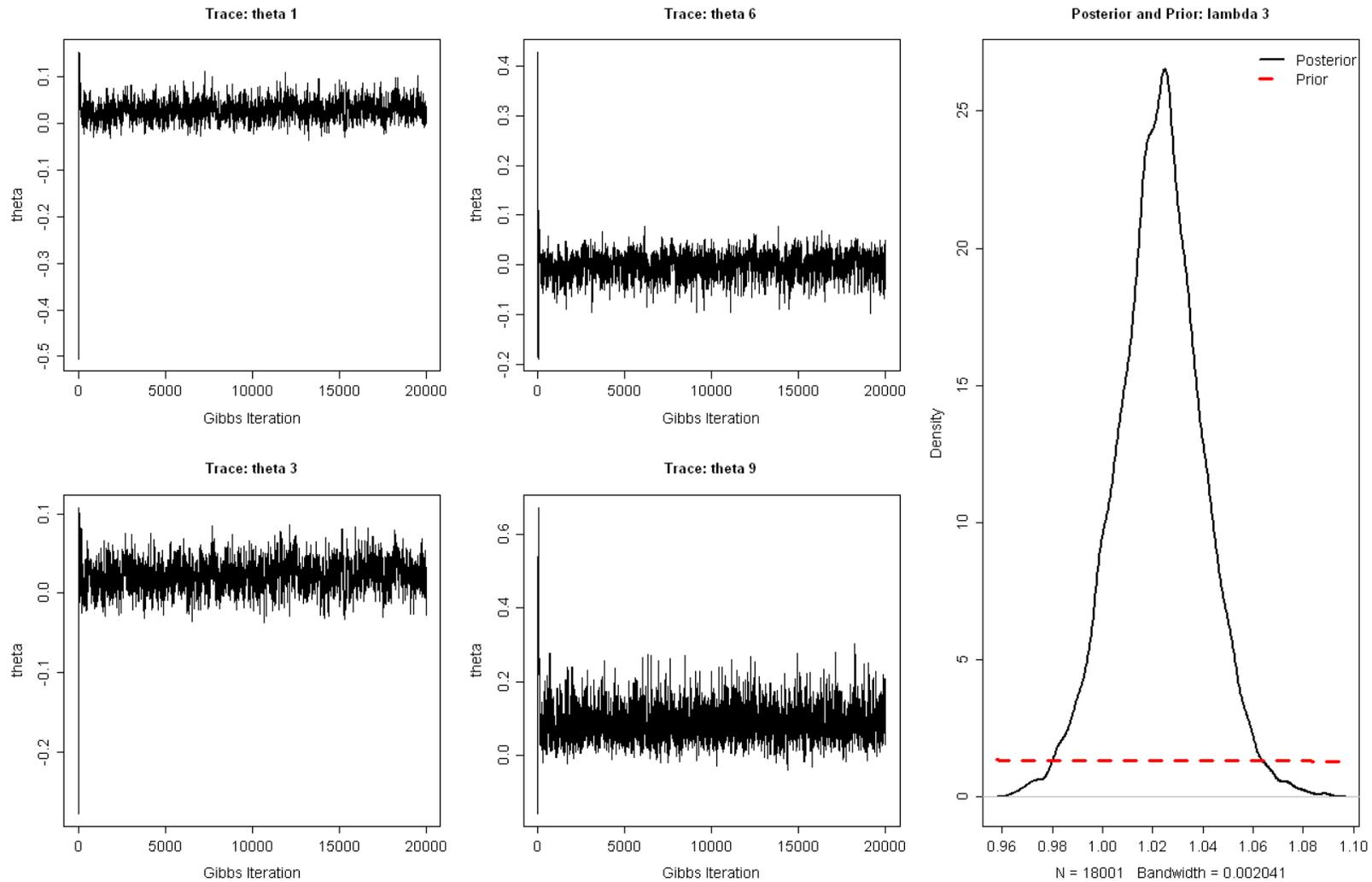
### Calculate starting population value
mo=rpois(1,m.tune)
init.pop=2.96*mo

### Save samples
###
lambda1=exp(theta)

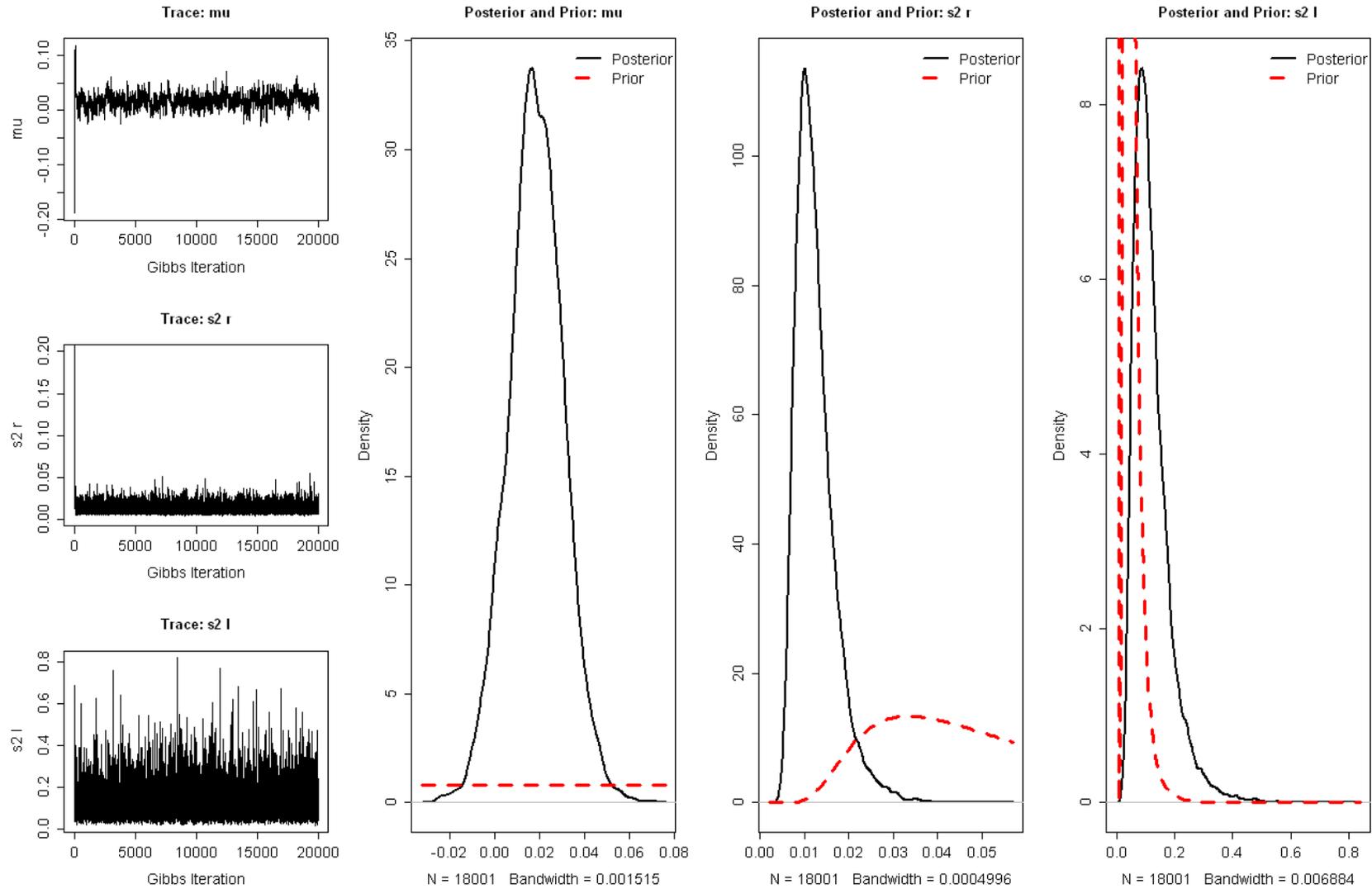
mursave[k]=mu.r
s2rsave[k]=s2.r
s2lsave[k]=s2.l
thetasave[k,]=(theta)
lambsave[k,]=exp(theta)
ipop.save[k]=init.pop
a.save[k]=a
b.save[k]=b
}

```

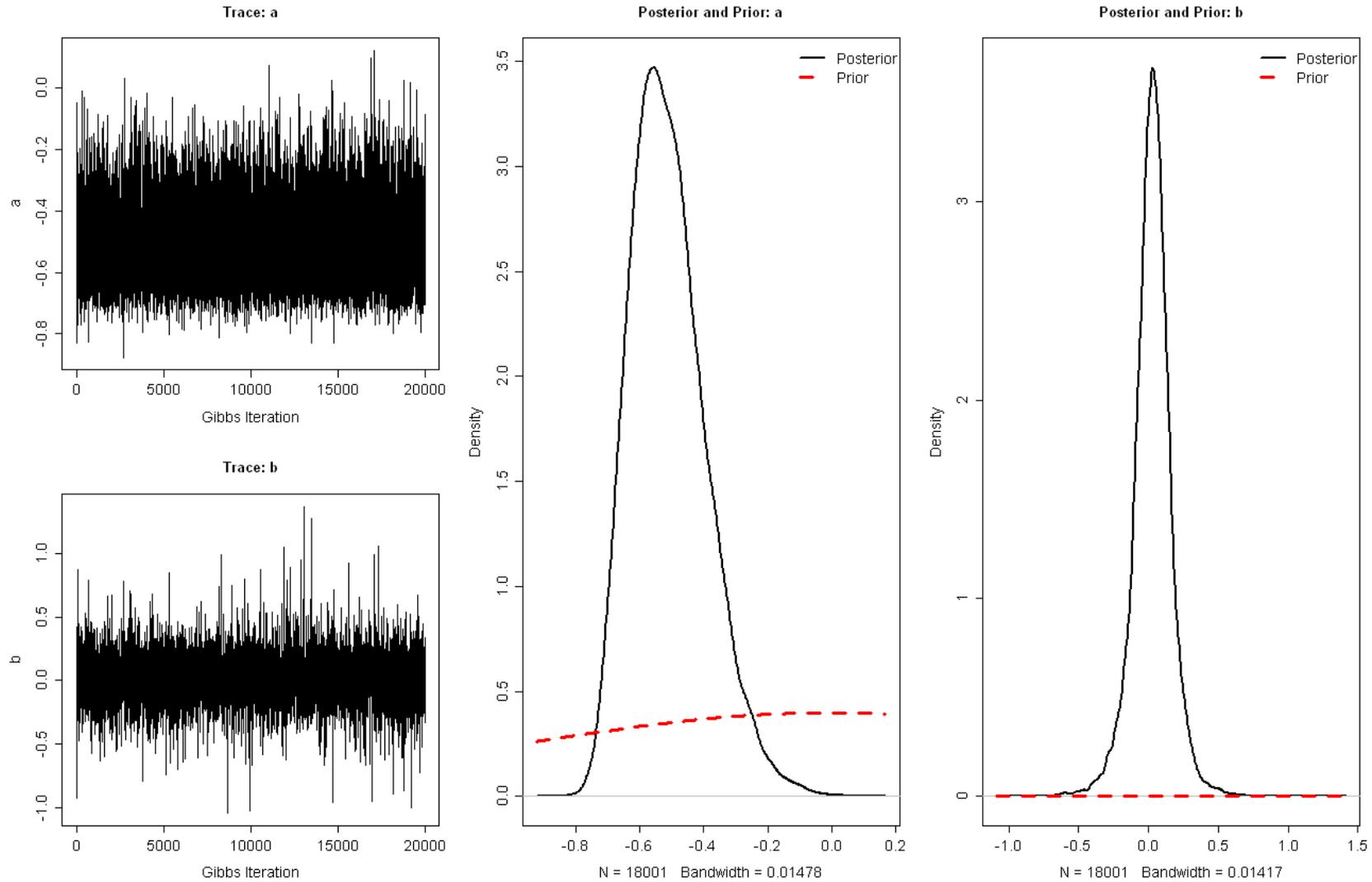
**APPENDIX 5.D.** Trace plots for a sample of  $\theta_t$  ( $\log \lambda_t$ ) values for the integrated model of Gunnison Sage-grouse population data. Trace plots show convergence occurred quickly (usually within 100 iterations) and good mixing. The plot on the right shows an example posterior density of population growth ( $\lambda$ ), the red dashed line represents the prior distribution for  $\lambda$ , and the vertical line is the maximum likelihood estimate for that value.



**APPENDIX 5.E.** Trace plots and density plots for the mean and variance priors on the log of the growth rate for the lek count data ( $\mu_r - \mu$ ,  $\sigma_r^2 - s2$ ) and the variance parameter for the log of the growth rate for the demographic data ( $\sigma_\lambda^2 - s2.l$ ).



