

GREATER SAGE-GROUSE ECOLOGY, CHICK SURVIVAL, AND POPULATION  
DYNAMICS, PARKER MOUNTAIN, UTAH

by

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

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

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2009

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## ABSTRACT

Greater Sage-Grouse Ecology, Chick Survival, and Population Dynamics,

Parker Mountain, Utah

by

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Utah State University, 2009

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We estimated survival of ~ 1-day-old chicks to 42 days based on radio-marked individuals for the Parker Mountain greater sage-grouse (*Centrocercus urophasianus*) population. Chick survival was relatively high (low estimate of 0.41 and high estimate of 0.50) compared to other studies. Brood-mixing occurred for 21 % of radio-marked chicks, and within 43 % of radio-marked broods. Our study showed that brood-mixing may be an important ecological strategy for sage-grouse, because chicks that brood-mixed experienced higher survival. Additionally, modeling of chick survival suggested that arthropod abundance is important during the early brood-rearing period (1 – 21 days). We also used life-cycle modeling (perturbation analyses and Life Table Response Experiments) to assess the importance of various vital rates within this population. We determined that adult hen survival and production (chick and fledgling survival) had the most influence on growth rate. Moreover, we assessed various methods (walking, spotlight, and pointing dog) for counting sage-grouse broods. Spotlight and pointing dog

iv  
methods were more effective than walking flush counts, and the latter may underestimate chick survival.

(146 pages)

## ACKNOWLEDGMENTS

I thank Terry Messmer for the many years of mentorship and guidance throughout my graduate education. I have learned from him the importance of working with people while working for wildlife. I have come to see the importance of his mantra “if it is not good for the community it is not good for wildlife.” This research could not have been accomplished without his support and guidance.

I appreciate the Parker Mountain Adaptive Resource Management partnership (PARM) for their organization and support. They have inspired many worthwhile efforts in the name of conservation for the Parker Mountain sage-grouse population. Their continued support will be critical for the future of that population.

I acknowledge the Utah Division of Wildlife Resources (UDWR), the Jack H. Berryman Institute, the Quinney Professorship for Wildlife Conflict Management, and the S.J. and Jessie Quinney Foundation for their in-kind and monetary support. I would like to specifically thank Jim Lamb, UDWR regional biologist. He spent many long hours helping the Parker Mountain sage-grouse project move forward. I would also like to thank Dean Mitchell and Dave Olsen for their oversight in the upland game program.

I would like to thank members of my committee, Dr. Chris Call, Dr. D. Layne Coppock, Dr. Roger Banner, and Dr. John (Jack) Connelly, for their input and support. I specifically thank Jack for his mentorship as a sage-grouse expert. I have become a better scientist and upland game biologist because of his association. Additionally, I thank Susan Durham for her statistical expertise and her ability to help me through the analyses of my data. Also, I thank Dr. David Koons for his editing and expertise in analysis for much of this dissertation.

I am grateful to all technicians who have been part of this work, namely Mike and Rene Richins, Chris Perkins, and Mandy Moss.

I give special thanks to Renee Chi and Joel Flory, for without these two exemplary graduate students, much of this thesis would not have been produced.

The trapping of sage-grouse hens is very taxing work. I thank all who volunteered their time in this activity for this research.

I send much love and gratitude to my family and friends who provided the needed moral support in my life to keep my head above water. Thanks to my grandfather, Dr. Robert Dahlgren, who inspired my career choice. Also, many of my family members volunteered their time to collect data. My dogs have been a big part of this work, and I have been blessed to be able to include them, so thanks to Buddy, Parker, Scout, and Rebel, and a mournful good bye to Sissy.

Last, but not least, I thank my wonderful wife. We started dating at the beginning of this research, and got married before it ended. How she made it through those long summers I will never know. She stuck with me through the thick and thin of it. She spent as many days as possible in the remotes of southern Utah, and has many fond memories of Loa, Utah. Her support in my life cannot be put into words. It has meant everything, and has given me true purpose.

David K. Dahlgren

## CONTENTS

	Page
ABSTRACT.....	iii
ACKNOWLEDGMENTS .....	v
LIST OF TABLES .....	ix
LIST OF FIGURES .....	xi
CHAPTER	
1. INTRODUCTION AND LITERATURE REVIEW .....	1
DESCRIPTION.....	1
GENERAL HABITAT REQUIREMENTS .....	1
Wintering .....	2
Pre-laying.....	2
Lekking .....	2
Nesting .....	3
Brood-rearing .....	4
RANGE-WIDE POPULATION STATUS.....	5
POPULATION STATUS IN UTAH.....	5
PARKER MOUNTAIN GREATER SAGE-GROUSE POPULATION.....	7
Study Area .....	7
Sage-grouse Population Status.....	10
Previous Research.....	10
LITERATURE CITED .....	13
2. ACHIEVING BETTER ESTIMATES OF GREATER SAGE-GROUSE CHICK SURVIVAL .....	20
INTRODUCTION .....	20
STUDY AREA .....	22
METHODS.....	23
Field Methods .....	23
Statistical Analysis.....	25
RESULTS.....	28
DISCUSSION.....	32
MANAGEMENT IMPLICATIONS .....	37
LITERATURE CITED .....	37

3. ESTIMATION OF GREATER SAGE-GROUSE SURVIVAL, PRODUCTIVITY FACTORS, AND LIFE-CYCLE MODELING .....	49
INTRODUCTION .....	49
STUDY AREA .....	53
METHODS .....	54
Estimation of Survival and Reproductive Rates .....	54
Life-cycle Modeling.....	58
RESULTS .....	62
Estimation of Survival and Reproductive Rates .....	62
Life Cycle Modeling.....	63
DISCUSSION .....	64
MANAGEMENT IMPLICATIONS .....	72
LITERATURE CITED .....	73
4. EFFECTIVENESS OF VARIOUS TECHNIQUES FOR SURVEYING SAGE- GROUSE BROODS .....	89
INTRODUCTION .....	89
STUDY AREA .....	92
METHODS .....	93
Data Analysis .....	95
RESULTS .....	96
DISCUSSION .....	96
MANAGEMENT IMPLICATIONS .....	98
LITERATURE CITED .....	99
5. CONCLUSIONS .....	105
LITERATURE CITED .....	111
APPENDICES .....	115
APPENDIX A: Alternative Analysis Actions for Chick Survival Analysis.....	116
INTRODUCTION .....	116
ANALYSIS ACTION 2: MISSING CHICKS WERE ASSIGNED MORTALITY .....	117
ANALYSIS ACTION 3: MISSING CHICKS WERE ASSIGNED SURVIVAL .....	117
APPENDIX B: Vegetation Analysis .....	124
INTRODUCTION .....	124
LITERATURE CITED .....	127
CURRICULUM VITAE.....	128



## LIST OF TABLES

Table	Page
2-1. Models of weekly greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick survival for both non- and brood-mixed brood, and covariate comparison of brood type (regular or mixed), hatch date (Julian days), and year (2005 or 2006), Parker Mountain, Utah, 2005-2006.....	44
2-2. Estimates of greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick daily survival rates for non- and mixed broods based on our best model (QAIC <sub>c</sub> ; brood-type), Parker Mountain, Utah, 2005-2006. ....	45
2-3. Models assessing the impact of greater sage-grouse ( <i>Centrocercus urophasianus</i> ) brood hen age (restricted data set without mixed broods because hen age was not determined for broods that radio-marked chicks mixed to) on chick survival, Parker Mountain, Utah, 2005-2006. ....	46
2-4. Models for greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick survival during the early brood-rearing period (days 1 – 21) based on arthropod sampling at brood sites (data set restricted to arthropod sampling periods, which did not change based on differing assumptions), Parker Mountain, Utah, 2005-2006.....	47
3-1. Female-based life table for the greater sage-grouse ( <i>Centrocercus urophasianus</i> ) population Parker Mountain, Utah, 1998-2006. ....	81
3-2. Female sage-grouse ( <i>Centrocercus urophasianus</i> ) survival models, Parker Mountain, Utah, 1998-2006.....	82
3-3. Female sage-grouse ( <i>Centrocercus urophasianus</i> ) nest initiation models, Parker Mountain, Utah, 1998-2006.....	82
3-4. Female sage-grouse ( <i>Centrocercus urophasianus</i> ) nest survival models, Parker Mountain, Utah, 1998-2006.....	83
3-5. Sage-grouse ( <i>Centrocercus urophasianus</i> ) brood success models, Parker Mountain, Utah, 1998-2006.....	83
3-6. Greater sage-grouse ( <i>Centrocercus urophasianus</i> ) population sensitivity, elasticity, and Life Table Response Experiment (LTRE) analyses, Parker Mountain, Utah, 1998-2006.....	84
3-7. Hunting season, bag and possession limits, harvested wing sample sizes, and reported radio-marked hen mortality for the greater sage-grouse ( <i>Centrocercus urophasianus</i> ) on Parker Mountain, Utah, 1998-2006. ....	86
3-8. Greater Sage-grouse ( <i>Centrocercus urophasianus</i> ) male lek count growth rate ( $\lambda_{\text{lek}}$ ), Parker Mountain, Utah, 1998-2006.....	87
3-9. Covariances for female greater sage-grouse ( <i>Centrocercus urophasianus</i> ) vital rates, Parker Mountain, Utah, 2006. ....	88

4-1.	Walking, nocturnal spotlight, and pointing-dog flush count data for method comparison at Parker Mountain, Utah, 2006-2007. ....	104
A-1.	Models for greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick survival based on the analysis action where missing chicks are considered mortalities (analysis action 2) for weekly chick age, Parker Mountain, Utah, 2005-2006. ....	118
A-2.	Models assessing the impact of greater sage-grouse ( <i>Centrocercus urophasianus</i> ) brood hen age (restricted data set without mixed broods because hen age was not determined for broods that radio-marked chicks mixed to) on chick survival based on the analysis action where missing chicks are considered mortalities (analysis action 2), Parker Mountain, Utah, 2005-2006. ....	119
A-3.	Estimates of greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick daily survival rates for analysis action 2 of non- and mixed broods, Parker Mountain, Utah, 2005-2006. ....	120
A-4.	Models for greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick survival across week age groups based on the analysis action where missing chicks were considered to have survived within their natural broods (analysis action 3), Parker Mountain, Utah, 2005-2006. ....	121
A-5.	Estimates of greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick daily survival rates for analysis action 3 of non- and mixed broods, Parker Mountain, Utah, 2005-2006. ....	122
A-6.	Models assessing the impact of greater sage-grouse ( <i>Centrocercus urophasianus</i> ) brood hen age (restricted data set without mixed broods because hen age was not determined for broods that radio-marked chicks mixed to) on chick survival based on the analysis action where missing chicks are considered surviving within their original broods (analysis action 3), Parker Mountain, Utah, 2005-2006. ....	122
B-1.	Models for greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chick survival based on vegetation measurements at brood sites (this dataset was restricted to only those survival periods immediately following vegetation sampling at brood sites), Parker Mountain, Utah, 2005-2006. ....	126

## LIST OF FIGURES

Figure	Page
1-1. Parker Mountain Study Area (PSA), Utah, 2005-2007.....	19
2-1. Survivorship curve for greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chicks (see Table 2 for precision estimates), Parker Mountain, Utah, 2005-2006. ....	48
3-1. Comparison of harvested (missing 2004-2005 data) and modeled age distributions for adult hen greater sage-grouse ( <i>Centrocercus urophasianus</i> ) (note: because yearling hen age distribution is proportional to adults, the inverse of this graph is the proportion of yearling hens in harvested and modeled distributions; and harvest information, including sample sizes, are reported in Table 7), Parker Mountain, Utah, 1998-2006.....	85
3-2. Comparisons of greater sage-grouse ( <i>Centrocercus urophasianus</i> ) lek-based and model-based growth rate ( $\lambda$ ), Parker Mountain, Utah, 1998-2006. ....	87
A-1. Survivorship curve for greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chicks with analysis action 2: where missing chicks are presumed mortalities (see Table A-3 for precision estimates), Parker Mountain, Utah, 2005-2006.....	120
A-2. Survivorship curve greater sage-grouse ( <i>Centrocercus urophasianus</i> ) chicks with Analysis action 3: missing chicks were presumed to survive within their original Broods (see Table A-5 for precision estimates), Parker Mountain, Utah, 2005-2006 . ....	123



## CHAPTER 1

### INTRODUCTION AND LITERATURE REVIEW

#### **DESCRIPTION**

Greater sage-grouse (*Centrocercus urophasianus*) is the largest species of native grouse in North America. Males may weigh up to 3.2 kg and females 1.5 kg (Patterson 1952, Autenrieth 1981). Sage-grouse are considered sagebrush (*Artemisia* spp.) obligates and depend on sagebrush habitat throughout their life cycle (Patterson 1952, Braun et al. 1977, Connelly et al. 2000a). Greater sage-grouse range includes southeast Alberta and southwest Saskatchewan; southwest North Dakota and northwest South Dakota; most of Montana and Wyoming; western Colorado; parts of southern and eastern Idaho; north, northeast, and southern Utah; northern Nevada; east to northeast California; southeast Oregon; and north-central Washington (Connelly and Braun 1997, Schroeder et al. 2004). Gunnison sage-grouse (*C. minimus*) occur in small, isolated populations in southwest Colorado and southeast Utah (Young et al. 2000). Greater sage-grouse have been extirpated from the fringes of their range in Arizona, New Mexico, Nebraska, and British Columbia (Schroeder et al. 2004).

#### **GENERAL HABITAT REQUIREMENTS**

Sage-grouse depend on sagebrush communities to complete their life cycle (Connelly et al. 2000a). These ecosystems provide wintering, pre-laying, lekking, nesting, and brood-rearing habitat.

## **Wintering**

Preferred winter habitat consists of medium to tall (25 to 80 cm, or 25 to 35 cm above snow) sagebrush with canopy coverage from 15 to 20% (Connelly et al. 2000a). Sage-grouse depend on sagebrush almost exclusively for their winter diet (Patterson 1952). Big (*A. tridentata*), low (*A. arbuscula*), and black (*A. nova*) sagebrush provide thermal cover, escape cover, and food for sage-grouse (Connelly et al. 2000a). Greater sage-grouse may actually gain weight during the winter (Beck and Braun 1978), and have been reported to not be impacted by severe weather conditions unless snow completely covers the sagebrush (Hupp and Braun 1989). Moynahan et al. (2006) documented the negative impact of severe winter weather (snowfall covered the sagebrush) by monitoring survival of radio-marked female sage-grouse in north-central Montana.

## **Pre-laying**

During pre-laying periods, 50 to 80% of a hen's diet consists of sagebrush leaves with the remainder being various forbs (Barnett and Crawford 1994). Nutrient content primarily comes from the forb component of a hen's diet, and appears to enhance reproductive success (Barnett and Crawford 1994).

## **Lekking**

During the spring breeding season, lek sites are used for displaying and breeding activities. Males display from these areas to attract females. Lekking habitat consists of bare ground or sparsely vegetated areas with little or no shrub canopy (Patterson 1952). Sage-grouse may take advantage of disturbances that provide this habitat type if sparsely vegetated areas are scarce (Connelly et al. 1981).

## Nesting

Sage-grouse nests are typically located under sagebrush plants, and are often under the tallest sagebrush in the stand (Wallestad and Pyrah 1974, Apa 1998). Connelly et al. (1991) in Idaho reported that 79% of 84 nests were located under sagebrush. Nests under sagebrush had higher rates of success than nests under non-sagebrush plants. Lowe (2006) found that big sagebrush support more nest success compared to threetip sagebrush (*A. tripartita*). Sveum et al. (1998) reported that nest sites in Washington exhibited higher shrub canopy coverage and more ground and lateral cover than random sites. Gregg et al. (1994) noted that high canopy cover (i.e., 41%) and tall (>18 cm) residual bunchgrass cover were a characteristic common to successful nests. Residual forbs also may provide nest-screening cover, though exotic herbaceous species may not (Sveum et al. 1998). Sage-grouse hens can renest following nest failure. Schroeder (1997) reported an unusually high (87%) renesting effort by hens in central Washington, while Connelly et al. (1993) observed much lower renesting rates (15% average for yearlings and adults). Distance between nests and the nearest lek varies and nests sites are selected independent of lek locations (Wakkinen et al. 1992).

One of the most common reasons for sage-grouse nest failure is predation (which is true for most ground-nesting species). Ample vegetation structure may reduce predation (Gregg et al. 1994, Schroeder and Baydack 2001). Common nest predators include ground squirrel (*Spermophilus* spp.), badger (*Taxidea taxus*), coyote (*Canis latrans*), and common raven (*Corvus corax*) (Shroeder and Baydack 2001). Common predators of sage-grouse adults and young include golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*), Swainson's hawk (*B. regalis*), northern harrier (*Circus*

*cyaneus*), common raven, weasel (*Mustela* spp.), and coyote (Schroeder and Baydack 2001). Most biologists believe that predation can be managed best by enhancing habitat quality (Messmer and Rohwer 1998). In areas where habitat fragmentation and increased densities of exotic predators have isolated and decreased populations of sage-grouse, direct predator management may be necessary (Schroeder and Baydack 2001).

### **Brood-rearing**

Brood-rearing can be divided into early and late periods. Early brood-rearing is closely associated with nesting habitat (Connelly et al. 2000a). For late brood-rearing activities, shrub canopy cover tends to be less, while herbaceous understory is higher (Connelly et al. 2000a). As sagebrush communities desiccate through the summer, birds tend to move to more mesic areas (Klebenow 1969, Braun 1998, Connelly et al. 2000b).

Insects are the major portion of a chick's diet during the early brood-rearing period (up to 3 weeks), and then forbs and a minor component of insects through the late brood-rearing period when sagebrush starts to be consumed (Patterson 1952, Klebenow and Gray 1968, Peterson 1970). Availability of forbs and insects is positively correlated with chick recruitment into a population (Drut et al. 1994). Agricultural habitats, such as alfalfa fields, may be used heavily by sage-grouse adults and chicks during the summer months (Patterson 1952). Brood-rearing takes place until early fall when the birds group into flocks for the winter.

Sagebrush communities that exhibit an abundant herbaceous understory are important for brood-rearing habitat (Connelly et al. 2000a). Direct intervention within late brood-rearing areas, especially areas where shrub canopy cover may be limiting the understory, can benefit sage-grouse (Dahlgren et al. 2006).



## **RANGE-WIDE POPULATION STATUS**

Greater sage-grouse populations have decreased as the quality and quantity of sagebrush habitat within their range has declined (Connelly et al. 2004). Connelly et al. (2004), in their range-wide assessment, reported that greater sage-grouse populations declined 3.5% per year from the mid-1960s to the mid-1980s, and 0.4% per year from the mid-1980s to 2003. Braun et al. (1976, 1977) and Connelly and Braun (1997) argued that mismanagement of the sagebrush-steppe ecosystem has led to the decline of sage-grouse populations and their habitats.

Connelly and Braun (1997) pointed out that sage-grouse populations have declined between 17 to 47% throughout much of their range. Connelly et al. (2000a), Wisdom et al. (2000), and West and Young (2000) expressed concerns that long-term loss, degradation, and fragmentation of sagebrush vegetation throughout the Intermountain West have hastened sage-grouse decline. The overall relationship between habitat degradation and sage-grouse population decline can be demonstrated by the remaining sage-grouse populations' close association with intact habitats in relatively northern latitudes, high elevations, and/or mesic environments (Connelly and Braun 1997).

## **POPULATION STATUS IN UTAH**

Utah has not been exempt from factors causing sage-grouse population decline (Beck et al. 2003). Sage-grouse once inhabited all of Utah's 29 counties (Beck et al. 2003). Now only five counties (i.e., Box Elder, Garfield, Rich, Uintah, and Wayne) contain abundant (> 500 breeding sage-grouse based on a moving average from 1996-2000) sage-grouse numbers (Beck et al. 2003). Beck et al. (2003) reported a 60 and 70%

decline in potential habitat for greater sage-grouse and Gunnison sage-grouse in Utah, respectively. However, in recent years sage-grouse populations seem to be stable or increasing, especially in those Utah counties that contain abundant populations (Beck et al. 2003, Connelly et al. 2004).

Greater sage-grouse are identified as a “species of special concern” by the Utah Division of Wildlife Resources (UDWR). To address these concerns, UDWR prepared the Utah Strategic Management Plan for Sage-grouse (UDWR 2002). This plan, approved by the Utah Wildlife Board in 2002, and identified 13 “Management Areas” to facilitate conservation efforts. The UDWR is updating and revising the 2002 plan (D. Olsen, UDWR Upland Game Coordinator, personal communication). Currently a community-based conservation effort is underway in these areas. This effort will culminate in implementation of conservation measures to stabilize and increase Utah’s sage-grouse populations (T. Messmer, Utah State University, personal communication).

Because of concerns about declining populations and habitat degradation, several groups have petitioned the U. S. Fish and Wildlife Service (USFWS) to list the greater sage-grouse under the Endangered Species Act (ESA) of 1973 (K. Kritz, USFWS, unpublished data). Sage-grouse occur on lands managed by the Bureau of Land Management (BLM), U. S. Forest Service (USFS), state of Utah, and private entities. The UDWR estimates that about 50% of sage-grouse habitat and populations inhabit private lands in Utah (UDWR 2002). Thus, listing the species would affect both state and federal management actions on public and private lands.

Sage-grouse conservation actions will involve many stakeholders including federal land management agencies, state wildlife agencies, private livestock operations,

and environmental organizations. The USFWS concluded in 2004 that a range-wide listing was not warranted for greater sage-grouse (L. Romin, USFWS, Salt Lake City, personal communication). This decision was overturned in December 2007. Thus, local working groups and their sage-grouse habitat recovery plans will continue to play a major role in sage-grouse conservation in Utah.

## **PARKER MOUNTAIN GREATER SAGE-GROUSE POPULATION**

### **Study Area**

The Parker Mountain study area (PSA) is in Garfield, Sevier, Piute, and Wayne counties of Utah. It encompasses both the Aquarius and Awapa Plateaus (Fig. 1-1). The Awapa Plateau lies on an east/west interface, the elevation increasing gradually from east to west and north to south, and meets the Aquarius Plateau to the south. Although it shares some of the vegetation characteristics of other sagebrush-steppe zones, its high elevation and unique weather patterns create a distinctive environment. The elevation ranges from 2,134 to 3,018 meters above sea level.

Parker Mountain consists of ~ 107,478 ha: 21,685 ha managed by the USFS, 36,398 ha by BLM, 43,863 ha by Utah School and Institutional Trust Lands Administration (SITLA), and 5,532 ha are in private ownership. The predominant land use in the area is grazing by domestic livestock (sheep and cattle). The sagebrush habitat on Parker Mountain is one of the largest contiguous tracts in Utah. Because of its high elevation and remoteness the area has escaped many of the development pressures that have impacted lower elevation sagebrush communities. Subsequently, Parker Mountain continues to be one of the few areas remaining in Utah that exhibits relatively high densities of greater sage-grouse (Beck et al. 2003).

Annual precipitation on Parker Mountain varies by elevational gradient. Higher elevations (> 2700 m) may receive 40 to 51 cm/year. Lower elevations receive 25 to 40 cm/year. Precipitation comes mostly in the form of winter snow and rain during the late summer monsoon. There are a small number of natural springs located at higher elevations (> 2700 m). Over 80 man-made water developments are scattered throughout Parker Mountain. These provide seasonal water for both wildlife and livestock.

Livestock stocking rate is 1.46 ha per animal unit month (AUM); (R. Torgerson, SITLA , personal communication). The area is grazed by sheep and cattle that are rotated through 10 grazing allotments. Grazing is initiated at lower elevations in June. Livestock are subsequently herded to higher elevation allotments as the desired forage utilization is achieved (R. Torgerson, SITLA, personal communication). Additionally, Parker Mountain is used by hunters, off-highway vehicles (OHV), camper, and other recreationists.

The majority of the Awapa Plateau is dominated by black sagebrush (*A. nova*). Lower lying draws and higher elevation areas on the western edge of the Awapa Plateau are dominated by mountain big sagebrush (*A. t. spp. vaseyana*). Some silver sage (*A. cana*) occurs in the more mesic bottoms and dominates uplands at the very highest elevations where the southern border of the Awapa Plateau meets the Aquarius Plateau. Common forb species include cinquefoil (*Potentilla* spp.), phlox (*Phlox* spp.), dandelion (*Taraxacum* spp.), lupine (*Lupinus* spp.), daisy (*Erigeron* spp.), penstemon (*Penstemon* spp.), and milkvetch (*Astragalus* spp.). Common grass species include wheatgrass (*Agropyron* spp.), bluegrass (*Poa* spp.), grama grass (*Bouteloua* spp.), squirrel tail

(*Elymus* spp.), and June grass (*Koeleria* spp.). Also, dry-land sedge (*Carex siccata*) is common on Parker Mountain uplands.

Common mammal species observed on Parker Mountain include mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), jack rabbits (*Lepus* spp.), mountain cottontail (*Sylvilagus nuttallii*), coyote (*Canis latrans*), and badger (*Taxidea taxus*). Common avian species include horned lark (*Eremophila alpestris*), red-tailed hawk (*Buteo jamaicensis*), American kestrel (*Falco sparverius*), golden eagle (*Aquila chrysaetos*), prairie falcon (*F. mexicanus*), American robin (*Turdus migratorius*), sage sparrow (*Amphispiza belli*), sage thrasher (*Oreoscoptes montanus*), Brewer's sparrow (*Spizella breweri*), northern flicker (*Copates auratus*), and common raven (*Corvus corax*). Greater short-horned lizards (*Phrynosoma hernandesi*) are common in black sagebrush habitat. Sensitive species, according to Utah that have been recorded on the PSA include the burrowing owl (*Anthene cucularia*), ferruginous hawk (*B. regalis*), pygmy rabbit (*Brachylagus idahoensis*), and greater sage-grouse. The only federally listed species that inhabits the study area is the Utah prairie dog (*Cynomys parvidens*).

Because of the presence of livestock on the study area, technicians employed by the United States Department of Agriculture Wildlife Services (USDA-WS) conduct predator control operations for livestock protection on Parker Mountain (K. Dustin, USDA-WS, personal communication). Coyotes are common predators. This work is also conducted under an agreement with the UDWR to increase pronghorn fawn survival. Coates (2007) indicated that ravens can be controlled with chicken-egg baits (though not likely a 1:2 kill ratio, as purported by USDA-WS). Because of concerns about the impact

of common ravens on sage-grouse nests, the USDA-WS contract was expanded to include raven control. Ravens are controlled with an avacide, DRC-1339, injected into chicken eggs.

### **Sage-grouse Population Status**

Natural fluctuation occurs for the Parker Mountain sage-grouse population, and the overall trend has followed range-wide trends (Connelly et al. 2004). The area has undergone limited development (no paved roads, no power lines, etc.) over the past century. However, Parker Mountain sage-grouse populations gradually declined from 1970–1997.

The area has been grazed annually by domestic livestock for many years, with a shift from sheep towards cattle over the last few decades and a reduction in overall grazing AUMs. Additionally, in recent years sagebrush habitat manipulation projects, designed to increase the quality of brood-rearing habitat, have been completed (Dahlgren et al. 2006; R. Torgerson, SITLA Biologist, personal communication). Based on male lek count data, the Parker Mountain sage-grouse population has been gradually increasing since 1998, with more dramatic increases reported recently (UDWR, unpublished data). The observed increases are likely the result of a combination of factors (i.e. range wide trends, improved surveys, improved habitat and weather conditions, and predator control).

### **Previous Research**

Jarvis (1974) conducted the first research on the Parker Mountain sage-grouse population. He concluded that golden eagles were a major predator of adult sage-grouse

and that the population may be limited by forb cover in brooding habitats, except in extremely wet years.

In 1998 the Parker Mountain Adaptive Resource Management (PARM) working group was formed, and Utah State University (USU) Extension began a research project to study female reproductive ecology using telemetric techniques (J. Flory, USU graduate student, unpublished data). The goal of this research was to identify limiting factors for the population, and then begin experimental management. Similar to Jarvis' (1974) findings, researchers reported low forb abundance in brooding habitat to be a limiting factor along with low chick survival (J. Flory, USU graduate student, unpublished data).

To determine if brood-rearing habitat could be improved, PARM implemented several management experiments from 2000-2002. In Parker Lake Pasture, they treated randomly-selected plots of mountain big sagebrush in brooding habitat with either Tebuthiuron (spike: 1.6 kg/ha at 0.3 active ingredient, 20P, N-[5-(1,1-dimethylethyl)-[5-<sup>14</sup>C]-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea, Dow AgroSciences 9330 Zionsville Road, Indianapolis, IN,USA), a Dixie harrow (mechanical), or a Lawson aerator (mechanical) to determine which management action would be most efficient at restoring herbaceous understory and elicit the most use by sage-grouse broods (Chi 2004, Dahlgren 2006).

The plots treated with Tebuthiuron showed the greatest improvement in forb cover and grouse-use response (Dahlgren et al. 2006). Following guidelines given in the above research, SITLA and the USDA Natural Resources Conservation Service (NRCS) have used a lower rate of active ingredient of Tebuthiuron application to treat more acreage of mountain big sagebrush within brooding habitat on Parker Mountain.

Recent research on the Parker Mountain sage-grouse population has led to other important research questions. Researchers have attempted to document juvenile survival by following radio-marked brood hens, though it has likely been underestimated due to a lack of marked chicks. This is because it is difficult to flush all chicks with a brood hen (Schroeder 1997), and the possibility of brood mixing/hopping can complicate observations. Once baseline juvenile survival rates are clarified, population modeling - given fecundity and survival of female sage-grouse - could be used to fully assess the population dynamics (i.e. future risks, management scenarios, and specific life-stage value to population trends). Brood counts have taken place on Parker Mountain for many years (L. Bogedahl, UDWR Biologist, personal communication). Brood counts are important measures for research and management, and currently, methods for sage-grouse brood counts are being refined (Walker et al. 2006). Additionally, sage-grouse harvest information from wing characteristics can yield important information for better understanding of population dynamics (Johnson and Braun 1997, Hagen et al. 2006). Recent research on Parker Mountain using telemetry could be used to verify harvest information.

The overall goals of this research were to; 1) improve our knowledge of chick survival, 2) gain a better understanding of population dynamics, and 3) evaluate monitoring methods for sage-grouse broods. The results of this research will give a more focused direction for managing greater sage-grouse. Due to the collaborative effort involved in this research, I used first person plural throughout this thesis. I used Journal of Wildlife Management guidelines for literature citations, figures, and tables (Chamberlain and Johnson 2008).



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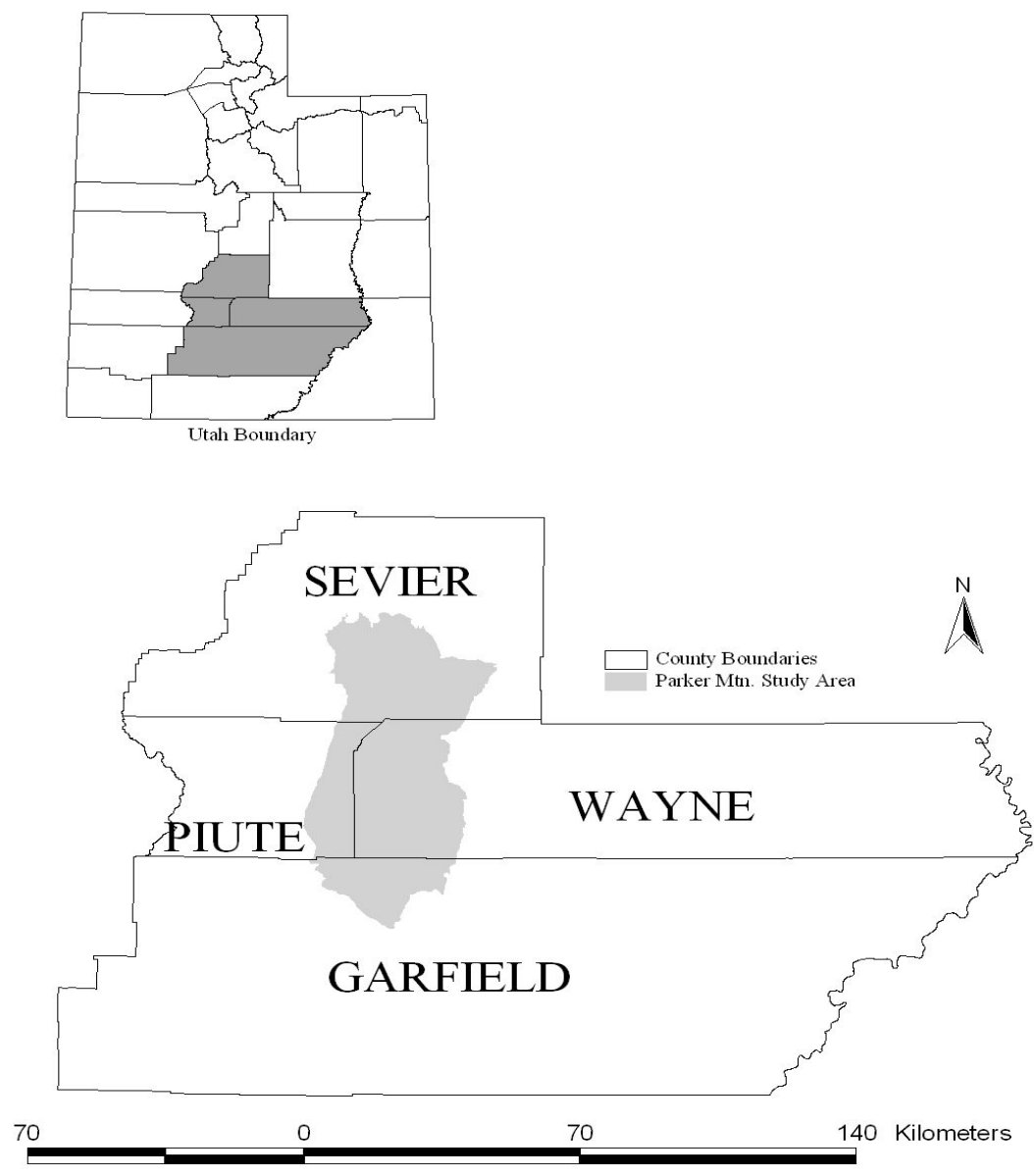


Figure 1-1. Parker Mountain Study Area (PSA), Utah, 2005-2007.

## CHAPTER 2

## ACHIEVING BETTER ESTIMATES OF GREATER SAGE-GROUSE

## CHICK SURVIVAL

**INTRODUCTION**

Range-wide greater sage-grouse (*Centrocercus urophasianus*) population declines have been attributed, in part, to environmental factors affecting production (Connelly and Braun 1997, Connelly et al. 2004). Recruitment, a key and highly variable component of production in North American grouse species (Tetraoninae), largely depends on chick survival (Bergerud 1988, Gotelli 2001). The qualities of brooding-rearing habitats are important components in greater sage-grouse (hereafter sage-grouse) recruitment (Drut et al. 1994, Connelly et al. 2000, Aldridge and Boyce 2007, Gregg et al. 2007).

Arthropod abundance can be especially important for the survival of young chicks (< 21 days old; Peterson 1970, Klebenow and Gray 1968, Johnson and Boyce 1990). Thompson et al. (2006) found sage-grouse productivity (measured by harvested wing samples and hens with broods) to be positively associated with arthropods (medium-sized Hymenoptera and Coleoptera) and herbaceous components of sagebrush habitats. Insect abundance may be related to plant diversity within sagebrush systems (especially intact sagebrush communities), but may be more highly associated with annual productivity (moisture dependent) within specific habitats (Wenninger and Inouye 2008). Thus, the relationship between insect availability and sage-grouse chick survival in a natural setting is poorly understood.

In addition to habitat quality and arthropod abundance, the age and experience of brood hens may also influence chick survival and productivity (Newton 1998). Curio



(1982) found that young birds (avian species in general) reproduce more poorly than older birds. In general, adult sage-grouse hens have a higher probability of nesting (Connelly et al. 1993), and may have higher chick survival than yearling hens (Gregg 2006).

Chick survival in sage-grouse has been difficult to study. Estimates reported from field studies have been low, even among studies where chicks were individually radio-marked (12% to 22% for the first few weeks of survival; Aldridge and Boyce 2007, Gregg et al. 2007). Additionally, post-hatch brood amalgamation (termed brood-mixing in precocial species), as a form of alloparental care may confound survival estimates from studies that did not include both radio-marked brood hens and chicks (Flint et al. 1995). Sage-grouse, when compared to other gallinaceous species, are relatively long-lived with lower reproductive output (Patterson 1952, Schroeder et al. 1999). Thus, they share life strategy characteristics with other species that brood-mix. However, this phenomenon has rarely been discussed in sage-grouse literature. Brood-mixing may afford adoptive parents several selective advantages to include increased survival of their progeny by earlier detection of predators and dilution of predation on natal offspring because of increased brood sizes (Riedman 1982). Concomitantly, younger, inexperienced mothers may improve their offspring's chances of survival by giving them up to older more experienced mothers (Eadie and Lumsden 1985, Eadie et al. 1988).

We monitored radio-marked sage-grouse brood hens and ~ 1-day-old sage-grouse chicks (Burkpile et al. 2002) to evaluate the temporal effects of chick age, brood-hen age, brood-mixing, hatch date, year, and arthropod abundance on chick survival. We hypothesized that yearling females are more likely to lose offspring *via* brood-mixing

events, and that offspring that leave their natal broods experience higher survival. Additionally, we hypothesized that arthropod abundance is associated with higher chick survival during the early brood-rearing period (< 21 days), when chicks are most susceptible to mortality due to lack of nutrition (Johnson and Boyce 1990). This research was conducted under protocols approved by the Utah State University International Animal Care and Use Committee (IACUC) permit # 945R.

## **STUDY AREA**

Parker Mountain is located in south-central Utah and is on the southern edge of greater sage-grouse range. The area is a high elevation (~ 2000-3000 meters) plateau that is largely dominated by black sagebrush (*Artemisia nova*), however there are also landscapes of mountain big (*A. tridentata vaseyana*) and silver (*A. cana*) sagebrush at the highest elevations (south and west sagebrush boundaries). This area has one of the largest contiguous blocks of sagebrush and one of the remaining stable populations of greater sage-grouse in Utah (Beck et al. 2003). Parker Mountain is largely public land including Bureau of Land Management (BLM), U.S. Forest Service (USFS), and State Institutional Trust Lands (SITLA). In general, the sage-grouse population uses lower elevation sagebrush landscapes for wintering, pre-laying, and lekking habitat; while hens gradually move up in elevation for nesting and brood-rearing activities, using the highest elevations and habitats along the southern and western boundaries of the Awapa Plateau (Chi 2004, Dahlgren 2006). Thus, late brood-rearing activities are concentrated at these elevations in most years. For more detailed information concerning the study area refer to Chapter 1.