**APPENDIX 5.F.** Trace plots and density plots for the parameters estimating the intercept (a) and slope (b) for the linear relationship between the growth rates from the demographic data and the lek count data for Gunnison Sage-grouse.



## MANAGEMENT IMPLICATIONS

Currently, many strategies are employed to manage Gunnison Sage-grouse (*Centrocercus minimus*, GUSG) by the Colorado Division of Parks and Wildlife (CPW). These methods include (but are not limited to) habitat restoration, area closures to vehicle and cattle, translocation, conservation easements for private land owners that manage their property to benefit the grouse, and predator control. In order to establish baseline demographic rates and test hypotheses with regards to those rates, CPW funded and conducted this demographic study, of which I was a part. Based on the information collected and analyzed, I have developed some management recommendations that I think will benefit this species and potentially improve the viability of the populations of GUSG.

The GUSG are known to reside primarily in one large population in the Gunnison Basin (GB, in Gunnison and Saguache counties, Colorado) with about 10% of individuals distributed in six isolated populations in the southwest of Colorado and into the eastern part of Utah. My research focused on the large GB population and one of the smaller populations, San Miguel (SM). The sample sizes from the SM population are small and thus population-specific effects were difficult to detect. However, the one strong result that was specific to SM was the almost complete lack of chick survival (hatch-30 days of age). The other vital rates that were measured for SM (nest success, yearling and adult survival) were not found to be different from GB. This highlights the need for immediate action to help improve chick survival in this population in order to improve the probability this population will persist.