## **METHODS**

### **Field Methods**

We captured and radio-marked female greater sage-grouse on or near leks during March and April of 2005 and 2006 (Geisen et al. 1982). Captured hens were fitted with 19g necklace-style radiotransmitters (Holohil Systems, Carp, Ontario, Canada). We re-located hens on their nest using telemetry and visually observed them using binoculars from > 10 meters to avoid disturbing the hen. We estimated the approximate hatch date using an incubation period of 27 days (Schroeder 1997). Throughout the incubation period we monitored nest fate every other day using binoculars. As the approximate hatch date approached we began daily monitoring of the nest. When a hen had ceased incubation we inspected the nest bowl to determine nest fate. If  $\geq 1$  egg hatched the nest was considered successful.

Within 24 - 48 hours of hatch we flushed successful radio-marked brood hens and captured all detected chicks by hand. Most broods were captured just before or after sunrise or sunset. We placed captured chicks in a brooding box with a heat source (a small lunch cooler with a hot water bottle) during handling. All chicks were weighed to the nearest gram, and a random subset were externally radio-marked with 1.5 gram transmitters (Advanced Telemetry Systems, Isanti, MN in 2005 and Holohil Systems, Carp, Ontario, Canada in 2006) using a suture technique (Burkepile et al. 2002). All chicks were radio-marked at the capture location, and we attempted to mark at least 3 chicks (maximum of 8) per brood.

Radio-marked broods were monitored every 1-2 days until chicks were 42 days old; however some monitoring periods were longer because of difficulty in locating the

radio-marked brood. The brood and brood capture sites were monitored the day after capture to assess chick death due to capture and handling. Ground-based telemetry was used throughout the 42 day monitoring period, and chicks in close proximity (~ 50 meters) to the radio-marked hen were assumed to be alive. Radio-marked chicks that were not detected near the radio-marked hen were subsequently searched for to attain a visual observation. If a radio-marked chick was found alive in another brood with an unmarked hen, the chick was classified as a brood-mixed chick (i.e., post-hatch brood amalgamation; Eadie et al. 1988). If a radio-marked chick was found dead, the remains, radio, and immediate vicinity were searched to determine cause of death.

Cause of death was classified as predation, exposure, and unknown. We recorded exposure as the cause of death if we found an intact chick body with no indication of predation. We identified predation as cause of death when the remains or radio indicated teeth or talon marks, or only the radio remained with some feathers and skin attached to sutures. It is possible that chicks may have died due to causes other than predation and were subsequently scavenged, though it was impossible to determine this outcome. Chicks that were found dead at the capture/marketing site with intact bodies and no signs of predation were determined to have died due to handling. Some chicks were not detected with the radio-marked hen at some point during the monitoring period, and were not found in another brood. These chicks were rigorously searched for in the last known location, and then radiating out (~ up to 3 km or more), for  $\geq 2$  consecutive days. Chick radios had a limited range (~ 300-400 meters straight line), and signals were very difficult to detect once a chick left the radio-marked hen. Additionally, missing chick frequencies were scanned for periodically throughout the remainder of the field season.

Arthropod sampling was conducted only in 2006. Sampling occurred once per week for each brood; however no random sites were used. Arthropod sampling sites were centered on the brood hen location. To capture arthropods, we used tin can (6.6 cm diameter, 11 cm depth) traps filled to ~ 4 cm from the bottom with a 50% water and 50% ethylene glycol (antifreeze) solution. Traps (n = 5 per site) were set at the crossing and ends of two 20-meter transects (random directions), and left open for approximately 48 hours. Arthropods were gathered and subsequently categorized by order (Orthoptera, Coleoptera, Hymenoptera, Lepidoptera, and miscellaneous, i.e., spiders). Ants were separated from the Hymenoptera order to be analyzed separately because of their availability, abundance, and importance to sage-grouse chicks compared to the rest of the order (Klebenow and Gray 1968, Peterson 1970, Fischer et al. 1996, Nelle et al. 2000). Volume (ml) displacement was used as the unit of measurement for arthropod abundance for each category and brood site. In addition to arthropod sampling, we conducted vegetation sampling at brood sites. However, we found no significant relationship between vegetation and chick survival. Methods and results for vegetation analyses are presented in Appendix B. We also assessed the relationship of arthropods and habitat (vegetation characteristics) using linear regression (Appendix B).

### **Statistical Analysis**

We first examined the influence of hen age on the probability of chicks leaving their broods in a brood-mixing event using logistic regression (Hosmer and Lemeshow 2000). We then estimated chick survival. Chicks classified as missing were assigned the following survival histories: analysis action; 1) missing chicks were right-censored from the dataset; analysis action, 2) missing chicks were treated as mortalities in a separate

analysis; and analysis action (Appendix A), and 3) missing chicks were treated as though they survived within their original broods in a separate analysis (Appendix A). Missing chicks may have resulted from radio failure (though never documented directly), death due to predation or exposure with subsequent scavenging that precluded our detection ability (i.e., burial by scavenger or predator, or carried off by an avian predator etc.), and/or an undetected (due to the weak signal from the small chick radio) brood-mixing event.

Right-censoring a missing chick (analysis action 1) provided our most unbiased estimate of chick survival if ‘missing’ occurred at random. However, analysis actions 2 and 3 provide a lower and upper limit to possible non-random fates of missing chicks as well as the estimates of chick survival (Appendix A).

Radio-marked chicks that were classified as ‘brood-mixed’ were right-censored from their original broods, and were assigned to a new brood. If a chick went missing after it brood-mixed, it was always right-censored from the dataset. We based this decision on our inability to detect weaker chick signals in broods where the hen was not radio-marked relative to the stronger signal from a natal radio-marked hen.

We estimated chick survival using a maximum likelihood extension to the Mayfield estimator (Manly and Schmutz 2001). To accommodate potential lack of independence among brood mates (Flint et al. 1995), the Manly and Schmutz model (2001) estimates the dependence in fates among brood members (denoted as  $D$ ) using a quasi-likelihood model with a normal approximation to binomial variance multiplied by  $D$ , a constant dispersion factor (Schmutz et al. 2001, Fondell et al. 2008). Estimating  $D$  takes into account all forms of heterogeneity (but does not distinguish between them)

influencing chick survival, including factors such as single predation events killing multiple chicks (i.e., fate dependence) and the influence of a brood hen on such events over the entire survival period. As the estimate of  $D$  nears the average brood size, the greater the dependence of fate among brood members, whereas the closer  $D$  is to 1, the more independent each brood member's fate is from the others. Moreover, the effects of chick age (measured categorically) and covariates (continuous or categorical) on chick survival can be estimated using a log-link function (McCulloch and Nelder 1989, Manly and Schmutz 2001).

Using this flexible modeling approach, we evaluated the impact of various combinations of a chick's age (7 day age classes up to a single 42 day age class), temporal variables (year: 2005 or 2006; hatch date denoted in Julian days), and individual characteristics of brood hens (hen age: yearling or adult; and brood type: mixed or not) on chick survival. When evaluating hen age we used a restricted data set that did not include 'mixed broods' because we could not collect information about these variables for unmarked hens of broods that marked chicks mixed into. To compare models we used a quasi-likelihood version of Akaike's Information Criterion explicitly calculated with the estimated  $D$  of each model, adjusted for sample size ( $QAIC_c$ ; Akaike 1973, Burnham and Anderson 2002). Unlike the *ad hoc* approach of calculating a  $\hat{\phi}$  value to correct AIC for overdispersion in the data,  $D$  is uniquely estimated for each model. As such, if the estimates of  $D$  between two competing models are different, their  $QAIC_c$  values can differ; even among the top few models (Manly and Schmutz 2001, Fondell et al. 2008). We further assessed the statistical precision of the  $\beta_i$ 's in our best models based on the extent to which 95% confidence intervals overlapped zero (Graybill and Iyer 1994).

We then evaluated the best parameterization of age-structured chick survival to 21 days, and further assessed the influence of arthropods on chick survival during this early brood-rearing period (days 1-21). Because sage-grouse chicks depend most on an arthropod diet during the early brood-rearing period (Johnson and Boyce 1990, Fischer et al. 1996), we modeled the effect of arthropod availability (based on volume displacement measures of abundance; continuous variables) on chick survival during this period alone. Measures of arthropod abundance included that for ants, bees, Hymenoptera (all families), Coleoptera, Orthoptera, Lepidoptera, miscellaneous (spiders etc.), and total arthropods. For this analysis we used a restricted dataset (only 2006 data were available) in which only observations of survival following arthropod sampling were used for each brood. Model selection was performed according to the methods described above. For all covariate analyses described above we included a null model in our *a priori* candidate set of models, designated as that with the best parameterization of age-structured chick survival but no covariates (Tables 2-1 and 2-3 – 2-4). All survival analyses were performed using recently updated statistical software developed by Manly and Schmutz (2001).

## RESULTS

In 2005 we had 21 radio-marked brood hens ( $n = 2$  unknown age,  $n = 11$  yearlings, and  $n = 8$  adults); while in 2006 we had 21 radio-marked brood hens ( $n = 21$  adults), 7 of which had broods in 2005. We captured and radio-marked 89 chicks in 21 broods and 61 chicks in 21 broods in 2005 and 2006 ( $n = 150$ ), respectively. Only 2.6% of the chicks ( $n = 3$  in 2005, and  $n = 1$  in 2006) were classified as deaths due to handling or radio-marking and all were excluded from survival analyses. Therefore, 146



individual chick survival histories were used to estimate survival to 42 days. During this study we recovered 2 radios with no feathers or skin attached to the sutures, which could have possibly torn out of the skin or radio casing (sloughed off). These 2 chicks, along with 24 others ( $n = 26$ ) had unknown fates (missing from the original radio-marked hen broods), and were right-censored from the data set. All other recovered radios ( $n = 44$ ) had direct indications of predation or scavenging. Captured chicks per brood ranged from 1 to 8. The mean mass of chicks was 29.5 g ( $SE = 0.16$ ) and thus radio transmitters averaged 5.1% ( $SE = 0.0003$ ) of chick body mass at capture time. All marked hens returned to their brood by the following day and most within a few minutes of brood release.

Brood-mixing occurred with 21% (31/146) of radio-marked chicks, and within 43% (18/42) of monitored broods. We documented 2 radio-marked brood hen mortalities during the brood monitoring period. In each case all radio-marked chicks were assimilated into unmarked broods within 48 hours of the documented hen mortality. In 45% (9/20) of brood-mixing events, multiple radio-marked chicks (2 or 3) left their original broods and joined new broods (unmarked hens) at the same time; one multiple-mixing event was due to brood hen mortality. The probability of brood-mixing differed by hen age ( $\beta_{\text{hen age}} = 1.57$ ,  $SE = 0.75$ ) and was notably higher in broods with yearling hens ( $P_{\text{yearling}} = 0.63$ ) relative to adult hens ( $P_{\text{adult}} = 0.27$ ). In 2005 all but 1 (a hen of unknown age) of the brood-mixing events occurred with yearling hens, though we were unable to test for year effects because in 2006 all radio-marked brood hens were adults. Disregarding mixing events due to brood hen mortality, multiple chick mixing occurred in 71% (5/7) of yearling hen broods, and in only 20% (2/10) of adult hen broods

Brood-mixing occurred during weeks 1 to 6 of chick development, with 70% (14/20) of brood-mixing events taking place within weeks 2 and 3. Additionally, we found chicks from unmarked broods mixing into marked broods. We documented chicks that exceeded the range of chick weights (24-36g) for 1 or 2 day old chicks when capturing broods within 24-48 hours of hatch, and presumably mixed into radio-marked broods during this time. Moreover, observations recorded when chicks were inadvertently flushed later in the monitoring period suggested a marked increase in the number and size (relative to known age) of flushed chicks within a given brood. We assumed this a consequence of brood-mixing into the marked brood.

Predation accounted for 32% (38/120) of known chick fates. Of the documented chick predations, we attributed predation to avian (n = 8), mammalian (n = 8), and unknown (n = 22) causes. For the mammalian depredated chicks, 50% (n = 4) were found underground in long-tailed weasel (*Mustela frenata*) dens. We attributed 6 deaths to exposure.

The top-ranked model for age-specific chick survival indicated differences in survival among weeks 1, 2, 3, 4, and 5-6 (Table 2-1), and a 0.60 (95% CI: 0.51 - 0.72) probability of sage-grouse chicks surviving to 42 days. The  $\beta_i$ 's for the age-specific mortality hazards were as follows: week 1 ( $\hat{\beta} = 0.019$ , SE = 0.006); week 2 ( $\hat{\beta} = 0.018$ , SE = 0.006); week 3 ( $\hat{\beta} = 0.006$ , SE = 0.004); week 4 ( $\hat{\beta} = 0.017$ , SE = 0.007); and weeks 5-6 ( $\hat{\beta} = 0.007$ , SE = 0.003). Estimated heterogeneity of chick survival (D) in our top-ranked model for age-specific chick survival was 1.31 (95% CI: 0.97 – 1.65), indicating low dependence in fates among brood mates. When additional covariates were

added to this model, we found little support for year or hatch-date effects on chick survival (based on QAIC<sub>c</sub> and 95% CIs for  $\beta_i$ 's that greatly overlapped zero; Table 2-1).

We did, however, find that brood type (mixed or not) affected chick survival (top model based on QAIC<sub>c</sub>, Tables 2-1 and 2-2). Based on the age and brood-type model, the effect of brood-type on chick survival was likely of biological importance but imprecisely estimated (95% CI overlapped zero;  $\hat{\beta}_{mixed} = 0.0072$ , 95% CI: -0.01 – 0.02). Averaged together, chicks in both brood types had a survival rate of 0.50 to 42 days (95% CI: 0.41 – 0.61), and separately chicks in non-brood-mixed broods had a survival rate of 0.48 (95% CI: 0.37 – 0.58) to 42 days, while chicks in brood-mixed broods had a survival rate of 0.65 (95% CI: 0.42 – 0.88) to 42 days. Accordingly, brood-mixed chicks had consistently higher estimates of daily survival rates to 42 days (Fig. 2-1, and Table 2-2). According to our best models for analysis actions 2 (low) and 3 (high) chick survival estimates were 0.41 (SE = 0.05) and 0.61 (SE = 0.10), respectively (Appendix A). Estimated heterogeneity of chick survival (D) in our brood-type (best) model was 1.01 (95% CI: 0.49 – 1.54), indicating even lower dependence in fates among brood mates when the brood-type covariate is added to the age-effects model. When we assessed brood hen characteristics (restricted data set) our best model included an effect of hen age ( $\hat{\beta} = -0.01$ , 95% CI: -0.0223 – -0.0017) indicating higher chick survival for yearling hens.

During the early brood-rearing period (days 1-21), arthropod abundance, specifically Orthoptera, Lepidoptera, Coleoptera, and ants, appeared to influence chick survival (based on QAIC<sub>c</sub> criteria that beat the null model; Table 2-4). However, all  $\beta_i$ 's in the top models were imprecisely estimated (95% CIs greatly overlapped zero).

This may have occurred because of our restricted sample size ( $n = 59$  survival periods), and thus, we were not able to attain precise estimates of these biologically important relationships.

## **DISCUSSION**

Our best estimates of greater sage-grouse chick survival to 42 days exceeded previously published reports. Gregg et al. (2007) reported a considerably lower survival rate of 0.22 to only 28 days for chicks marked with subcutaneous implanted radios. Furthermore, Aldridge and Boyce used radio-marked chicks (same methods as we used) and reported a survival probability of 0.12 to 56 days. Our chick survival was also higher than estimates reported in studies that assessed survival (0.33) of unmarked sage-grouse chicks during the same approximate period (Schroeder 1997).

Brood-mixing was a common occurrence among our radio-marked chicks and broods, and was our most important factor in model structure based on covariates. Eadie et al. (1988) hypothesized that density of broods may influence brood-mixing. Our findings from Parker Mountain may support this hypothesis because sage-grouse broods generally concentrate in high elevation late brood-rearing habitat at southern and western edges of Parker Mountain. Further research testing this hypothesis is warranted.

The estimated effects of brood-mixing on chick survival differed by our analysis actions concerning missing chicks. When we right censored missing chicks (analysis action 1), the higher survival rates in brood-mixed chicks was associated with some uncertainty (95% CI overlapped zero). However, when missing chicks were classified as dead (analysis action 2), we could be more certain that brood-mixed chicks had a higher

survival than their counterparts that did not mix (95% CI did not overlap zero). Lastly, when missing chicks were classified as surviving within their original broods, the brood type model did not rank higher than the null model and beta estimates were not significant. However, in all cases marked chicks that brood-mixed had relatively higher daily survival estimates (Fig. 2-1, Table 2-2, and Appendix A), suggesting that brood-mixing may be advantageous for chick survival (Eadie et al. 1988, Nastase and Sherry 1997).

Nastase and Sherry (1997) indicated that brood-mixing for Canada geese (*Branta canadensis*) aided survivorship of native brood members. However, our results, suggest that brood-mixing may increase the survival of chicks that are adopted into unmarked broods. We could not determine whether brood-mixing actions were initiated by chicks in an attempt to improve their fitness, or by adoptive mothers attempting to improve their fitness by increasing the chances of survival in their natal offspring.

Eadie et al. (1988) hypothesized that parental age or experience may influence brood-mixing behavior. Although we could not address yearly effects (no yearling brood hens in 2006), in 2005 brood-mixing and more multiple-chick mixing occurred in broods reared by yearling hens. This suggests that brood hen age may be an important factor concerning brood-mixing in sage-grouse. Our results lend support for the hypothesis that chicks born to a young female are more likely to join the brood of an experienced female, such that the young female may increase her own fitness by abandoning her young rather than bearing the cost of raising them herself (Eadie et al. 1988).

On our study area brood-mixing appeared to abate the potentially deleterious impact of brood hen mortality when orphaned chicks were quickly assimilated into

surrogate hens broods. Brood-mixing of young in the event of parental mortality has not been discussed in previous works as an adaptive survival strategy, nor in relation to avian alloparental care (Riedman 1982, Eadie et al. 1988). The frequency and biological importance of this novel finding warrants further study.

Our monitoring may have increased the amount of brood-mixing by potentially simulating a predatory event. We found that brood hens would often spread their chicks out and attempt to decoy us away from their broods. If other brood hens were in the area following our departure, distressed chicks could have easily been adopted (mixed) by other, unmarked brood hens. The monitoring/observer effect on the probability of brood-mixing needs further investigation, and could potentially be examined by using observer-effect nest survival (also a probability of “occurrence”) models (Rotella et al. 2000).

Schroeder (1997) reported that hen age did not appear to be an important factor in chick survival. Gregg (2006) reported the opposite. We found a possible inverse effect of hen age on chick survival with analysis actions 1 and 3 (but not with analysis action 2), indicating that yearling hens had higher chick survival than adult hens. This was an unexpected finding given the importance of adult females in long-lived, low reproductive species, such as sage-grouse (Johnson and Braun 1999, Connelly et al. 2000), and our finding that yearling hens had a higher probability of losing chicks to brood-mixing. Higher chick survival for yearling hens may have been the consequence of only the “best” yearling hens making it to the brooding stage and rearing their own chicks. The majority of yearling hens were eliminated from the brood hen sample due to lower nest initiation rates and lower nesting success. Moreover, the chicks of yearling hens were more apt to mix into other broods with unmarked hens. In these events, chicks were right-

censored from yearling hen broods due to brood mixing, and were not included in the hen age analysis, which further decreased the sample size of chicks within yearling hen broods. Thus, for a number of reasons, within-generation selection may have resulted in only the best yearling hens being included in most of our sample (Vaupel and Yashin 1985). In addition, we only had yearling hens in 2005 and were not able to assess temporal effects by hen age. Though it is possible that yearling hens could experience higher average chick survival than adult hens, we strongly suggest caution concerning interpretation of our results.