Predation is the primary cause of chick mortality (Chapter 2). Anecdotal evidence suggests that SM has a particularly high abundance of coyotes, and that may be the cause of the high rates of mortalities for chicks. Therefore, a predator control program might be warranted to mitigate the predation pressures on GUSG chicks. In the year following my study a predator control program was conducted in SM and preliminary results have found some juvenile recruitment as a result. This shows promise for the ability to bolster this declining population in the short-term. However, the predator control program was

instituted as a management action and not a research project. Data are being collected in this population. However, our ability to learn from this information would be enhanced by treating this as a research or adaptive management project. I would also like to note that predator control is not a viable option for management long-term, but instead can be considered until the population rebounds or is sustainable by other management strategies (e.g., habitat improvement).

In the GB population, the rates of juvenile survival have declined steadily over the six years of my study (Chapter 2). This decline seems to coincide with a decline in the population index data (i.e., lek counts) for the same time period. Juvenile survival was also found to be a parameter that was both highly influential to population growth and highly variable (Chapter 4). This combination often suggest that such a parameter would make a good management target as it is both likely to positively affect the population and well as there is a high potential for improvement in the vital rate given its high variability. My analyses do suggest that survival of juveniles in the fall and winter is similar to that of yearlings and adults; the lowest survival rates of juveniles are in the summer months (June-Sept, Chapter 2). Therefore efforts made to improve juvenile survival might be more effective in the summer when there is a higher variability in survival. Unfortunately, my data were not collected in such a manner that tested relationships between juvenile survival and habitat characteristics or predator levels, which might help guide management of this vital rate. However, location data were collected for juveniles and this might have potential for future work in examining juvenile survival with respect to a spatially explicitly population model.

My sensitivity analyses suggested that nest success might also be an attractive management target since it is both relatively influential to population growth and highly variable (Chapter 4). Vegetation characteristics were not found to be strongly correlated with nest success (based on the method I used to measure them, Chapter 1). Although vegetation manipulation is a more attractive management target based on its relative ease of implication, more work needs to be done to examine the relationship between nest success and vegetation characteristics at different scales or possibly different metrics in order to

better guide management. If habitat management is conducted, concentrated monitoring before and after management actions would help us learn about the potential effects of such strategies; which would lead to more effective management in the future.

Translocation has been used on GUSG over the past ten years to move birds from the larger, more stable GB population to the six smaller populations. The goal of translocation is to help bolster the sizes and viabilities of these populations. The results of my translocation simulations (Chapter 4) suggest that moving birds more frequently is likely to have a larger impact on the destination population than simply moving a large number of birds at one time. Keep in mind my translocation results are only based on moving females as this is a female-based population model and females are assumed to be the limiting sex in this species. Based on my analysis, over the course of 30 years, if 300-500 birds are moved at a frequency of every five years or more often (e.g., 300 birds total moved every year is 10 birds a year, 500 birds total moved every five years is ~83 birds) the population size in SM will remain over 100 individuals (including chicks as my basis is a post-birth pulse model). However, the impact to the source population (GB) should be considered as well as projections for this population over the six year time frame suggest this population is also declining (Chapters 4 and 5).

The translocation method is based on some preliminary information from the translocations that have occurred for GUSG. I have no estimates of reproductive success for translocated birds and the estimates I have of survival for translocated birds are rough. This management strategy lends itself well to adaptive management procedures, which would allow for updating of models as new information became available and management would be guided based on the best information. One key aspect to adaptive management is monitoring. Continually monitoring the population of interest is crucial to assess current status of the species, to evaluate effects of management actions, and direct future management efforts. I recognize that resources are limited for wildlife research and monitoring. I believe that if financial costs are included formally in the evaluation of potential monitoring programs coupled with the desired results,

which is possible in adaptive management plans, then the resulting management would be economical and effective.

One form of monitoring of GUSG that has been conducted for several decades is of lek counts. These counts are not only long-running, but relatively inexpensive and have the benefit of engaging the community to collect. However, there are many issues with the collection of this type of data (outlined in Chapter 5). Through the use of a Bayesian integrated model I added strength from the demographic data to improve the utility of this extensive count data (Chapter 5). The protocol for collecting lek count data was standardized in 1996. This is the time frame in which I was able to make use of the lek count information. This 16-year data series helped reduce the potential bias in the shorter term demographic data (6 years), without which our predictions about the future of the species would be negatively skewed (based on Chapter 4). The lek count data that were collected previous to 1996 were too varied for any inference to be drawn from them. Therefore there is value in continuing to collect lek count data, but it is important to keep the standardized protocol. However, they should not be relied on solely for population assessment as the high level of variability inherent in maximum count data will possibly lead to spurious conclusions if not tempered by more rigorous information.