We did not find any indication of life-fate dependence among brood mates within our analyses. By explicitly estimating  $D$ , the Manly and Schmutz (2001) method accounts for the amount of heterogeneity/dependence in survival among brood mates. Our estimate of  $D$  for our survival model with the best parameterization of chick age (Table 2-1) did not differ from 1.00 (nor with analysis actions 2 and 3; Appendix A). Moreover, our model that best captured variation in chick survival (chick age plus brood-type model) yielded an estimate that also did not differ from 1.00 (based on 95% C.I.). The estimate of brood-mate dependence in survival improved by including brood-type (i.e., more covariate structure) in our model, but still indicated no dependence in fates among brood mates. Thus, sage-grouse chick mortality may very well be independent of other brood members, which may be associated to the habitats in which they live, the predator community, and the behavior of brood hens in response to predators.

Aldridge (2005) found that herbaceous and shrub cover had important impacts on sage-grouse chick survival at various landscape scales. Additionally, Gregg (2006) found that vegetation at brood sites influenced chick survival. The vegetation parameters we

measured and brood sites could not predict chick survival (Appendix B). We measured vegetation characteristics at relatively small scales (40-meter transect per brood location site). Furthermore, predation was our most common cause of mortality, and the relationships between habitat, predation, and early life-cycle survival likely occur at much larger scales than we measured (Stephens et al. 2005). Dahlgren et al. (2006) found that sage-grouse broods on the same study differentially selected habitat during the late brood-rearing period based on 40.5 ha plots.

Though we found no relationship between arthropods and vegetation measurements (Appendix B), our results suggested that arthropod abundance in the immediate vicinity of broods may have influenced chick survival during the early brood-rearing period. This is consistent with findings for captive reared sage-grouse chicks (Johnson and Boyce 1990). Fischer et al. (1996) found that sage-grouse broods were selecting specific habitat that had higher abundance of Hymenoptera than random sites. All arthropods were important for our analysis, but specifically Orthoptera, Lepidoptera, Coleoptera, and ants (within Hymenoptera) accounted for more variation in chick survival than other orders. Connelly and Braun (1997) suggested that low quality early brood-rearing habitat was related to declines in sage-grouse population recruitment. However, our vegetation modeling results lacked significant estimates of the covariate coefficients ( $\beta_i$ 's). This could be an artifact of low sample sizes. Therefore, more research and evaluation with larger sample sizes may be needed to better estimate the relationships between arthropod abundance and sage-grouse chick survival, particularly for the early brood-rearing period.



## MANAGEMENT IMPLICATIONS

The Parker Mountain greater sage-grouse population we studied exhibited the highest chick survival rates and occurrences of brood-mixing reported in published literature. The increased incidences of brood-mixing, which may be a reflection of the availability of brood-rearing habitat and thus brood density, afforded the Parker Mountain sage-grouse population a novel adaptive survival strategy. Because of the role of long-lived adult hens in brood-mixing, and ultimately production, it is important to conserve this segment of the population. Our study also confirmed that in areas where brood-mixing may occur, chick survival rates obtained without radio-marking individuals, and other non-radio-marking methods (e.g., pit tags, leg bands, etc.) will underestimate survival.

In a captive setting, sage-grouse chick survival during the first few weeks of life depended on arthropod availability (Johnson and Boyce 1990). Our field research confirmed that arthropod availability was related to sage-grouse chick survival. However in our study, we could not detect any relationship between the vegetation parameters measured and arthropod abundance. More information is needed regarding the factors that influence arthropod abundance (e.g. precipitation, habitat management, etc.) as it relates to annual sage-grouse production and population dynamics.

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Table 2-1. Models of weekly greater sage-grouse (*Centrocercus urophasianus*) chick survival for both non- and brood-mixed brood, and covariate comparison of brood type (regular or mixed), hatch date (Julian days), and year (2005 or 2006), Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age = (week1)+(week2)+(week3)+(week4)+(weeks5-6)	6	93.96	0.00	0.99999
age = (week1)+(week2)+(week3)+(weeks4-6)	5	121.01	27.04	0.00000
age = (weeks1-2)+(weeks3-4)+(weeks5-6)	4	124.33	30.36	0.00000
age = (weeks1-2)+(weeks3-6)	3	134.22	40.25	0.00000
age = (week1)+(week2)+(weeks3-6)	4	135.83	41.86	0.00000
age = (week1)+(weeks2-6)	3	156.17	62.20	0.00000
age = (weeks1-3)+(weeks4-6)	3	164.64	70.67	0.00000
age = (weeks 1-6)	2	168.88	74.91	0.00000
<u>Covariate Model Comparison</u>				
age* + brood type	7	39.21	0.00	0.99999
age* (Null Model)	6	93.96	54.76	0.00000
age* + hatch date	7	111.96	72.75	0.00000
age* + year	7	126.37	87.16	0.00000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (week1) + (week2) + (week3) + (week4) + (weeks5-6), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.



Table 2-2. Estimates of greater sage-grouse (*Centrocercus urophasianus*) chick daily survival rates for non- and mixed broods based on our best model (QAIC<sub>c</sub>; brood-type), Parker Mountain, Utah, 2005-2006.

*Age	$\beta_i$ 's	SE	Non Brood-mixed		Brood-mixed	
			DSR	SE	DSR	SE
Week 1	0.023	0.007	0.977	0.007	0.984	0.010
Week 2	0.026	0.008	0.975	0.009	0.982	0.011
Week 3	0.007	0.003	0.993	0.003	1.000	0.008
Week 4	0.023	0.007	0.977	0.008	0.984	0.010
Week 5-6	0.013	0.004	0.987	0.004	0.994	0.008

DSR: daily survival rate for each week

SE: standard Error

\* the null model age structure (in weeks) was determined by QAIC<sub>c</sub> values in Table 1.

Table 2-3. Models assessing the impact of greater sage-grouse (*Centrocercus urophasianus*) brood hen age (restricted data set without mixed broods because hen age was not determined for broods that radio-marked chicks mixed to) on chick survival, Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age = (week1)+(week2)+(week3)+(week4)+(weeks5-6)	6	152.86	0.00	0.99999
age = (week1)+(week2)+(week3)+(weeks4-6)	5	171.62	132.41	0.00000
age = (weeks1-2)+(weeks3-4)+(weeks5-6)	4	176.90	137.69	0.00000
age = (week1)+(week2)+(weeks3-6)	4	181.85	142.64	0.00000
age = (weeks1-2)+(weeks3-6)	3	182.88	143.68	0.00000
age = (week1)+(weeks2-6)	3	185.11	145.91	0.00000
age = (weeks 1-6)	2	198.15	158.95	0.00000
age = (weeks1-3)+(weeks4-6)	3	198.83	159.63	0.00000
<u>Covariate Model Comparison</u>				
age* + hen age (yearling or adult)	7	41.31	0.00	0.99999
age* (Null Model)	6	152.86	111.60	0.00000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (week1) + (week2) + (week3) + (week4) + (weeks5-6), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.

Table 2-4. Models for greater sage-grouse (*Centrocercus urophasianus*) chick survival during the early brood-rearing period (days 1 – 21) based on arthropod sampling at brood sites (data set restricted to arthropod sampling periods, which did not change based on differing assumptions), Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age = (weeks 1-2)+(week3)	3	30.41	0.00	0.565476
age = (week1)+(week2)+(week3)	4	32.11	1.70	0.241165
age = (weeks 1-3)	2	33.13	2.73	0.144562
age = (week1)+(week2-3)	3	35.31	4.90	0.048797
<u>Covariate Model Comparison</u>				
age* + Orthoptera	5	15.60	0.00	0.473688
age* + each arthropod type separately	9	15.99	0.39	0.389495
age* + Lepidoptera	5	18.11	2.51	0.135037
age* + Coleoptera	5	28.62	13.02	0.000705
age* + ants	5	29.24	13.64	0.000517
age* (Null Model)	3	30.41	14.80	0.000289
age* + bees	5	31.24	15.64	0.000190
age* + total arthropods	5	33.65	18.05	0.000000
age* + Hymenoptera	5	35.60	20.00	0.000000
age* + Miscellaneous	5	45.26	29.66	0.000000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (weeks 1-2) + (week3), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.

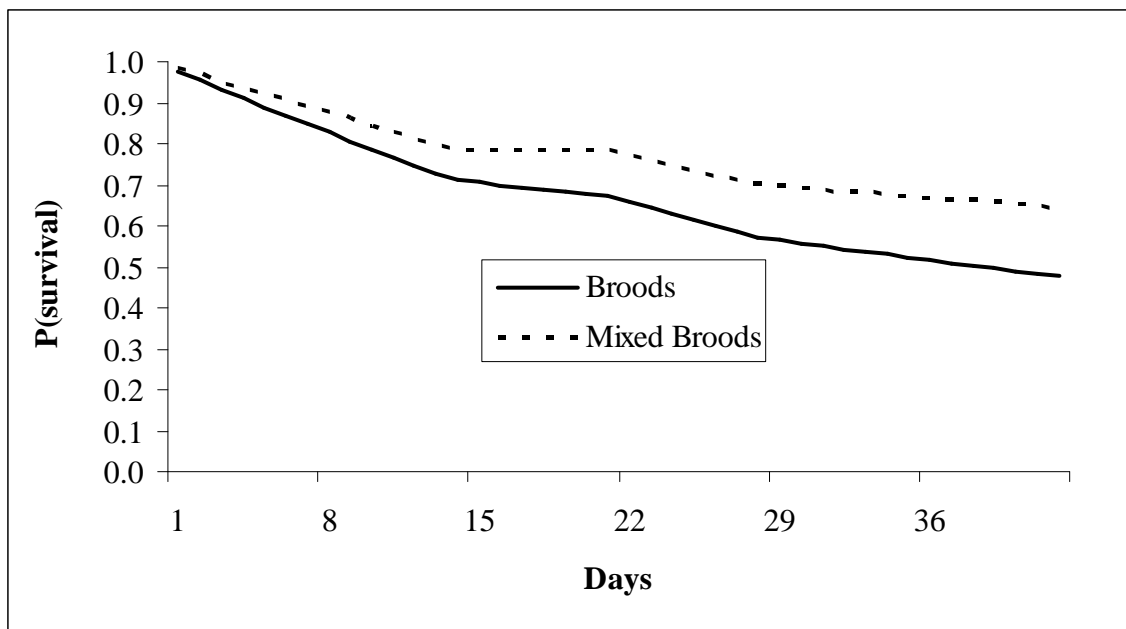


Figure 2-1. Survivorship curve for greater sage-grouse (*Centrocercus urophasianus*) chicks (see Table 2 for precision estimates), Parker Mountain, Utah, 2005-2006.

## CHAPTER 3

ESTIMATION OF GREATER SAGE-GROUSE SURVIVAL,  
PRODUCTIVITY FACTORS, AND LIFE-CYCLE MODELING**INTRODUCTION**

The largest of North American grouse (tetraonid), greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) inhabit sagebrush (*Artemisia* spp.) dominated landscapes in western North America. They depend on sagebrush for food and habitat throughout their life cycle (Connelly et al. 2000a, Schroeder et al. 2004). Conversion and fragmentation of these sagebrush habitats, anthropogenic developments, mismanagement of grazing, cheatgrass invasion and wildfire, other habitat degradation, and disease have led to the decline of many sage-grouse populations (Braun et al. 1977, Connelly and Braun 1997, Connelly et al. 2004). In response to rangewide population declines, several organizations have petitioned the U. S. Fish and Wildlife Service (USFWS) to list the species for protection under the Endangered Species Act. In 2005, the USFWS ruled that listing the species was unwarranted. However, in response to a federal ruling in 2007 the USFWS is currently reviewing the species' status (USFWS 2008).

Although sage-grouse are a relatively long-lived species, their relatively low reproduction rate and high dependence on sagebrush habitats creates a conservation dilemma (Schroeder et al. 1999, Connelly et al. 2000a). To address this dilemma, better information is needed regarding the impact of biological factors on reproductive success, and ultimately productivity, for application to landscape management.

Life-cycle modeling may help address this information need. Parameterization of known life-cycle data through modeling can facilitate an objective examination of the amount and quality of existing demographic data for a specific species and/or population (Koons et al. 2006). In this way, modeling can help managers identify information gaps. Projection and perturbation of life-cycle models also help managers and scientists understand how vital rates (e.g., clutch size, chick survival, adult survival, etc.) and age structure affect population dynamics (Caswell 2001). Crude predictions about these functional relationships can be derived from basic attributes of a species' life history (Sæther and Bakke 2000).

In the case of sage-grouse, reproductive parameters may be the most important factors to consider when trying to reverse population declines (Connelly and Braun 1997, Connelly et al. 2000a, Crawford et al. 2004). Differences in these parameters across age classes may also be important. For example, Connelly et al. (1993) showed that adult hens are more successful at initiating nests than yearling hens.

Without a validated population model to guide management decisions, it would be more difficult to select the appropriate tool to best achieve management goals (e.g., habitat conservation, habitat manipulation, harvest regulation, predator management, or various combinations). Prospective analysis of a life-cycle model (e.g., sensitivity and elasticity analysis) developed from available life-history data can be used to estimate the effect of hypothetical changes in various vital rates on population dynamics such as the rate of population growth (e.g., Caswell 1978). Sensitivity analysis measures the effect of unit changes in demographic parameters on population growth rate, while elasticity analysis measures the effect of relative changes (i.e., percentage changes) in demographic

parameters on population growth rate (de Kroon et al. 2000). These metrics can be used to identify key parameters that require better statistical estimation, and thus direct future research efforts (Caswell 2001). Sensitivity and elasticity analyses can also provide insight into the aspects of a life-cycle that may be the most appropriate targets for management, with the confidence in inference being contingent on the quality of available data (Akçakaya and Raphael 1998, Cooch et al. 2001, Clutton-Brock and Coulson 2002).

Additional insight into mechanisms of population change can be gained by conducting retrospective perturbation analyses, such as Life Table Response Experiments (LTRE; Horvitz et al. 1997). The LTRE can be used to quantify the contribution of “actual” change in vital rates to historic changes in population growth rate (Caswell 2001, Oli et al. 2001, Dobson and Oli 2001). Even if a vital rate has a small to moderate sensitivity value, it can still contribute greatly to actual changes in population growth if the vital rate changes by a higher degree over time (or space) than other vital rates. Retrospective information such as this can identify those vital rates that may be more malleable to management actions and have important impacts on population dynamics (Caswell 2000).

Johnson and Braun (1999) used prospective perturbation techniques and population viability analysis to examine the dynamics of the North Park, Colorado, sage-grouse population. Yet, they based their survival and reproductive parameters on data from harvested wing samples and had to make the following assumptions: 1) that age and sex ratios do not change from breeding to the start of the hunting season, 2) all classes of birds are exploited by hunters in proportion to their abundance in the population, and 3)

winter survival is not sex-biased. By using radio-telemetry data, these limiting assumptions could be relaxed. However, life-cycle models for sage-grouse have not yet been developed with data from uniquely marked individuals and this is likely due to the lack of long-term (multiple years) monitoring of radio-marked individuals in a single population.

Population change of sage-grouse has often been assessed using lek counts (Connelly et al. 2004, Reese and Bowyer 2007); leks are areas where sage-grouse males conduct mating displays (Patterson 1952). Habitat around lek sites typically offers high visibility, and this - combined with the prominent visual and auditory displays of male sage-grouse - make lek sites relatively easy to find (Schroeder et al. 1999). Additionally, lek locations are relatively temporally persistent (Dalke et al. 1963). Thus, this mating strategy has provided managers with an opportunity to collect information about the status of populations by counting the number of males during the breeding season. Counts of male sage-grouse have occurred throughout much of this species' range since the 1960s (Connelly et al. 2004).

The Utah Division of Wildlife Resources (UDWR) has compiled lek count data into their annual upland game reports (UDWR 2008). However, the use of lek count data for assessing population trend has come under increased scrutiny (Beck and Braun 1980, Walsh et al. 2004, and Reese and Bowyer 2007). By comparing both female-based population modeling and lek count data a better understanding of population assessment may be gained.

The purpose of this paper is to describe biological factors affecting the productivity and viability of the Parker Mountain greater sage-grouse population. To



accomplish this we first estimated survival and reproductive parameters using 9 consecutive years (1998-2006) of data collected on a radio-marked sample of female sage-grouse at Parker Mountain, Utah. We then use these estimates to develop a matrix projection model and conduct both prospective (sensitivity and elasticity) and retrospective (LTRE) perturbation analyses to evaluate the contribution of age-structured vital rates to the finite population growth rate ( $\lambda$ ). We developed four hypotheses; 1) adult hens have higher nest initiation rates, nest success, and brood success when compared to yearling hens, 2) adult survival and reproductive parameters have the greatest influence on finite growth rate for the Parker Mountain sage-grouse population, 3) hunter harvest is proportional to modeled age distribution, and 4) population growth rates resulting from modeling do not differ from growth rates derived from lek counts. Data for this research was collected by three graduate students; Joel Flory (1998-1999), Renee Chi (2000-2002), and David Dahlgren (2003-2006). This research was completed under Utah Division of Wildlife Resources (UDWR) Certificate of Registration (COR) # 5BAND3969, and the Utah State University International Animal Care and Use Committee (IACUC) # 945R.

## **STUDY AREA**

Parker Mountain is located in south-central Utah and is on the southern edge of greater sage-grouse range. The area is a high elevation (~ 2000-3000 meters) plateau that is largely dominated by black sagebrush (*A. nova*); however, there are also landscapes of mountain big (*A. tridentata vaseyana*) and silver (*A. cana*) sagebrush at the highest elevations (south and west sagebrush boundaries). This area has one of the largest contiguous blocks of sagebrush and one of the larger populations of greater sage-grouse

remaining in Utah (Beck et al. 2003). Parker Mountain is largely public land including Bureau of Land Management (BLM), U.S. Forest Service (USFS), and State Institutional Trust Lands (SITLA). In general, the sage-grouse population uses lower elevation sagebrush landscapes for wintering, pre-laying, and lekking habitat; while hens gradually move up in elevation for nesting and brood-rearing activities, using the highest elevations and habitats along the southern and western boundaries of the Awapa Plateau (Chi 2004, Dahlgren 2006). For more detailed information concerning the study area refer to Chapter 1.

## **METHODS**

### **Estimation of Survival and Reproductive Rates**

*Field methods.*— In the spring of 1998-2006 female sage-grouse were captured on or near leks and marked with 21-gram (1998-2004, Advance Telemetry Systems, Isanti, MN, USA) or 19-gram (2005-2006, Holohil Systems, Carp, Ontario, Canada) necklace-style radios (Geisen et al. 1982). Both radio types produced a mortality signal 8 hours after movement ceased. During late April (1998-2000) and May (1998-2006) radio-marked hens were monitored to assess nest initiation rates. We visually re-located hens on their nest by carefully circling the nest using telemetry gear and binoculars from >10 meters to avoid disturbing the hen and inadvertently flushing her from the nest. When possible, we estimated the approximate hatch date using an incubation period of 27 days (Schroeder 1997). For the majority of the incubation period we monitored nest fate every other day using binoculars. When a hen had ceased incubation we inspected the nest bowl to determine nest fate. If >1 egg hatched the nest was considered successful.