## COMPLETE LITERATURE CITED

- Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010a. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* **91**:7-14.
- Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub. 2010b. Estimation of immigration rate using integrated population models. *Journal of Applied Ecology* **47**:393-400.
- Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. University of Alberta, 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.
- American Ornithological Union, A. 2000. Forty-Second supplement to the American Ornithologists Union Check-list for North American Birds. *The Auk* **117**:847-858.
- Anthony, R. G. and M. J. Willis. 2009. Survival Rates of Female Greater Sage-Grouse in Autumn and Winter in Southeastern Oregon. *Journal of Wildlife Management* **73**:538-545.
- Apa, A. D. 2004. Habitat use, movements, and survival of Gunnison Sage-Grouse in southwestern Colorado. Unpublished Report. Colorado Division of Wildlife, Colorado, USA.
- Barbieri, M. M. and J. O. Berger. 2004. Optimal predictive model selection. *Annals of Statistics* **32**:870-897.
- Battazzo, A. M. 2007. Winter Survival and Habitat Use by Female Greater Sage-grouse (*Centrocercus urophasianus*) in South Phillips County, Montana 2004-2006. University of Montana, Missoula, MT USA.
- Baxter, R. J., J. T. Flinders, D. G. Whiting, and D. L. Mitchell. 2009. Factors affecting nest-site selection and nest success of translocated greater sage grouse. *Wildlife Research* **36**:479-487.
- Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin* **34**:1070-1078.

- Beck, T. D. I., R. B. Gill, and C. E. Braun. 1975. Sex and age determination of sage grouse from wing characteristics. *in* C. D. o. Wildlife, editor. Game Information Leaflet, Fort Collins, CO, USA.
- Beissinger, S. R. and D. R. McCullough. 2002. Population viability analysis. University of Chicago Press, Chicago, IL.
- Bell, S., M. Marzano, J. Cent, H. Kobierska, D. Podjed, D. Vandzinskaite, H. Reinert, A. Armaitiene, M. Grodzinska-Jurczak, and R. Mursic. 2008. What counts? Volunteers and their organisations in the recording and monitoring of biodiversity. *Biodiversity and Conservation* **17**:3443-3454.
- Benton, T. G. and A. Grant. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution* **14**:467-471.
- Besbeas, P., S. N. Freeman, and B. J. T. Morgan. 2005. The potential of integrated population modelling. Pages 35-48. Blackwell Publ Ltd.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* **58**:540-547.
- Besbeas, P., J. D. Lebreton, and B. J. T. Morgan. 2003. The efficient integration of abundance and demographic data. *Journal of the Royal Statistical Society Series C-Applied Statistics* **52**:95-102.
- Bishop, C. J., G. C. White, and P. M. Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. *Journal of Wildlife Management* **72**:1085-1093.
- Brockwell, P. J. and R. A. Davis. 2002. Introduction to Time Series and Forecasting. 2nd edition. Springer-Verlag New York, Inc., New York, NY USA.
- Bromley, R. G., D. C. Heard, and B. Croft. 1995. VISIBILITY BIAS IN AERIAL SURVEYS RELATING TO NEST SUCCESS OF ARCTIC GEESE. *Journal of Wildlife Management* **59**:364-371.
- Broms, K., J. R. Skalski, J. J. Millspaugh, C. A. Hagen, and J. H. Schulz. 2010. Using Statistical Population Reconstruction to Estimate Demographic Trends in Small Game Populations. *Journal of Wildlife Management* **74**:310-317.

- Brooks, S. P., R. King, and B. J. T. Morgan. 2004. A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* **27**:515-529.
- Buhnerkempe, M. G., N. Burch, S. Hamilton, K. M. Byrne, E. Childers, K. A. Holfelder, L. N. McManus, M. I. Pyne, G. Schroeder, and P. F. Doherty. 2011. The utility of transient sensitivity for wildlife management and conservation: Bison as a case study. *Biological Conservation* **144**:1808-1815.
- Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. *Wildlife Society Bulletin* **30**:93-96.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference- a practice information-theoretic approach. 2nd edition. Springer, New York.
- Cam, E., W. A. Link, E. G. Cooch, J. Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: Seeing the trees despite the forest. *American Naturalist* **159**:96-105.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* **39**:388-394.
- Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. *Conservation Biology* **19**:1821-1826.
- Caswell, H. 1989. Analysis of Life Table Response Experiments. 1. Decomposition of Effects on Population-growth Rate. *Ecological Modelling* **46**:221-237.
- Caswell, H. 1996. Analysis of life table response experiments .2. Alternative parameterizations for size- and stage-structured models. *Ecological Modelling* **88**:73-82.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology* **81**:619-627.
- Caswell, H. 2001. *Matrix Population Models*, 2nd ed. Sinauer Associates Inc, Sunderland, MA.
- Caswell, H. 2007. Sensitivity analysis of transient population dynamics. *Ecology Letters* **10**:1-15.
- Caswell, H. 2010. Life table response experiment analysis of the stochastic growth rate. *Journal of Ecology* **98**:324-333.

- Catchpole, E. A., S. N. Freeman, B. J. T. Morgan, and M. P. Harris. 1998. Integrated recovery/recapture data analysis. *Biometrics* **54**:33-46.
- Caughley, G. 1974. Bias in Aerial Survey. *Journal of Wildlife Management* **38**:921-933.
- Chee, Y. E. and B. A. Wintle. 2010. Linking modelling, monitoring and management: an integrated approach to controlling overabundant wildlife. *Journal of Applied Ecology* **47**:1169-1178.
- Coates, P. S. and D. J. Delehanty. 2008. Effects of Environmental Factors on Incubation Patterns of Greater Sage-grouse. *Condor* **110**:627-638.
- Coates, P. S. and D. J. Delehanty. 2010. Nest Predation of Greater Sage-Grouse in Relation to Microhabitat Factors and Predators. *Journal of Wildlife Management* **74**:240-248.
- Colorado Sage Grouse Working Group. 1997. Gunnison Sage-grouse Conservation Plan, Gunnison Basin, Colorado. Colorado Division of Wildlife.
- 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., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting by Sage Grouse in Southeastern Idaho. *Condor* **95**:1041-1043.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies Unpublished Report, Cheyenne, Wyoming, USA.
- Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage-grouse ecology final report. Idaho Department of Fish and Game.
- Connelly, J. W., Reese, K.P., and Schroeder, M.A. 2003. Monitoring of Greater Sage-Grouse Habitats and Populations. University of Idaho, Moscow, Idaho.
- 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.
- Curio, E. 1983. Why Do Young Birds Reproduce Less Well. *Ibis* **125**:400-404.

- Dahlgren, D. K. 2009. Greater Sage-grouse Ecology, Chick Survival, and Population Dynamics, Parker Mountain, Utah. Utah State University.
- Dahlgren, D. K., T. A. Messmer, and D. N. Koons. 2010. Achieving Better Estimates of Greater Sage-Grouse Chick Survival in Utah. *Journal of Wildlife Management* **74**:1286-1294.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* **33**:43-64.
- Desholm, M. 2009. Avian sensitivity to mortality: Prioritising migratory bird species for assessment at proposed wind farms. *Journal of Environmental Management* **90**:2672-2679.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**:3476-3488.
- Doak, D. F., W. F. Morris, C. Pfister, B. E. Kendall, and E. M. Bruna. 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. *American Naturalist* **166**:E14-E21.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater Sage-Grouse Nesting Habitat: The Importance of Managing at Multiple Scales. *Journal of Wildlife Management* **74**:1544-1553.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* **152**:317-323.
- Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Technical Note- Diets and Food Selection of Sage Grouse Chicks in Oregon. *Journal of Range Management* **47**:90-93.
- Emmons, S. R. and C. E. Braun. 1984. Lek Attendance of Male Sage Grouse. *The Journal of Wildlife Management* **48**:1023-1028.
- Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* **41**:263-274.
- Fischer, J. and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. *Biological Conservation* **96**:1-11.

- Gauthier, G., P. Besbeas, J. D. Lebreton, and B. J. T. Morgan. 2007. Population growth in snow geese: A modeling approach integrating demographic and survey information. *Ecology* **88**:1420-1429.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for Trapping Sage Grouse in Colorado. *Wildlife Society Bulletin* **10**:224-231.
- Gladwell, M. 2008. *Outliers: The Story of Success*. Little, Brown and Company Hachette Book Group, New York, NY USA.
- Gregg, M. A. and J. A. Crawford. 2009. Survival of Greater Sage-Grouse Chicks and Broods in the Northern Great Basin. *Journal of Wildlife Management* **73**:904-913.
- Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. Delong. 1994. Vegetational Cover and Predation of Sage Grouse Nests in Oregon. *Journal of Wildlife Management* **58**:162-166.
- Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted radiotransmitters to estimate survival of greater sage-grouse chicks. *Journal of Wildlife Management* **71**:646-651.
- Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and reneating by greater sage-grouse. *Journal of Wildlife Management* **70**:472-478.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a Species Conservation Tool - Status and Strategy. *Science* **245**:477-480.
- Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-Grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
- Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology* **81**:654-665.