Following a successful nest, radio-marked hens and their broods were monitored regularly (~ every 3 days 1998-2004, and ~ every 2 days 2005-2006). We noted inadvertent flushing of chicks during the first 6 weeks following hatch, but attempted to keep disturbance of the brood to a minimum. Throughout the study period (1998-2006) brood success (or fledgling success; as defined in Aldridge and Brigham 2001) was estimated as the proportion of successfully hatched broods where  $\geq 1$  chick (marked or unmarked) was observed alive  $\geq 42$  days following hatch. From 2002-2006 pointing dogs were used during this time to assist with detection of chicks. In 2005-2006 we radio-marked a sample of individual chicks within 24-48 hours following hatch within our radio-marked hen broods (see Chapter 2). If by 42 days all radio-marked chicks had left the brood, radio-marked hen broods were still monitored using telemetry and pointing dogs for detection of unmarked chicks. This approach largely ignored brood-mixing behavior which may underestimate brood success (see Chapter 2), but was used for consistency across all 9 years.

Survival of yearling and adult hens was monitored throughout the study. We made a rigorous effort (ground and aerial) each spring (April-May) to locate all extant radio-marked hens. Those hens that did not produce a brood were monitored ~ once per week (1998-2004), or at least once again in July or August (2005-2006). Aerial monitoring by a fixed-wing aircraft occurred in the majority of years during late fall and/or late winter. Additionally, a small sample of radio-marked hens were harvested and reported during the Fall UDWR sage-grouse hunting season (1998-2006). The UDWR also collected samples of wings (1998-2003 and 2006) for harvested grouse using

wing barrels at each exit from the study area. Wings were characterized by age and sex using the protocol in Beck et al. (1975).

Clutch size was monitored when possible. We were able to obtain clutch size by counting hatched egg parts, observing the nest while the hen was not incubating (rare), or when accidental flushing occurred (also rare). Generally, we were careful not to disturb radio-marked hens during incubation. We did not include depredated nests in our clutch size sampling. Infertility of eggs in entire or partial clutches was also noted.

*Data Analysis.*— Program MARK was used to estimate survival and various reproductive rates of radio-marked female sage-grouse (White and Burnham 1999). For each demographic parameter we developed alternative models designed to capture potential age (yearling vs. adult) and time variation, or both. We considered continuous time covariates for factors (all years different), and constrained factors (dummy variables representing low, medium, and high, or simply low and high survival and/or reproductive rates in a given year based on preliminary estimates). Null models were also considered (i.e., no age, or no time variation). For all demographic parameters the best model for age and time variation was selected using Akaike's Information Criterion adjusted for sample size (AICc; Akaike 1973, Burnham and Anderson 2002) within program MARK.

Specifically, logistic regression (known fate analysis in program MARK) was used to examine age and temporal variation in nest initiation and brood success rates. Other than 2005-2006, we had no reliable telemetry-based data concerning the number of chicks fledged per 'successful' brood. Thus, the number of chicks fledged per successful brood was estimated as the proportion of radio-marked chicks still alive 42 days after

hatch in the sample of broods that were successful in 2005-2006 (see Chapter 2). This measure was later extrapolated across all study years in the life-cycle models.

Nest checks and eventual fates (survived or failed) were used to estimate daily survival rates (DSR) of nests as well as variation in DSRs across years and age (nest survival module in program MARK). The sage-grouse nesting period consisted of 7 days for laying (1 day per egg using the average clutch size; Schroeder 1997) and 27 days of incubation, yielding a total of 34 days. Overall nest survival was thus estimated as:  $DSR^{34}$ . Because modeling was done on a logit-transformed response variable, we estimated the variance and standard errors of DSRs and nest survival (using an exposure time of 34 days) using the delta method (Seber 1982).

The irregular monitoring of radio-marked yearlings and adults throughout a given year was best suited for attaining direct estimates of monthly survival (MSR). Variation in MSR across ages and years was modeled using the logit-link and nest survival module in program MARK. Rather than a known-fate analysis, this approach was used because it allows for staggered entry, right-censoring, and irregular monitoring of marked individuals (Rotella et al. 2004). Occasionally, individual hens “disappeared” (a radio signal was not detected during ground and aerial searches) from our sample, and were right-censored at their last known survival period. Annual survival for a given year and age class was then estimated as  $MSR^{12}$ . Corresponding estimates of variances and standard errors were attained using the delta method, as described above.

The only demographic parameter for which we did not have data was fledgling survival. Therefore, we approximated fledgling survival (survival from 6 weeks post-hatch to the next breeding season) using the MSRs for yearling females on our Parker

Mountain study area. This period of survival is 8 months long (August–March), and thus fledgling survival in a given year was estimated as MSR<sup>8</sup>. Beck et al. (2006) reported estimates for fledgling survival on two different study areas (0.64 and 0.86) that we could have used; however, our approach yields estimates that are within their reported range, and we further feel that basing the calculations on data for yearlings at Parker Mountain may be more representative of the local environmental conditions that 1<sup>st</sup>-year individuals experience on our study area.

### **Life-cycle Modeling**

Once vital rates (survival and reproduction) were estimated across years and age-classes, a female-based table of vital rates was constructed for the Parker Mountain sage-grouse population from 1998-2006 (Table 3-1). Based on the best-performing statistical model for each vital rate the data consisted of: survival rates for yearling and adult hens, age-specific nest initiation rates, average clutch size, average infertility measures, age-specific nest survival, brood success, proportion of chicks fledged per successful brood, and fledgling survival rate. From these data, a 2-stage projection matrix (**A**) was computed for each year assuming a pre-breeding census and birth-pulse reproduction. Each matrix consisted of yearling (<sub>1</sub>) and adult (<sub>2</sub>) fertility (*f*) and survival (*S*):

$$\mathbf{A} = \begin{pmatrix} f_1 & f_2 \\ S_1 & S_2 \end{pmatrix}$$

Age-specific survival is described above. Age-specific fertility was computed for each age-class using the following equation:

$$f_x = NI_x * (CS - INF) * 0.50 * NS_x * BS * PCSB * FS ,$$

where

$NI_x$  = age-specific nest initiation rate

$CS$  = average clutch size

$INF$  = average number of infertile eggs in a clutch

$NS_x$  = age-specific nest survival rate

$BS$  = brood success

$PCSB$  = proportion of chicks fledged per successful brood

$FS$  = fledgling survival

The 0.50 in the fertility equation accounts for the fraction of offspring that are female, assuming an equal sex ratio. Using the year-specific matrices we calculated an average matrix across all years. A basic eigen-analysis was performed on the average matrix to calculate the finite population growth rate ( $\lambda$ ), stable age distribution, reproductive values, expected lifetime number of replacements by age class, and generation time ( $\mu_1$ ; Caswell 2001). I calculated the sensitivity of  $\lambda$  according to:

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}},$$

where  $a_{ij}$  is the  $i,j$ th entry of  $\mathbf{A}$  (Caswell 1978). Furthermore, we calculated the elasticity of  $\lambda$  to proportional changes in vital rates as (deKroon et al. 2000):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}.$$

Although some vital rates may have large sensitivity or elasticity values, they may not vary temporally within a population, and thus may not contribute significantly to actual historic changes in population growth rate. The LTRE, however, can be used to decompose the vital-rate contributions to historic changes in population growth rate (i.e., a retrospective perturbation analysis). We used the year-specific vital rates and matrices

in a random-effects LTRE design to analyze how past changes in vital rates on the Parker Mountain study area contributed to actual change in population growth rate.

Contribution values from a LTRE analysis incorporate vital rate sensitivities and historic changes in survival and fertility estimates between years (or locations, treatments, etc.).

We decomposed the variance in  $\lambda$  among annual matrices  $V(\lambda)$  as:

$$V(\lambda) \approx \sum_{ij} \sum_{kl} C(ij, kl) s_{ij} s_{kl} ,$$

where,  $C(ij, kl)$  is the covariance of matrix elements  $a_{ij}$  and  $a_{kl}$ , and  $s_{ij}$  and  $s_{kl}$  are the vital rate sensitivities for these matrix elements evaluated at a reference matrix (Caswell 2001). Hence, variation in a vital rate will have a large contribution to variation in growth rate ( $\lambda$ ) when  $\lambda$  is sensitive to changes in that vital rate, and/or when the vital rate changes by a large amount across years. In our analysis, year was the random effect, and the mean matrix (across all years) was the reference matrix. I used the “covariance method” to calculate a single contribution value ( $\chi_{ij}$ ) for each vital rate (Horvitz et al. 1997):

$$\chi_{ij} = \sum_{kl} C(ij, kl) s_{ij} s_{kl}$$

This sum results in a single contribution value of  $a_{ij}$  to  $V(\lambda)$  by using the contribution of a single vital rate and its covariance with other vital rates. This analysis assumes a stable age structure and asymptotic growth rate, and is therefore a deterministic modeling approach. Following the LTRE analysis, a comparison was made between the results of prospective and retrospective analyses. By comparing which vital rates are the most important in both a prospective and retrospective manner, a more thorough assessment of how management directions should be focused on the life cycle of an organism can be developed. All prospective and retrospective analyses were completed in the R statistical



package (R version 2.8.0, Copyright © 2008, The R Foundation for Statistical Computing).

To assess the impacts of harvest on each age-class, we compared annual age distributions for the modeled population to annual age distributions within the harvested wing sample. To calculate age distributions for the modeled population we assumed that the first year (1998) had a stable age distribution, and then calculated  $\eta$  (next year's age distribution) by multiplying the previous year's age distribution with the following year's projection matrix. The results were then scaled such that abundance across age classes summed to unity in order to represent the proportional age distribution. This yielded a modeled age distribution for females in each year of the study. For the harvest-based age distribution, we simply totaled the yearling and adult hen harvest, and calculated proportions by age-class for each year of harvested data. This allowed assessment of whether hunter harvest was selecting hens proportional to modeled estimates of availability, or whether hunters (perhaps inadvertently) select female age-classes disproportionately.

Male lek count data were obtained from the UDWR. Using these data, we calculated the number of males per lek for the Parker Mountain population from 1998-2006. Finite population growth rate based on lek counts ( $\lambda_{\text{lek}}$ ) was then calculated as:

$$\lambda(t) = \frac{\sum_{i=1}^n M_i(t+1)}{\sum_{i=1}^n M_i(t)}$$

Where  $M_i(t)$  = number of males counted at lek  $i$  in year  $t$ , across  $n$  leks counted in both years  $t$  and  $t+1$ , and their precision (variance and standard error, SE) estimated by treatment as a standard ratio estimator (Scheafer et al. 1996):

$$\text{Var}(\lambda_t) = \frac{fpc}{n\overline{M}(t)^2} \frac{\sum_{i=1}^n [M_i(t+1) - \lambda(t)M(t)]^2}{n-1}, \text{ where } fpc \text{ is assumed to be } 1.0.$$

By using these formulas to estimate lek-based population growth rate and error rates we were able to use all leks monitored within the study area, even if individual leks were added to the data set within the sampling period.

## RESULTS

### Estimation of Survival and Reproductive Rates

From 1998-2006 we captured, radio-marked, and monitored 180 hens, totaling 276 annual survival histories (adults  $n = 136$ , yearlings  $n = 140$ ; some hens lived multiple years changing age-classes). Nest survival was monitored for 153 nests. Clutch size and infertility was estimated from 125 and 100 nests, respectively. Brood success was determined from 99 broods and the number of chicks fledged per successful brood was calculated from 30 successful radio-marked broods in 2005-2006.

Annual hen survival did not differ by age ( $\beta_{\text{hen age}} = 0.10$ , SE = 0.23), but did fluctuate by low ( $S^{\ddagger} = 0.42$ , SE = 0.12,  $n = 1$ ), medium ( $S^{\ddagger} = 0.56$ , SE = 0.04,  $n = 6$ ), and high survival years ( $S^{\ddagger} = 0.78$ , SE = 0.10,  $n = 2$ ; Table 3-2). Nest initiation (NI) rates, however, differed by hen age ( $\beta_{\text{hen age}} = 1.20$ , SE = 0.33) and varied between low ( $n = 4$  years) and high ( $n = 5$  years) years (yearling low year NI = 0.56, SE = 0.001; yearling

high year NI = 0.70, SE = 0.027; adult low year NI = 0.81, SE = 0.059; and adult high year NI = 0.89, SE = 0.095; Table 3-3).

Nest survival did not differ by hen age ( $\beta_{\text{hen age}} = 0.46$ , SE = 0.30), but the best model, based on the AICc criterion nevertheless indicated that age-specific differences in nest survival were important and varied between normal and high years (yearling normal  $\beta = 0.38$ , SE = 0.054, n = 6; yearling high  $\beta = 0.67$ , SE = 0.017, n = 3; adult normal  $\beta = 0.54$ , SE = 0.020, n = 6; and adult high  $\beta = 0.78$ , SE = 0.043, n = 3; Table 3-4). Mean clutch size did not differ by hen age ( $t = 1.64$ , df = 123,  $P = 0.10$ ), and was  $\bar{x} = 6.38$  (SE = 0.11), while infertile eggs per nest was  $\bar{x} = 0.53$  (SE = 0.14). Therefore, the effective clutch size was 5.85. Brood success did not differ by hen age ( $\beta_{\text{hen age}} = 0.44$ , SE = 0.54), but did fluctuate (based on the best model's AICc) between low, medium, and high success years (low year  $\beta = 0.59$ , SE = 0.004, n = 3; medium year  $\beta = 0.81$ , SE = 0.061, n = 5; and high year  $\beta = 0.94$ , SE = 0.339, n = 1; Table 3-5). The number of chicks fledged per successful brood was 0.55 (n = 30). Fledgling survival (MSR<sup>8</sup>) followed patterns of yearling hen survival (above) and thus fluctuated between low, medium, and high survival years (low year  $\beta = 0.56$ , SE = 0.154, n = 1; medium year  $\beta = 0.68$ , SE = 0.050, and n = 6; and high year  $\beta = 0.85$ , SE = 0.062, n = 2; Table 3-1).

### **Life Cycle Modeling**

The finite growth rate ( $\lambda$ ) for the Parker Mountain sage-grouse population (based on the average matrix) indicated that our population should be stable over the long term ( $\lambda = 1.002$ ), given the estimated levels for each vital rate. The stable age distribution for yearlings and adult females was 0.41 and 0.59, respectively. The reproductive value for

yearlings and adult females was 0.44 and 0.56, respectively. The expected lifetime number of replacements was 1.004 for yearlings and 1.27 for adults; generation time was 2.84 years. Sensitivity, elasticity, and LTRE analyses showed that adult hen survival and production parameters were most important for changes in growth rate (Table 3-6). Season dates, bag and possession limits, and wing sample sizes are reported in Table 3-7. The selection of harvested females by age was disproportionate toward yearling hens for modeled age distributions across all years (Figure 3-1). The number of males per lek and associated yearly growth rates are reported in Table 3-8 for comparison with female-based finite growth rates computed from the life-cycle matrix models. The average growth rate based on lek counts ( $\lambda_{\text{lek}} = 1.20$ ) was much higher than that for modeling ( $\lambda = 1.002$ ).

## **DISCUSSION**

We found strong support for our second hypothesis. Adult hen survival and production (chick and fledgling survival) were the two most important factors contributing to population growth rate for the Parker Mountain sage-grouse population. Adult hen reproduction was consistently higher and thus the relative importance of adult hen survival contribution to the population. Yearling hen survival and reproduction had much less influence on population growth rate. Fledgling survival was the second most important vital rate. We made the most assumptions with this parameter, and thus future research needs to focus on this portion of the sage-grouse life-cycle. Production was also very important to population growth rate. In our study, production was represented by brood survival and chicks/successful brood, which when combined approximated a chick survival parameter. Both production vital rates had high sensitivity and elasticity values,

and thus have a large potential to impact population growth rate. Interestingly, brood survival had a negative LTRE value because it was negatively correlated with adult and yearling survival, yearling nest initiation, and both age-class nest survivals (Table 3-9). This indicates that historically when these other vital rates have been low, compensation may have occurred with increased production. This could be an indication of density dependence occurring within the population, but more investigation with a larger time frame is needed. Lastly, adult hen nest survival was also important to population growth rate. All other vital rates had much less potential and historic contribution to population growth rate.

Fledgling survival (August to March) was similar to reported estimates of 0.64 and 0.86 for Idaho mountain valley and lowland populations, respectively (Beck et al. 2006; Table 3-1). Fledgling survival varied by year because it was based on MSR for yearling hen survival estimates. We believe basing fledgling survival on MSR of hen survival estimates best reflected the environmental conditions for the Parker Mountain study area. Furthermore, the life form (body size) of a juvenile female sage-grouse is very similar to yearling hens by autumn, which may support our assumption that survival was similar. Further investigation into fledgling survival is needed for the Parker Mountain sage-grouse population. Monitoring survival of fledglings from August to March is the largest telemetry-based data gap for this population. Additionally, to our knowledge only one peer-reviewed study has been published concerning sage-grouse survival during this period (Beck et al. 2006).

Brood success (or fledgling success) was relatively high throughout the study, and did not differ by hen age, but did vary by low, medium, and high years (Tables 3-1 and 3-

5). Brood success in our study was much higher than other reported estimates. For example, Aldridge and Brigham (2001) reported brood success of 0.42 in Alberta, Canada, and Schroeder (1997) reported brood success of 0.50 for a population in Washington. However, Schroeder (1997) based brood success (or fledgling success) on the proportion of all hens which attempted a nest, while similar to our study, Aldridge and Brigham (2001) reported brood success based only on successful breeders.

Both Schroeder (1997) and Aldridge and Brigham (2001) discussed the difficulty in locating chicks when flushing broods at time of fledgling, which may underestimate brood success and chick survival estimates. For this reason, we used pointing dogs in 2002-2006 for locating chicks, which was valuable to this study (also see Chapter 4). However, pointing dogs were not used in 1998-2001, but this did not influence modeling of temporal effects on brood success for these years (Table 3-5).

Based on the definition of brood success, detection of only 1 chick is needed to confirm success within a brood. The probability of detecting at least one chick is likely much greater than the probability of detecting all chicks that survived to fledging within a brood (see Chapter 4). Therefore, underestimation of these estimates may be more relevant to chick survival than brood success. We did not estimate chick survival for all years in this study due to the uncertainty of locating all chicks within a brood using a traditional walking flush count (Schroeder 1997, Aldridge and Brigham 2001). Instead, we let brood success vary by yearly estimates based on radio-marked brood hens, and then calculated the proportion of radio-marked chicks that survived  $\geq 42$  days within 2005 and 2006 broods. By consistently using radio-marked data for all vital rate estimation, we felt the combination of these two estimates was the best method for

estimating juvenile production across all years. This yielded chick survival (multiplying brood success and chicks per successful brood) estimates close to those found in Chapter 2.

Interestingly, temporal impacts (years) on survival and reproductive rates were most evident when they were separated into qualitative categories (i.e. low, medium, and high or simply low and high survival and/or reproductive rates) for various years. In other words, by using dummy variables (i.e., categories of low, medium, and/or high) for each year based on survival and reproductive estimates, modeling resulted in better covariate structure and model fit. There was no apparent pattern of vital rates within years for these categories, except brood success (Table 3-9).