- Herman-Brunson, K. M., K. C. Jensen, N. W. Kaczor, C. C. Swanson, M. A. Rumble, and R. W. Klaver. 2009. Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. *Wildlife Biology* **15**:395-404.
- Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management* **69**:638-649.

- Hupp, J. W. and C. E. Braun. 1989. Topographic Distribution of Sage Grouse Foraging in Winter. *Journal of Wildlife Management* **53**:823-829.
- Huwer, S. L. 2004. Evaluating greater sage-grouse brood habitat using human-imprinted chicks. Colorado State University, Fort Collins, CO.
- Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. *Ecological Applications* **20**:1753-1765.
- Johnson, K. H. and C. E. Braun. 1999. Viability and conservation of an exploited sage grouse population. *Conservation Biology* **13**:77-84.
- Kolada, E. J., M. L. Casazza, and J. S. Sedinger. 2009. Ecological Factors Influencing Nest Survival of Greater Sage-Grouse in Mono County, California. *Journal of Wildlife Management* **73**:1341-1347.
- Koons, D. N., J. B. Grand, B. Zinner, and R. E. Rockwell. 2005. Transient population dynamics: Relations to life history and initial population state. *Ecological Modelling* **185**:283-297.
- Lane, V. R. 2005. Sage-grouse (*Centrocercus urophasianus*) nesting and brood rearing sagebrush habitat characteristics in Montana and Wyoming. Montana State University, Bozeman, MT.
- Larson, M. A., M. E. Clark, and S. R. Winterstein. 2001. Survival of ruffed grouse chicks in northern Michigan. *Journal of Wildlife Management* **65**:880-886.
- Link, W. A. and P. F. Doherty. 2002. Scaling in sensitivity analysis. *Ecology* **83**:3299-3305.
- Link, W. A. and J. D. Nichols. 1994. On the Importance of Sampling Variance to Investigations of Temporal Variation in Animal Population-Size. *Oikos* **69**:539-544.
- Link, W. A. and J. R. Sauer. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. *Ecological Applications* **8**:258-268.
- Link, W. A. and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology* **83**:2832-2840.

- Link, W. A., J. R. Sauer, and D. K. Niven. 2006. A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. *Condor* **108**:13-24.
- Lubow, B. C. 1996. Optimal translocation strategies for enhancing stochastic metapopulation viability. *Ecological Applications* **6**:1268-1280.
- Malthus, T. 1798. *An Essay on the Principle of Population*. Electronic Scholarly Publishing Project, London, UK.
- Mayfield, H. F. 1975. Suggestions for Calculating Nest Success. *Wilson Bulletin* **87**:456-466.
- McKelvey, K. S., K. B. Aubry, and M. K. Schwartz. 2008. Using anecdotal occurrence data for rare or elusive species: The illusion of reality and a call for evidentiary standards. *Bioscience* **58**:549-555.
- Morris, W. F. and D. F. Doak. 2002. *Quantitative Conservation Biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. Dissertation. University of Montana, Missoula, Montana.
- Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. *Journal of Wildlife Management* **71**:1773-1783.
- Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female Greater Sage-Grouse in Montana. *Ecological Applications* **16**:1529-1538.
- Nams, V. O. 1990. Locate II. Pacer, Truro, Nova Scotia, Canada.
- NCDC. 2004-2010. Climatological Data Annual Summary Colorado. National Oceanic and Atmospheric Administration (NOAA).
- Ott, L. and M. Longnecker. 2001. *An introduction to statistical methods and data analysis*. Duxbury.

- Peterson, M. J., W. E. Grant, and N. J. Silvy. 1998. Simulation of reproductive stages limiting productivity of the endangered Attwater's prairie chicken. *Ecological Modelling* **111**:283-295.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America* **95**:213-218.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Reed, J. M., N. Fefferman, and R. C. Averill-Murray. 2009. Vital Rate Sensitivity Analysis as a Tool for Assessing Management Actions for the Desert Tortoise. *Biological Conservation* **142**:2710-2717.
- Roff, D. A. 1992. *Evolution of Life Histories*. Prentice-Hall, New York.
- Rogers, G. E. 1964. Sage grouse investigations in Colorado. Colorado Game, Fish and Parks Department.
- Rout, T. M., C. E. Hauser, and H. P. Possingham. 2007. Minimise long-term loss or maximise short-term gain? Optimal translocation strategies for threatened species. *Ecological Modelling* **201**:67-74.
- Saether, B. E. and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642-653.
- Sandercock, B. K., W. E. Jensen, C. K. Williams, and R. D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. *Journal of Wildlife Management* **72**:970-982.
- Sauer, J. R. and W. A. Link. 2002. Hierarchical modeling of population stability and species group attributes from survey data. *Ecology* **83**:1743-1751.
- Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer Difference in the North American Breeding Bird Survey. *Auk* **111**:50-62.
- Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. *American Naturalist* **163**:429-441.
- Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conservation Biology* **21**:945-955.

- Schaub, M., T. S. Reichlin, F. Abadi, M. Kery, L. Jenni, and R. Arlettaz. 2012. The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia* **168**:97-108.
- Schroeder, M. A. 1997. Unusually high reproductive effort by Sage Grouse in a fragmented habitat in north-central Washington. *Condor* **99**:933-941.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-Grouse in North America. *Condor* **106**:363-376.
- Schroeder, M. A. and R. K. Baydack. 2001. Predation and the management of prairie grouse. *Wildlife Society Bulletin* **29**:24-32.
- Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Greater Sage-Grouse (*Centrocercus urophasianus*). The birds of North America. The Birds of Norther America Online, Ithiaca, NY: Cornell Lab of Ornithology.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.
- Shenk, T. and A. Franklin. 2001. Modeling in Natural Resource Mangement:Development, Interpretation, and Application. Island Press, Washington, D.C., USA.
- Stacey, P. B. and M. Taper. 1992. Environmental Variation and the Persistence of Small Populations. *Ecological Applications* **2**:18-29.
- Stearns, S. C. and T. J. Kawecki. 1994. FITNESS SENSITIVITY AND THE CANALIZATION OF LIFE-HISTORY TRAITS. *Evolution* **48**:1438-1450.
- Stinson, D. W., D. W. Hays, and M. A. Schroeder. 2004. Washington state recovery plan for the Greater Sage-grouse. . Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Stiver, J. A. 2007. Polygyny and effective population size in the lekking Gunnison Sage-grouse. University of Nebraska, Lincoln, Nebraska.

- Stiver, J. R., A. D. Apa, T. E. Remington, and R. M. Gibson. 2008. Polygyny and female breeding failure reduce effective population size in the lekking Gunnison sage-grouse. *Biological Conservation* **141**:472-481.
- 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.
- Swanson, C. C. 2009. Ecology of greater sage-grouse in the Dakotas. Ph.D. South Dakota State University, United States -- South Dakota.
- Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* **76**:336-347.
- Thomas, L., S. T. Buckland, K. B. Newman, and J. Harwood. 2005. A unified framework for modelling wildlife population dynamics. *Australian & New Zealand Journal of Statistics* **47**:19-34.
- Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. *Western North American Naturalist* **66**:332-342.
- Tirpak, J. M., W. M. Giuliano, C. A. Miller, T. J. Allen, S. Bittner, D. A. Buehler, J. W. Edwards, C. A. Harper, W. K. Igo, G. W. Normar, M. Seamster, and D. F. Stauffer. 2006. Ruffed grouse population dynamics in the central and southern Appalachians. *Biological Conservation* **133**:364-378.
- United States Fish and Wildlife Service, U. 2010. Determination of Gunnison Sage-grouse as a Threatened or Endangered Species. *in* D. o. t. Interior, editor. Federal Register
- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An Improved Spotlighting Technique for Capturing Sage Grouse. *Wildlife Society Bulletin* **20**:425-426.
- Walker, B. L. 2008. Greater Sage-grouse Response to Coal-bed Natural Gas Development and West Nile Virus in the Powder River Basin, Montana and Wyoming, USA. University of Montana, Missoula, MT.

- Wallestad, R. and D. Pyrah. 1974. Movement and Nesting of Sage Grouse Hens in Central Montana. *Journal of Wildlife Management* **38**:630-633.
- Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Game Management Division, Montana Dept. of Fish and Game, Helena, MT.
- Walsh, D. P., J. R. Stiver, G. C. White, T. E. Remington, and A. D. Apa. 2010. Population Estimation Techniques for Lekking Species. *Journal of Wildlife Management* **74**:1607-1613.
- Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Pages 56-68. *Wildlife Soc.*
- White, G. C. and K. P. Burhnam. 1999. Program MARK: Survival estimation from populations of marked animals. Fort Collins, CO.
- Wisdom, M. J. and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: Prairie-chickens as an example. *Journal of Wildlife Management* **61**:302-312.
- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. *Ecology* **81**:628-641.
- Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: Update and reanalysis of 1987 survey data. *Conservation Biology* **10**:1142-1154.
- Young, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence among sage grouse populations. . Dissertation. Purdue University, West Lafayette, Indiana, USA.
- Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000a. A new species of sage-grouse (Phasianidae : *Centrocercus*) from southwestern Colorado. *Wilson Bulletin* **112**:445-453.
- Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000b. A new species of sage-grouse (Phasianidae : *Centrocercus*) from southwestern Colorado. *Wilson Bulletin* **112**:445-+.
- Zablan, M. A. 1993. Evaluation of sage grouse banding program in North Park, Colorado. Colorado State University, Fort Collins, CO.

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.