Hen survival did not differ by hen age, and was similar to other studies. Wallestad (1975) reported 0.35 and 0.40 for yearling and adult survival, respectively. However, Zabland (1993) reported no difference in survival by female age-class. Our hen survival estimates, except in one low year (Table 3-1), were more similar to Zabland (1993) which reported annual survival of 0.55 for female sage-grouse in Colorado and Connelly et al. (1994) which reported annual survival of 0.68 to 0.85 for female sage-grouse in Idaho.

We found some support for our first hypothesis, where adult hens generally had higher reproductive rates than yearlings. For our study, nest initiation rates were influenced by hen age-class. Similarly, Connelly et al. (1993) reported a difference between yearling and adult sage-grouse. In other studies all females initiated nests (Schroeder 1997). Connelly et al. (2000a) suggested that pre-laying range conditions of the specific study area may influence initiation rates. Pre-laying habitat is likely low in

herbaceous cover for Parker Mountain because habitat near lek sites is dominated by black sagebrush (*A. nova*), and higher elevation forb-rich habitat is typically covered in snow during the pre-laying period. Favorable pre-laying conditions with available forbs are important to sage-grouse nesting and reproductive success (Barnett and Crawford 1994, Moynahan et al. 2007, Gregg et al. 2008). The influence of pre-laying habitat on this population needs further investigation.

Average clutch size in our study was in the lower end of the range reported for sage-grouse (6 – 9.5; Connelly et al. 2000a, Table 3-1), and this may be a reflection of low quality pre-laying habitat condition. Additionally, infertility rates may have reduced the effective clutch size. We noted 3 occasions where the entire nest was infertile, and had multiple occasions where 1 or more eggs within a successful nest were infertile. Throughout the study, we documented only 1 renesting event, where both nests were found. However, we documented multiple nests with only 3-4 eggs, which may have been renesting attempts (Schroeder 1997). Due to observer availability, rigorous monitoring of radio-marked hens did not occur until later (late April or May) in the nest initiation season, and therefore nest initiation rates and renesting attempts were likely underestimated.

Nest survival was relatively high during this study. Wallestad and Pyrah (1974) reported differences in nest success by hen age; however this was not true for all studies (Connelly et al. 1993, Schroeder 1997). Connelly et al. (2000a) reported a range of 0.12–0.86 for estimates of sage-grouse nest success range-wide, of which our estimates are relatively high. Our estimate of nest survival for yearlings was similar to range-wide averages of both age classes reported in Crawford et al. (2004); however our adult nest



survival was much higher. Nest survival in our study seemed to fluctuate between normal and high years for each age-class (Table 3-1 and 3-4). We did not evaluate factors influencing nest survival (i.e. habitat parameters, precipitation regimes) besides hen age and temporal (annual) variation. These factors need further investigation.

Sage-grouse have a historic precedence of harvest throughout their range (Patterson 1952). Historically, impacts of harvest on sage-grouse were thought to be negligible (Crawford 1982, Braun and Beck 1985). However, recent literature reveals different implications for sage-grouse harvest. Johnson and Braun (1999) determined that harvest was likely additive to the population. Connelly et al. (2003) assessed different levels of exploitation on sage-grouse populations in Idaho. They found that even moderate levels of harvest slowed population response, this was especially apparent for populations in suboptimal habitat (xeric sagebrush) close to population centers or highly fragmented habitat. They also suggested more conservative harvest management that reflected individual population trend and the quality of habitat. They were criticized by Sedinger and Rotella (2005) for study design, but Reese et al. (2005) refuted these claims. Connelly et al. (2000b) found that female, and especially adult female, sage-grouse have a higher susceptibility to harvest. Sage-grouse have a low population turnover rate due to their long-lived nature (Connelly and Braun 1997). Harvest selection of highly productive females in long-lived species could be detrimental to grouse populations (Connelly et al. 2000b, Ellison 1991), especially compounding the implication of low juvenile success in sage-grouse due to the decreasing quantity and quality of early brood-rearing habitat (Connelly and Braun 1997). Our sensitivity and elasticity analyses confirm that adult hen survival is one of the most important factors for

a sage-grouse population. Connelly et al. (2000b) recommended conservative season lengths and bag limits, and delaying the season in the fall to allow population mixing so successful hens are not targeted while still brooding.

We did not find support for our third hypothesis. Our comparison of harvested female age distribution to modeled age-distribution indicated that current Utah sage-grouse harvest management is likely selecting for yearling, not adult hens (Figure 3-1). This may be due to the relatively (compared to other states) conservative harvest regulations, and seasons starting later in September. The UDWR attempts to align their sage-grouse harvest with harvest management principles by using population inventory, setting population and harvest goals, and setting regulations to meet these objectives (Connelly et al. 2005). In Utah only those populations with estimates of  $\geq 500$  breeding adults are harvested (Beck et al. 2003). The UDWR regulates sage-grouse harvest by estimating sage-grouse populations based on male lek counts (J. Robinson, UDWR Upland Game Program Coordinator, personal communication). Population estimates have been calculated according to the following assumptions: spring breeding population is based on maximum male lek counts with an assumption that 75% of male lek attendance and a male:female sex ratio of 1:2; and then starting with the spring population estimate, fall populations are calculated based on 65% male survival to fall, 84% female survival to fall, and 1.2 - 2.2 (1.7 most years) chicks/hen in the fall population (Connelly et al. 2000a, Crawford et al. 2004). The number of tags is then calculated at 10% of the fall population estimate; with a slight inflation based on hunter success for the previous 2 years is then taken into account.

Our results of the proportion of age-class harvest (more yearlings than adults) are contrary to results in Connelly et al. (2000b). We also compared low hen survival years (based on modeling efforts) to reported hunter harvest of radio-marked hens. Only 6 radio-marked hens (3 yearlings and 3 adults) were harvested during this study period (1998-2006). Another 6 hen mortalities were detected shortly (< 1 month) after the regular hunting season, and were possibly hunter wounded mortalities, but there was no certainty because all carcasses were scavenged. Our study was not designed to assess whether harvest was additive or not, and adult hens that are harvested, although below availability, may still be additive to overwinter survival. Moreover, yearling hens that survive to the fall are within ~ 6 months of being adult hens. Therefore, considering the relatively high over-winter survival of sage-grouse (Connelly et al. 2000a), harvest of yearling hens may be comparable to harvest of adult hens.

Further research is needed to test current UDWR harvest regulations for additive impacts on sage-grouse populations. Modeling that included more age-classes and seasonality may help assess the impacts of harvest on sage-grouse. Furthermore, our results suggest that age-specific harvest is not proportional to population age distribution, and therefore harvested wing data is likely biased by age-class, at least for hens.

We did not find support for our fourth hypothesis. Modeled growth rate and average lek-based growth rate from 1998-2006 were very different (Table 3-7). Modeled growth rate indicated a relatively stable population throughout our study, while lek counts suggested an overall increasing population. The reasons for the discrepancy between lek-based and modeled telemetry-based population trends are difficult to ascertain. Lek counts have been criticized for their high degree of variability (Reese and

Bowyer 2007); however they have still been used to assess long-term population trends because lek counts are considered the best available data (Connelly et al. 2003, Connelly et al. 2004). Additionally, there may be biases associated with marking sage-grouse, and thus biased estimates derived from telemetry-based data (Murray and Fuller 2000). We do not have enough information to determine which estimate is most accurate, though telemetry-based data is likely more precise.

## **MANAGEMENT IMPLICATIONS**

The Parker Mountain sage-grouse population was stable to increasing during this study period. Our population vital rates were relatively high compared to other studies. This was interesting because even with higher vital rates our population was merely stable, suggesting that sage-grouse populations need similar vital rates to maintain stability. Surprisingly, hen survival was variable year to year, especially for a relatively long-lived species. Yet, adult hen survival was the most important factor, because of higher reproductive rates, for population growth. Production (chick and fledgling survival) was also extremely important. Management activities that target adult female survival and production parameters would be the most influential for this population. Additionally, more research is needed to assess the specific factors that influence adult and juvenile survival. Based on preliminary information, harvest (based on UDWR regulations) that occurred during 1998-2006 likely did not influence overall adult hen survival. However, our modeling results suggested that increased adult hen mortality/harvest could potentially have large negative impacts to the population. Our results also suggested that harvested wing data was biased toward the yearling female

age-class. Lastly, there was a discrepancy between lek count data and telemetry-based data for this population. Further research is needed to rectify this issue.

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Table 3-1. Female-based life table for the greater sage-grouse (*Centrocercus urophasianus*) population Parker Mountain, Utah, 1998-2006.

Year	Sample Size (n)		HS <sup>c</sup>		NI <sup>d</sup>		ECS <sup>e</sup>	NS <sup>f</sup>		BS <sup>g</sup>	Ch/SB <sup>h</sup>	FS <sup>i</sup>
	Y <sup>a</sup>	A <sup>b</sup>	Y <sup>a</sup>	A <sup>b</sup>	Y <sup>a</sup>	A <sup>b</sup>		Y <sup>a</sup>	A <sup>b</sup>			
1998	19	10	0.56	0.56	0.56	0.81	5.85	0.67	0.78	0.81	0.55	0.68
1999	17	26	0.56	0.56	0.56	0.81	5.85	0.38	0.67	0.81	0.55	0.68
2000	8	19	0.56	0.56	0.70	0.89	5.85	0.67	0.78	0.59	0.55	0.68
2001	15	10	0.56	0.56	0.70	0.89	5.85	0.38	0.67	0.81	0.55	0.68
2002	14	15	0.56	0.56	0.70	0.89	5.85	0.38	0.67	0.59	0.55	0.68
2003	13	13	0.42	0.42	0.70	0.89	5.85	0.38	0.67	0.81	0.55	0.56
2004	0	9	0.78	0.78	0.56	0.81	5.85	0.67	0.78	0.59	0.55	0.85
2005	38	17	0.78	0.78	0.56	0.81	5.85	0.38	0.67	0.81	0.55	0.85
2006	13	46	0.56	0.56	0.56	0.89	5.85	0.38	0.67	0.95	0.55	0.68
<b>mean</b>			<b>0.59</b>	<b>0.59</b>	<b>0.62</b>	<b>0.85</b>	<b>5.85</b>	<b>0.48</b>	<b>0.71</b>	<b>0.75</b>	<b>0.55</b>	<b>0.70</b>

a = yearling hen, or female sage-grouse between their first and second breeding season, which become adult hens at the beginning of their second breeding season.

b = adult hen, or those hens that survived to their second or more breeding seasons.

c = annual hen survival, based on monthly survival rates (MSR<sup>12</sup>). Survival did not differ by hen age. Survival was modeled, which resulted in low, medium, and high (dummy variables) survival years (Table 2).

d = nest initiation, a hen must have been positively located on a nest using telemetry and binoculars. Nest initiation differed by hen age and low or high initiation years (Table 3; note: because of scheduling difficulties and field conditions, often hens were not searched for until early May, which may underestimate nest initiation rates).

e = effective clutch size, which takes into account infertility rates

f = nest survival, based on 7 day laying and 27 day incubation periods. Nest survival differed by hen age and low or high survival years (Table 4).

g = brood survival using annual variation in data (low, medium, and high survival years; see Table 5)

h = proportion of chicks per successful brood that survived  $\geq 42$  days using data in 2005 and 2006.

i = fledgling survival, was based on hen MSR<sup>8</sup> because we did not have radio-marked fledglings.

Table 3-2. Female sage-grouse (*Centrocercus urophasianus*) survival models, Parker Mountain, Utah, 1998-2006.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K <sup>a</sup>
DVQyear <sup>b</sup>	560.56	0	0.67133	1	3
Henage <sup>c</sup> + DVQyear	562.38	1.82	0.2695	0.4014	4
Year <sup>d</sup>	567.60	7.04	0.0199	0.0296	2
S(.) <sup>e</sup>	567.62	7.06	0.01969	0.0293	1
Hen age + year	569.58	9.02	0.00737	0.011	3
Hen age	569.62	9.06	0.00724	0.0108	2
DVyear <sup>f</sup>	571.08	10.52	0.00349	0.0052	9
henage + DVyear	572.79	12.23	0.00148	0.0022	10

a = number of parameters

b = dummy variable for low, medium, or high survival years

c = hen age of yearling or adult

d = continuous year variable (1998-2006)

e = the null model where there is no covariate influence

f = dummy variable for individual year (discrete)

Table 3-3. Female sage-grouse (*Centrocercus urophasianus*) nest initiation models, Parker Mountain, Utah, 1998-2006.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K <sup>a</sup>
Henage <sup>b</sup> + DVQyear <sup>c</sup>	255.23	0	0.58813	1	3
Hen age	256.57	1.35	0.29974	0.5096	2
Hen age + year <sup>d</sup>	258.61	3.39	0.10826	0.1841	3
Hen age + DVyear <sup>e</sup>	266.27	11.04	0.00236	0.004	10
DVQyear	267.32	12.10	0.00139	0.0024	2
S(.) <sup>f</sup>	272.93	17.71	0.00008	0.0001	1
year	274.27	19.05	0.00004	0.0001	2
DVyear	281.09	25.87	0	0	9

a = number of parameters

b = hen age of yearling or adult

c = dummy variable for low or high years

d = continuous year variable (1998-2006)

e = dummy variable for individual year (discrete)

f = the null model where there is no covariate influence

Table 3-4. Female sage-grouse (*Centrocercus urophasianus*) nest survival models, Parker Mountain, Utah, 1998-2006.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K <sup>a</sup>
Hen age <sup>b</sup> + DVQyear <sup>c</sup>	345.58	0	0.32321	1	3
DVQyear	345.89	0.31	0.27655	0.8556	2
henage	347.09	1.50	0.15249	0.4718	2
S(.) <sup>d</sup>	347.28	1.70	0.13821	0.4276	1
Hen age + year <sup>e</sup>	349.09	3.51	0.05598	0.1732	3
year	349.22	3.64	0.05242	0.1622	2
Hen age + DVyear <sup>f</sup>	358.24	12.66	0.00058	0.0018	10
DVyear	358.26	12.67	0.00057	0.0018	9

a = number of parameters

b = hen age of yearling or adult

c = dummy variable for normal or high years

d = the null model where there is no covariate influence

e = continuous year variable (1998-2006)

f = dummy variable for individual year (discrete)

Table 3-5. Sage-grouse (*Centrocercus urophasianus*) brood success models, Parker Mountain, Utah, 1998-2006.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K <sup>a</sup>
DVQyear <sup>b</sup>	100.20	0	0.48629	1	3
Hen age <sup>c</sup> + DVQyear	101.70	1.50	0.22953	0.472	4
Hen age	103.71	3.51	0.08402	0.1728	2
Hen age + year <sup>d</sup>	104.09	3.89	0.06954	0.143	3
year	104.11	3.91	0.06891	0.1417	2
S(.) <sup>e</sup>	104.36	4.16	0.06077	0.125	1
DVyear <sup>f</sup>	113.34	13.14	0.00068	0.0014	9
Hen age + DVyear	115.26	15.06	0.00026	0.0005	10

a = number of parameters

b = dummy variable for low, medium, or high survival years

c = hen age of yearling or adult

d = continuous year variable (1998-2006)

e = the null model where there is no covariate influence

f = dummy variable for individual year (discrete)

Table 3-6. Greater sage-grouse (*Centrocercus urophasianus*) population sensitivity, elasticity, and Life Table Response Experiment (LTRE) analyses, Parker Mountain, Utah, 1998-2006.

Vital Rate	$S_{ij}^a$	$S_{ij}$ rank	$e_{ij}^b$	$e_{ij}$ rank	LTRE <sup>c</sup>	LTRE rank
<b>Yearling Survival</b>	<b>0.45</b>	<b>5</b>	<b>0.26</b>	<b>6</b>	<b>0.00199</b>	<b>5</b>
<b>Adult Survival</b>	<b>0.65</b>	<b>1</b>	<b>0.38</b>	<b>1</b>	<b>0.00429</b>	<b>3</b>
<b>Yearling Nest Initiation</b>	<b>0.14</b>	<b>9</b>	<b>0.09</b>	<b>9</b>	<b>-0.00045</b>	<b>7</b>
<b>Adult Nest Initiation</b>	<b>0.31</b>	<b>7</b>	<b>0.26</b>	<b>6</b>	<b>0.00026</b>	<b>8</b>
<b>Clutch Size</b>	<b>0.06</b>	<b>10</b>	<b>0.35</b>	<b>2</b>	<b>0.00000<sup>d</sup></b>	<b>9</b>
<b>Clutch Infertility</b>	<b>-0.060</b>	<b>10</b>	<b>-0.032</b>	<b>11</b>	<b>0.00000<sup>d</sup></b>	<b>9</b>
<b>Yearling Nest Survival</b>	<b>0.19</b>	<b>8</b>	<b>0.09</b>	<b>9</b>	<b>0.00676</b>	<b>2</b>
<b>Adult Nest Survival</b>	<b>0.37</b>	<b>6</b>	<b>0.26</b>	<b>6</b>	<b>0.00351</b>	<b>4</b>
<b>Brood Survival</b>	<b>0.47</b>	<b>4</b>	<b>0.35</b>	<b>2</b>	<b>-0.00121</b>	<b>6</b>
<b>Chicks/Successful Brood</b>	<b>0.64</b>	<b>2</b>	<b>0.35</b>	<b>2</b>	<b>0.00000<sup>d</sup></b>	<b>9</b>
<b>Fledgling Survival</b>	<b>0.50</b>	<b>3</b>	<b>0.35</b>	<b>2</b>	<b>0.00714</b>	<b>1</b>

a = sensitivity values, which are only comparable within the same column

b = elasticity values, which are only comparable within the same column

c = Life Table Response Experiment values, which are only comparable within the same column

d = constrained to be constant by model assumptions, therefore no contribution in LTRE



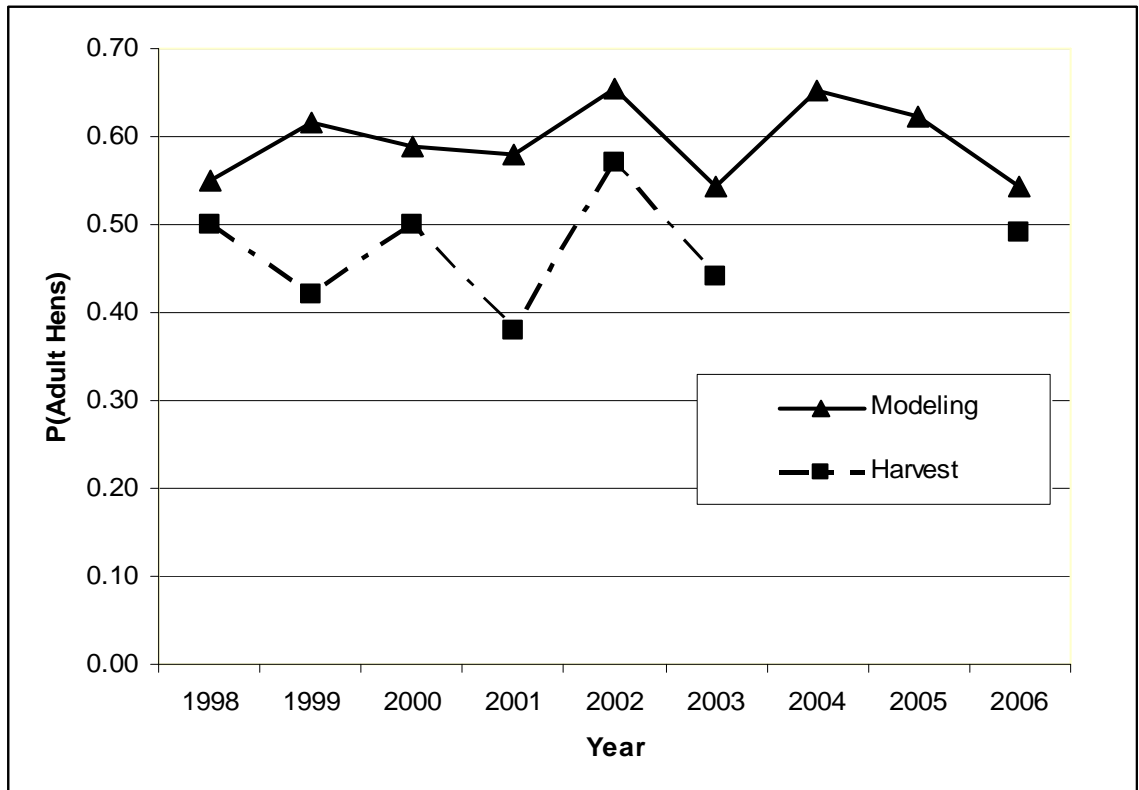


Figure 3-1. Comparison of harvested (missing 2004-2005 data) and modeled age distributions for adult hen greater sage-grouse (*Centrocercus urophasianus*) (note: because yearling hen age distribution is proportional to adults, the inverse of this graph is the proportion of yearling hens in harvested and modeled distributions; and harvest information, including sample sizes, are reported in Table 3-7), Parker Mountain, Utah, 1998-2006.

Table 3-7. Hunting season, bag and possession limits, harvested wing sample sizes, and reported radio-marked hen mortality for the greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, 1998-2006.

	1998	1999	2000	2001	2002	2003	2004	2005	2006
Opening date	Sept. 19	Sept. 18	Sept. 16	Sept. 15	Sept. 21	Sept. 20	Sept. 18	Sept. 17	Sept. 16
Season length (days)	7	9	9	9	9	9	9	9	9
Bag/Possession limits	1 / 2	1 / 2	<sup>a</sup> 1 / 2	<sup>a</sup> 1 / 2	<sup>b</sup> 2	<sup>b</sup> 2	<sup>b</sup> 2	<sup>b</sup> 2	<sup>b</sup> 2
Total wing sample	184	135	163	152	72	135	<sup>c</sup> N/A	180	281
Adult Hens	21	16	16	19	12	23	<sup>c</sup> N/A	<sup>d</sup> N/A	49
Yearling Hens	21	22	16	31	9	29	<sup>c</sup> N/A	<sup>d</sup> N/A	58
<sup>e</sup> Radio-marked hens	0	1	0	1	0	0	1	1	1
<sup>f</sup> wounded hens	1	2	0	0	3	0	0	0	0

a = limited sage-grouse permits were issued for the lawful take of sage-grouse, but bag and possession limits were in place for those with permits.

b = 2 individual tags were issued per hunter on a first come first serve basis, so that each hunter could only take 2 sage-grouse per season.

c = sage-grouse wings were not collected in 2004.

d = sage-grouse wings were collected in 2005, but wing characteristics were analyzed inappropriately and the sample was discarded before re-analyzing could take place.

e = Radio-marked hens that were harvested by hunters and reported to UDWR or USU personnel. Sample sizes of radio-marked hens are reported in Table 1.

f = Radio-marked hens that were found dead within a month following the sage-grouse season. There is much uncertainty about these mortalities because scattered remains were found at all mortality recoveries, but there is a possibility these hens died due to wounding during the regular hunting season.

Table 3-8. Greater Sage-grouse (*Centrocercus urophasianus*) male lek count growth rate ( $\lambda_{\text{lek}}$ ), Parker Mountain, Utah, 1998-2006.

Year	$\lambda_{\text{lek}}^a$	SE
1998	1.94	0.07
1999	0.92	0.04
2000	1.27	0.05
2001	0.96	0.06
2002	0.74	0.05
2003	1.29	0.08
2004	1.15	0.04
2005	1.31	0.06
2006	NA	NA
mean	1.20	0.05

a = finite growth rate based on lek count data

SE = Standard Error

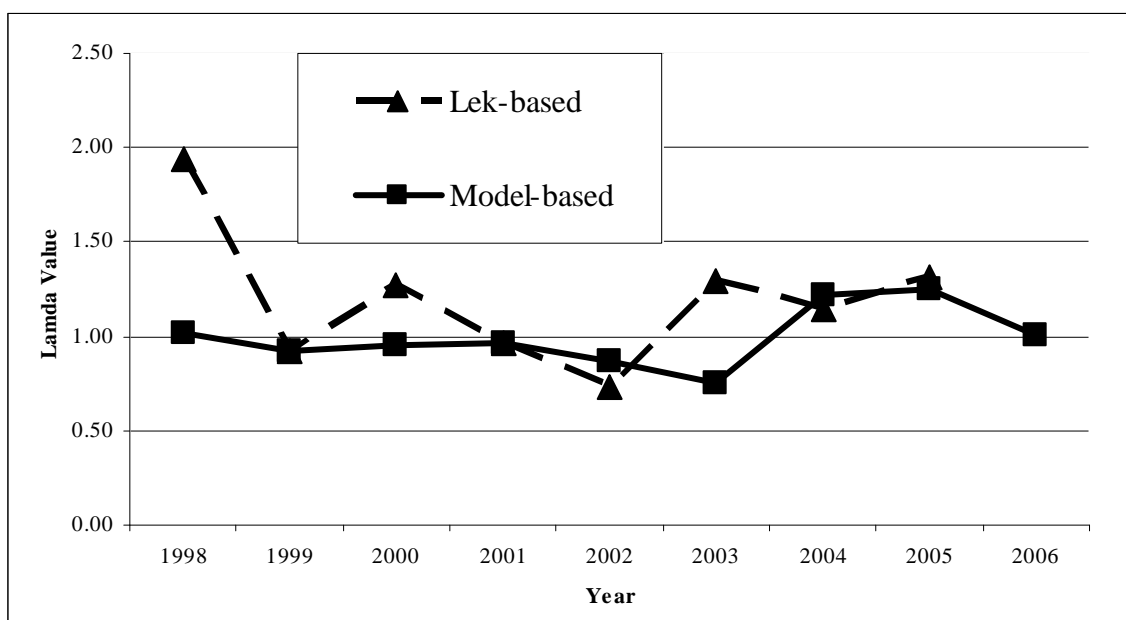


Figure 3-2. Comparisons of greater sage-grouse (*Centrocercus urophasianus*) lek-based and model-based growth rate ( $\lambda$ ), Parker Mountain, Utah, 1998-2006.

Table 3-9. Covariances for female greater sage-grouse (*Centrocercus urophasianus*) vital rates, Parker Mountain, Utah, 2006.

	YS	AS	YNI	ANI	CS	INF	YNS	ANS	BS	CH/SB	FS
YS	0.012										
AS	0.012	0.012									
YNI	-0.004	-0.004	0.005								
ANI	-0.003	-0.003	0.002	0.002							
CS	0.000	0.000	0.000	0.000	0.000						
INF	0.000	0.000	0.000	0.000	0.000	0.000					
YNS	0.004	0.004	-0.002	-0.002	0.000	0.000	0.019				
ANS	0.001	0.001	-0.001	-0.001	0.000	0.000	0.007	0.003			
BS	-0.003	-0.003	-0.003	0.000	0.000	0.000	-0.009	-0.003	0.015		
CH/SB	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
FS	0.009	0.009	-0.003	-0.002	0.000	0.000	0.003	0.001	-0.003	0.000	0.007

YS = yearling survival

AS = adult survival

YNI = yearling nest initiation

ANI = adult nest initiation

CS = clutch size

INF = infertility

YNS = yearling nest survival

ANS = adult nest survival

BS = brood survival/success

CH/SB = chicks per successful brood

FS = fledgling survival

CHAPTER 4  
EFFECTIVENESS OF VARIOUS TECHNIQUES FOR  
SURVEYING SAGE-GROUSE BROODS

## INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*), the largest North American grouse, live in sagebrush-dominated (*Artemisia* spp.) landscapes throughout western North America (Schroeder et al. 2004). Recent declines in greater sage-grouse (hereafter sage-grouse) populations have occurred due to many factors concerning declining habitat quantity and quality (Connelly et al. 2004). Measures of productivity are important for sage-grouse populations, and accurate measures of this population parameter have contained some uncertainty (Schroeder 1997, Aldridge and Brigham 2001, Aldridge 2005, Crawford et al. 2004).

Sage-grouse brood counts have been historically conducted to gather information on annual production (Patterson 1952, June 1963, Pyrah 1963, Wallestad 1975, Autenrieth 1981, Connelly et al. 2003), and to assess chick survival (Schroeder 1997, Aldridge and Brigham 2001, Aldridge 2005). Brood counts have been subject to criticism because of their variability (Strickland et al. 1996). Though brood counts may be highly variable, they may be useful for prediction of harvest at large scales (Rice 2003). In recent years sage-grouse production has been commonly evaluated with harvested wing information (Connelly et al. 2003, Hagen and Loughin 2008). However, Hagen and Loughin (2008) suggest historically reported sample sizes have been too low for accurate inference. For many sage-grouse populations harvest levels that produce enough wing data ( $n \geq 300$ ; suggested by Hagen and Loughin 2008) might exceed

conservative harvest criteria suggested by Connelly et al. (2000b). Furthermore, many sage-grouse populations are no longer harvested because of population declines and limited habitat, and therefore no harvest-based production information are available.

Additionally, some states use production information to set sage-grouse harvest regulations. Oregon currently uses lek count data along with brood counts to set sage-grouse harvest at  $\leq 5\%$  of the estimated fall population (Connelly et al. 2005). Because of these issues and concerns, and the need to gather as much information possible for sage-grouse populations, state agency interest in brood counts may be increasing (D. Olsen, Upland Game Coordinator, Utah Division of Wildlife Resources, and C. Hagen, Sage-grouse Biologist, Oregon Department of Fish and Wildlife, personal communication).

There are other important considerations for conducting brood counts. Past research has used counts of specific radio-marked hen broods to assess chick survival (Schroeder 1997, Aldridge and Brigham 2001, Aldridge 2005). In these studies an observer approached a radio-marked hen's brood on foot, attempting to flush all extant chicks. This yields an estimate of chick survival based on known hatched clutch size. Multiple studies have reported uncertainty in locating all sage-grouse chicks during walking flush counts, and thus noted that this technique may have underestimated juvenile survival (Schroeder 1997, Aldridge and Brigham 2001, Aldridge 2005). Recently, methods have been reported for radio-marking sage-grouse chicks (Burkepile et al. 2002, Gregg et al. 2007). Radio-marking may yield better estimates of chick survival than brood counts, however not all research or management activities can

expend the resources to monitor radio-marked chicks, especially at larger (i.e. statewide) population scales.

Walker et al. (2006) discussed using spotlight counts versus walking flush counts on sage-grouse broods to determine differences in survey methods and chick survival. They found that spotlight counts enhanced their ability to detect chicks in a given brood. However, they did not include pointing-dog surveys in their methodology and only compared walking observer counts to spotlight counts.

Zwickel (1980) reported that dogs can increase the quality of wildlife research. In our peer-reviewed literature search we found 49 publications where dogs had been used in grouse (Tetraonidae) research. The earliest publications by genus include; red grouse and ptarmigan (*Lagopus* spp.; Jenkins et al. 1963); sooty and dusky grouse (*Dendragapus* spp.; Buss et al. 1958); ruffed grouse (*Bonasa* spp.; Marshall 1946); black grouse (*Tetrao* spp.; Baines 1991); and spruce grouse (*Falci pennis* spp.; in Ellison 1974). Specifically, European grouse research has a long history of using pointing-dogs to aid assessment of various grouse populations (Jenkins et al. 1963, Thirgood et al. 2000). Moreover, recently European grouse biologists have developed more technical approaches for using pointing-dogs (Broseth et al. 2005, Warren and Baines 2007). Pointing-dogs have been used specifically for sage-grouse research (Autenrieth 1981, Connelly et al. 2000a, Connelly et al. 2003, Dahlgren et al. 2006). Connelly et al. (2003) recommended using pointing-dogs for sage-grouse brood surveys and specifically for capturing chicks. However, considering the body of grouse research which used pointing-dogs, we could not find any publications quantitatively assessing the effectiveness of pointing-dogs for detecting grouse.

The purpose of this study was to compare the effectiveness of methods used for detecting sage-grouse chicks within radio-marked hen broods. We hypothesized that spotlighting and pointing-dog survey methods will have superior detection when compared to walking flush counts. This is because each method provides a more reliable detector (e.g. high beam spotlight or a dog's nose and ground coverage) than the mere disturbance of a walking observer.

## **STUDY AREA**

Parker Mountain is located in south-central Utah and is on the southern edge of greater sage-grouse range. The area is a high elevation (~ 2000-3000 meters) plateau that is largely dominated by black sagebrush (*A. nova*), however there are also landscapes of mountain big (*A. tridentata vaseyana*) and silver (*A. cana*) sagebrush at the highest elevations (south and west sagebrush boundaries). This area has one of the largest contiguous blocks of sagebrush and one of the larger populations of greater sage-grouse remaining in Utah (Beck et al. 2003). Parker Mountain is largely public land including Bureau of Land Management (BLM), U.S. Forest Service (USFS), and State Institutional Trust Lands (SITLA). In general, the sage-grouse population uses lower elevation sagebrush landscapes for wintering, pre-laying, and lekking habitat; while hens gradually move up in elevation for nesting and brood-rearing activities, using the highest elevations and habitats along the southern and western boundaries of the Awapa Plateau (Chi 2004, Dahlgren 2006). For more detailed information concerning the study area refer to Chapter 1.



## METHODS

We used spotlight, walking, and pointing-dog flush counts to count sage-grouse chicks with radio-marked hens. We used all three methods on 5 to 8 week-old broods within a 36-hour (maximum) period during late July and August of 2006 and 2007. A random order in which the three methods occurred on a given brood was assigned *a priori* to our counts. We believe this was the best randomization possible given our limited sample size. If more than one hen flushed with chicks during the surveys, the number of chicks/brood was averaged by hen. In 2005 and 2006, radio-marked hen broods were captured at ~ one-day-old and marked with 1.5 gram radios according to protocol in Burkepile et al. (2002) in a study to estimate chick survival (see Chapter 2). For broods with marked chicks and a radio-marked hen, we used the hen's signal to locate the brood and search efforts were centered on her location. We counted all chicks flushed and then checked marked chick signals pre- and post-sampling efforts to record a separate sample of detection for radio-marked chicks. For consistency, when broods containing only marked chicks and no marked hen were located, we used the marked chicks' signal to get the brood's general location, and then an effort was made to flush the unmarked brood hen, and use her location as the center of our search effort.

Generally, the brood hen was the first to flush and reveal her location.

Because brood-mixing or chick mortality within a given brood could potentially bias results of this analysis if it occurred while sampling with the three methods, we completed all three methods on a single brood within a 36-hour period. By completing all three survey methods within this time frame, we minimized the probability of brood-mixing or mortality events. Brood-mixing is where a chick leaves its genetic mother's

brood and joins another hen's brood, and was common within this sage-grouse population (see Chapter 2).

We used spotlight techniques at night and located broods and counted them using binoculars. Our walking counts consisted of a single researcher approaching the brood during the day (usually morning or evening) and slowly walking a spiral pattern (~ 5 to 10 meter spacing between spirals) around the brood hen's location for 20 minutes. This time period was used for both walking and pointing-dog count methods for consistency and comparison, however spotlight counts were a single occurrence in time, and thus it was impossible to keep the survey time consistent across all methods.

Our pointing-dog flush counts consisted of locating the brood using telemetry and keeping the dog within relatively close proximity (< 100 meters) of the brood hen's flush location for 20 minutes. We approached broods downwind initially to give the dog the best scenting conditions possible (Gutzwiller 1990), though the dog inevitably covered the entire area regardless of wind direction during the search period. Our observer/handler tried to keep human disturbance to a minimum during this count. This was done to reduce or eliminate the influence of the handler on detection of chicks, and to minimize human scent in the dog's search pattern. Three dogs were used during this study and all were well trained and experienced on sage-grouse. One of the three dogs was used only once (Table 4-1), and we tried to minimize the use of different dogs for consistency (Gutzwiller 1990).

## Data Analysis

We used two different data analysis methods. Our first analysis assessed data from all flushed chicks (both marked and unmarked). Because of our precautionary measures (keeping all surveys within a 36-hour period), we assumed no brood-mixing and/or chick mortality occurred. If brood-mixing or chick mortality was detected for radio-marked chicks, the data was censored. We used a one-way ANOVA in a randomized block design where broods are blocks to test for count differences in flush count methodology at a  $P \leq 0.05$  alpha level.

Our second analysis was completed in support of the first analysis. Our second analysis only used data from marked chicks, which afforded absolute detection. For this analysis, we assumed all marked chicks were independent and equal in detectability. Our assumption of independence related to an individual chick's detection once the radio-marked brood hen was located. We realized that on a landscape-level independence did not exist between brood mates. However, for the purposes of this study we assumed once a radio-marked brood was located based on the brood hen's location, the detection of individual chicks was independent of each other within the general brood location. We believe this was a safe assumption at this small scale given the propensity of brood hens to scatter their chicks in random directions with an alarm call in a predation event. We compared detection proportions among the three methods by assessing overlap of confidence intervals; non-overlapping confidence intervals indicated a difference between two proportions. Confidence intervals were estimated using the calculator available at [http://www.causascientia.org/math\\_stat/ProportionCI.html](http://www.causascientia.org/math_stat/ProportionCI.html), accessed on August 31, 2007. We used a confidence of 85.6 %, following Payton et al. (2003) for a

ratio of standard errors equal to 2, which approximates a test of significance with  $\alpha = 0.05$  for non-overlapping confidence intervals. Due to the low variability of detection in spotlight and pointing-dog counts (Table 4-1), standard errors were calculable only for walking flush counts. Thus, we felt a conservative approach would be to assume that standard errors for pointing-dog and spotlight methods were not equal, but their ratios were not greater than 2. This allowed calculation of confidence intervals for these two methods when little variability existed.

## RESULTS

We surveyed a total of 21 broods (25 marked chicks) during the summers of 2006 and 2007 (Table 1). Most broods had a radio-marked hen, but some only had a marked chick due to brood-mixing prior to our survey efforts (Table 4-1). For the first analysis using all (marked and unmarked) chicks, detectability differed by technique ( $F = 7.25$ ,  $P = 0.001$ ). Pair-wise comparisons showed walking flush counts detected less chicks than spotlight and pointing-dog flush counts ( $t = 3.68$ ,  $P = 0.002$  and  $t = 2.73$ ,  $P = 0.03$ , respectively), and no difference between spotlight and pointing-dog flush counts ( $t = -1.01$ ,  $P = 0.57$ ). The second (supportive) analysis of marked chicks for walking, pointing-dog, and spotlight flush counts had probabilities of detection of 0.72 (CI: 0.58 - 0.83), 0.96 (CI: 0.87 - 0.99), and 1.00 (CI: 0.93 - 1.00), respectively.

## DISCUSSION

Walking flush counts were least reliable for detecting chicks within broods. Spotlight counts and pointing-dog flush counts were more reliable at detecting chicks and exhibited similar detectability. Spotlight counts produced the best detection, followed

very closely by pointing-dog flush counts. Therefore, our hypothesis that spotlight and pointing-dog methods would have better detectability was supported. Nocturnal activities of the broods seemed to bring chicks into closer proximity with the hen and each other compared to diurnal activities. This proximity factor also allowed observers to separate one brood from another more readily if multiple broods were in an area. Spotlight counts entailed the least amount of time/brood to conduct the survey. However nocturnal surveying was more logistically difficult (i.e. disruption of regular work schedules) on observers compared to daytime walking and pointing-dog flush counts.

We did encounter some mortality of marked chicks during our 36 hour (maximum) survey period, and one case of brood-mixing by a marked chick (data was censored). This may have unknowingly occurred with unmarked chicks and could have violated the assumptions and increased the variation within our analysis of all (unmarked and marked) chicks. Additionally, there is the possibility that surveying one brood with all three methods in such a short period of time may have increased the likelihood of brood-mixing and/or mortality due to disturbance. Flushing individual chicks may increase the chance of predation and/or contact with another brood. Though we may have encountered problems of violated assumptions, both analyses showed similar results, strengthening our conclusions.

All dogs used in this study had been trained on sage-grouse and specifically on the study site for at least a month prior to data collection. We believe this acclimation to the study area and to sage-grouse specifically were important components to the success of pointing-dog counts. Additionally, all three dogs had at least two full years of experience (> 30 days/year) searching for wild game birds. All dogs were trained to hold

point until the observer flushed the bird. Holding steady to flush would be even more desirable. No dog-related chick mortality occurred during our survey efforts. Trained and experienced dogs are a must when pointing-dogs are used for research (Gutzwiller 1990, Connelly et al. 2003).

## **MANAGEMENT IMPLICATIONS**

Our evaluation demonstrates that spotlight and pointing-dog flush counts were equal in efficiency at detecting sage-grouse broods, and superior to walking flush counts. The walking flush method consistently underestimated sage-grouse brood counts. This confirms the uncertainty of walking flush counts for assessing sage-grouse chick survival described in earlier studies (Schroeder 1997, Aldridge and Brigham 2001, and Aldridge 2005), and suggests their reports of chick survival may have been underestimated. Because of this uncertainty, we strongly recommend the use of spotlight counts and/or pointing-dog flush counts for assessing chick survival where radio-marked chicks are not used.

There are some concerns when using spotlight counts. Sage-grouse tend to roost in lower sagebrush types with less shrub cover (Connelly et al. 2003), which facilitates use of spotlighting techniques. Therefore, pointing-dog counts may be best for other game bird species that nocturnally roost in heavier cover, where the effectiveness of spotlighting may be limited. Moreover, feasibility of spotlight counts may be related to individual sage-grouse population characteristics. Distribution and roosting habitat type of the local broods during the late summer need to be considered, because we did not evaluate spotlight counts with unmarked hens at landscape scales. If pointing-dog flush counts are used, we recommend using trained dogs, with experience on wild game birds,

and specifically on the species of interest. We recommend using dogs of at least two years of age or more that are at least trained to hold point while the observer flushes the bird.

Our best methods (pointing-dog and spotlight counts) may be employed in both research endeavors to more reliably estimate chick survival, and for management activities, such as brood counts for assessing production. These may especially be useful tools for sage-grouse populations where harvest is not occurring, or where only limited harvested wing samples can be taken.

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Table 4-1. Walking, nocturnal spotlight, and pointing-dog flush count data for method comparison at Parker Mountain, Utah, 2006-2007.

Brood	Year	No. Marked Chicks	Walking		Spotlight		Pointing-dog		Dog ID
			All <sup>a</sup>	Marked Chick Detection	All <sup>a</sup>	Marked Chick Detection	All <sup>a</sup>	Marked Chick Detection	
PM1	2006	1	3	1.00	3	1.00	3	1.00	1
PM2	2006	2	1	0.50	3	1.00	4	1.00	1
PM3 <sup>c</sup>	2006	1	10	1.00	8	1.00	5	0.00	1
PM4	2006	1	2	1.00	1	1.00	1	1.00	2
PM5	2006	1	3	0.00	8	1.00	8	1.00	1
PM6	2006	0	3	n/a	5	n/a	6	n/a	1
PM7	2006	2	3	1.00	10	1.00	8	1.00	1
PM8 <sup>c</sup>	2006	1	5	1.00	8	1.00	6	1.00	1
PM9 <sup>c</sup>	2006	1	4	1.00	8	1.00	5	1.00	1
PM10	2006	2	1	0.50	2	1.00	2	1.00	1
PM11	2006	1	1	1.00	4	1.00	3	1.00	2
PM12	2006	1	0	0.00	3	1.00	3	1.00	3
PM13 <sup>c</sup>	2006	1	0.6	1.00	9	1.00	14	1.00	2
PM14	2006	1	0	0.00	4	1.00	4	1.00	2
PM15	2007	1	4	1.00	9	1.00	8	1.00	2
PM16	2007	2	1	0.50	2	1.00	2	1.00	2
PM17	2007	2	10	1.00	12	1.00	4	1.00	2
PM18	2007	2	3	0.50	4	1.00	2	1.00	2
PM19	2007	0	0.33	n/a	1	n/a	2.66	n/a	2
PM20	2007	1	n/a <sup>b</sup>	n/a <sup>b</sup>	2	1.00	2	1.00	2
PM21	2007	1	1	1.00	n/a <sup>b</sup>	n/a <sup>b</sup>	3	1.00	2

a - represents the total number of chicks (marked and unmarked) in each brood detected by each method

b - The marked chick died during our survey period, data was censored for that brood and method

c - These broods (n = 4) did not have a radio-marked hen, and the general brood location was found by a marked chick's (brood-mixed) signal, however the unmarked brood hen usually flushed first and we used her location similar to other marked hen broods

## CHAPTER 5

### CONCLUSIONS

Concerns about greater sage-grouse (*Centrocercus urophasianus*) population declines have been increasing in recent years (Connelly et al. 2004). The U. S. Fish and Wildlife Service (USFWS) has received several petitions to list this species rangewide (USFWS 2008). Sage-grouse occur throughout Utah (Beck et al. 2003). In recent years, some populations have been declining while others have remained stable (Utah Division of Wildlife Resources 2008, Beck et al. 2003, Connelly et al. 2004).

The Parker Mountain sage-grouse population is one of the four stable to increasing (> 500 breeding adults) greater sage-grouse populations in Utah (Beck et al. 2003). Parker Mountain exhibits one of the largest intact contiguous sagebrush (*Artemisia* spp.) landscapes in Utah. This may be one of the most important factors contributing to population stability (Connelly and Braun 1997).

We studied chick ecology and population dynamics of the Parker Mountain population to provide better information for application to management. Obtaining better chick survival estimates is key to determining the effects of specific management actions on population trends (Connelly et al. 2000a, Connelly and Braun 1997, and Crawford et al. 2004). New technology and radio-marking techniques now allow managers to obtain better estimates of chick survival, an information need within general sage-grouse ecology (Burkepile et al. 2002, Gregg et al. 2007, Aldridge 2005).

Past assessments regarding the status and trends for the Parker Mountain greater sage-grouse population has been based largely on male lek counts (Beck et al. 2003, Connelly et al. 2004). With better estimates of chick survival in concert with life-cycle

modeling procedures using telemetry-based data, assessment of population dynamics contributing to perceived stability is possible. Our research documented some of the highest rates of greater sage-grouse chick survival reported in the published literature and provided an unbiased assessment of the impact of this vital rate on population change.

The *a priori* assumptions we made concerning chick survival also affected these estimates. Actual chick survival is likely between my low (0.41) and high (0.60) estimates. Hen age was related to the probability of a chick brood-mixing, and brood-mixing may have been related to survival. Brood-mixing was much more common than expected, and may be an important ecological factor affecting Parker Mountain greater sage-grouse. Further research is needed to assess the impacts of brood-mixing, and the possible influence radio-marking and monitoring may have on brood-mixing rates. Additionally, alloparental care of adult hens (i.e. yearling hens donating chicks to adult hen broods) may be an important factor contributing to this population, which in turn may be related to the importance of adult hen survival. The critical influence of adult female survival on population dynamics is strongly supported by our life-cycle modeling. More research is necessary to assess the dynamics of these relationships.

The two years we studied chick survival (2005-2006) were relatively high production years compared to previous years based on pointing dog surveys of permanent plots (D. Dahlgren, unpublished data). To more completely assess variability in production, more research (additional years) with radio-marked chicks is needed. This will provide a broader view of production dynamics for Parker Mountain sage-grouse. Moreover, life-cycle modeling suggested that production (chick and fledgling survival) may compensate for lower vital rates in other population parameters, indicating density

dependence within the population. Further research with additional years is needed to verify this relationship.

Life-cycle modeling proved a useful exercise to assess the effect of specific population vital rates on population dynamics. By calculating sensitivity and elasticity values, we can project which vital rates are most important. Furthermore, Life Table Response Experiment (LTRE) aided a view of historic contributions of specific vital rates to variation in population growth rate. LTRE analysis was used in a temporal framework to consider all vital rates and their specific contributions to growth rate over time. For instance, those vital rates that may have large sensitivity and/or elasticity values, but do not change over time contribute little to actual population growth rate. However, LTRE analysis determines which vital rates actually contributed. These tools can help future conservation of sage-grouse populations by guiding management actions that target specific population dynamics, which allows use of limited resources to get the most for the “management dollar.” According to our results, adult female survival is the most important factor to consider, yet we currently have very little information on what impacts adult female survival for this population, and why survival estimates varied by low and high years. Further research is needed in this area.

A possible research avenue to consider for understanding adult female sage-grouse survival is within the predator/prey dynamics on Parker Mountain and the phenomenon of prey switching. Schroeder and Baydack (2001) in their discussion of predation of prairie grouse stated, “The dynamics of predator populations are determined typically by the abundance of their primary prey species, which usually are rodents or lagomorphs rather than grouse. In situations where populations of the primary prey

species fluctuate, grouse numbers can be influenced by the changing densities of predators and the effects that prey densities have on predator's foraging behavior." Past research on Parker Mountain has concluded that golden eagles (*Aquila chrysaetos*) are the main predator of adult sage-grouse (Jarvis 1974, Chi 2004, Dahlgren 2006). Additionally, coyote (*Canis latrans*) removal (due to continued sheep grazing) by USDA Wildlife Services (WS) is an annual occurrence on Parker Mountain (K. Dustin, USDA WS, personal communication).

Coyote predation has been shown to influence prey populations, and specifically lagomorphs (Wagner and Stoddart 1972, Henke 1995). Therefore, a hypothesis that might be considered is: by removing coyotes, the lagomorph population (black-tailed jackrabbit – *Lepus californicus* – is the most abundant on Parker Mountain) may be above natural levels, thus increasing golden eagle abundance, resulting in increased adult sage-grouse mortality. This negative impact to adult sage-grouse survival may especially be true when lagomorph populations suddenly decline and prey switching occurs. By experimentally managing coyote removal, adult sage-grouse survival may be indirectly impacted because of these predator/prey relationships.

Harvest may also pose risk to adult female sage-grouse (Connelly et al. 2000b). Currently, harvest of the Parker Mountain sage-grouse population occurs each fall. The prevailing paradigm for harvest of tetraonids (grouse family) is that hunting mortality is considered additive to natural mortality (Bergerud 1985, Bergerud and Gratson 1988, Ellison 1991, Connelly et al. 2005). Additive mortality does not mean that populations cannot sustain some level of harvest (Connelly et al. 2005). Connelly et al. (2003) determined that harvest was additive to sage-grouse populations in Idaho, especially



those with fragmented habitats and/or close to large urban areas. Connelly et al. (2000b) found that female sage-grouse may be more vulnerable to harvest than males.

When harvest occurs for a relatively long-lived low reproductive species (i.e., sage-grouse), taking of adult females may have the greatest negative impact (Ellison 1991, Connelly et al. 2005). The Utah Division of Wildlife Resources (UDWR) current regulations (see Chapter 3) for sage-grouse hunting attempt to base harvest on population levels, and keep harvest  $\leq 10\%$  of fall population estimates (D. Olsen, Upland Game Coordinator UDWR, personal communication). In our analysis of stable age distribution (based on modeling) and harvested age distribution (based on wing samples) yearling hens were harvested in greater proportion than adults. This suggests that harvest samples are biased by age class, but does not address the issue of additive harvest. Based on these analyses and radio-marked hen hunter-return rates, adult female harvest is minimal within current regulations. We believe the UDWR's conservative harvest regulations based on population estimates are important for ensuring sage-grouse harvest in the future, without negatively impacting population stability (Connelly et al. 2000b). However, population monitoring (radio-marking, leg bands, and harvested wing collection) should continue when harvest occurs.

Production, or chick and fledgling survival, is the second most important vital rate for the Parker Mountain population. This research has provided more specific information about what chick survival has been, and the factors that may be related to it. Other research of captive-reared sage-grouse chicks has shown that arthropod abundance was critical to chick survival during the early brood-rearing period (Johnson and Boyce 1990). In our study, arthropods were also important for survival of chicks in a natural

setting. However, our modeled relationships between arthropod abundance and survival were not definitive, which was likely due to our low sample sizes. Furthermore, we were unable to relate arthropod abundance to habitat characteristics that were measured. Future research, with larger sample sizes, may help clarify these relationships. Fledgling survival, based on our modeling assumptions, was extremely important to historic (LTRE analysis) variation in growth rate; however we did not assess this parameter directly using radio-marked individuals. Further research is needed concerning fledgling survival of marked individuals for this population, and sage-grouse in general.

Brood count method comparisons showed that the common method of walking flush counts likely has underestimated past chick survival estimates. Our results suggest that if radio-marking is not used on chicks, spotlight and pointing dog methods can be used to improve detection. However, these methods do not account for brood-mixing. Spotighting was effective, but taxing due to nocturnal activities of observers. Pointing dogs were also effective, but only well trained and experienced dogs should be used. Though spotighting was efficient at brood counts, we only used this method on radio-marked broods, and did not test this (or others) method at landscape scales. Future research could address the usefulness of these techniques at larger scales.

Based on this and past research, the future of the Parker Mountain sage-grouse population will be secure if; 1) the large contiguous nature of the sagebrush habitat is kept intact, 2) harvest regulations remain conservative (meaning adult hens are conserved), 3) development follows historically low levels, and 4) future management focuses on maintaining or improving adult female survival and production.

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APPENDICES

APPENDIX A: ALTERNATIVE ANALYSIS ACTIONS FOR  
CHICK SURVIVAL ANALYSIS

**INTRODUCTION**

The modeling we conducted to estimate greater sage-grouse (*Centrocercus urophasianus*) chick survival contained an important analysis action to accommodate radio-marked chicks that went “missing” from their original broods. After we thoroughly searched for them, these chicks were not detected dead or alive within or outside their original brood during the 42-day monitoring period. The most objective analysis action we could conduct concerning these missing chicks was to right-censor them from the dataset (the analysis used in the main text; analysis action 1).

However, there are possibly several fates that missing chicks could have experienced; such as, a predation or scavenging event where the chick was moved outside of our detection capabilities (death), an undetected brood-mix out of the original brood (survived), or the chick stayed in the original brood but experienced radio failure (survived).

By conducting additional analysis actions for these unknown fates, we can estimate high- and low-end survival probabilities for our sample of radio-marked chicks. To estimate lower survival limits we assumed that missing chicks died once we could not detect them within their original broods (analysis action 2). Conversely, to estimate upper survival limits, we assumed missing chicks lived (survival was assigned within the original brood) once they could not be detected (analysis action 3). By conducting survival modeling based on these assumptions we identified the full range of possible survival estimates during our study.



## ANALYSIS ACTION 2: MISSING CHICKS WERE ASSIGNED MORTALITY

Under this assumption, age and brood type was our best model according to model comparisons (Table A-1). Moreover, there was a difference between survival of chicks in the different brood types (Figure 2;  $\hat{\beta}_{mixed} = 0.012$ , 95% CI: 0.000 – 0.023) and together both brood types averaged a survival rate of 0.41 to 42 days (95% CI: 0.33 – 0.50). Separately, chicks in non brood-mixed broods had a survival rate of 0.38 (95% CI: 0.28 – 0.48) to 42 days, and in brood-mixed broods had a survival rate of 0.61 (95% CI: 0.45 – 0.77) to 42 days. For this analysis action  $D = 1.10$  (95% CI: 0.67 – 1.52). We found that analysis action 2 yielded a less precise estimate of the direct relationship between hen age and chick survival ( $\hat{\beta} = -0.008$ , 95% CI: -0.017 – 0.001; Table A-2).

## ANALYSIS ACTION 3: MISSING CHICKS WERE ASSIGNED SURVIVAL

Under this assumption, age and year was our best model according to model comparisons (Table A-4); however, the year effect was imprecisely estimated ( $\hat{\beta} = -0.006$ , 95% CI: -0.019 – 0.007). According to our best model (year) chicks averaged a survival rate of 0.61 to 42 days (95% CI: 0.43 – 0.88), and  $D = 1.39$  (95% CI: 0.39 – 2.39). Furthermore, the brood type model did not have a lower QAIC<sub>c</sub> value than the null model, and there was not a difference between survival of chicks in the different brood types ( $\hat{\beta}_{mixed} = 0.008$ , 95% CI: -0.010 – 0.026; Figure A-2, Table A-4). Modeling based on analysis action 3 yielded a difference between yearling and adult hens for chick survival ( $\hat{\beta} = -0.012$ , 95% CI: -0.022 – -0.002; Table A-6). The negative beta indicates that yearling hens had higher chick survival estimates than adult hens (for discussion on this result, see the main text).

Table A-1. Models for greater sage-grouse (*Centrocercus urophasianus*) chick survival based on the analysis action where missing chicks are considered mortalities (analysis action 2) for weekly chick age, Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age = (week1)+(week2)+(week3)+(week4)+(weeks5-6)	6	346.01	0.00	0.99999
age = (week1)+(week2)+(week3)+(weeks4-6)	5	362.53	16.51	0.00000
age = (weeks1-2)+(weeks3-4)+(weeks5-6)	4	369.04	23.02	0.00000
age = (weeks1-2)+(weeks3-6)	3	372.71	26.69	0.00000
age = (week1)+(week2)+(weeks3-6)	4	374.70	28.68	0.00000
age = (week1)+(weeks2-6)	3	398.44	52.42	0.00000
age = (weeks1-3)+(weeks4-6)	3	400.52	54.50	0.00000
age = (weeks1-6)	2	408.54	62.52	0.00000
<u>Covariate Model Comparison</u>				
age* + brood type (regular or mixed)	7	253.77	0.00	0.99999
age* + year (2005 or 2006)	7	332.43	78.66	0.00000
age* + hatch date (Julian days)	7	343.24	89.47	0.00000
age* (Null Model)	6	346.01	92.25	0.00000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (week1) + (week2) + (week3) + (week4) + (weeks5-6), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.

Table A-2. Models assessing the impact of greater sage-grouse (*Centrocercus urophasianus*) brood hen age (restricted data set without mixed broods because hen age was not determined for broods that radio-marked chicks mixed to) on chick survival based on the analysis action where missing chicks are considered mortalities (analysis action 2), Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age=(week1)+(week2)+(week3)+(week4)+(week5-6)	6	378.22	0.00	0.99999
age=(weeks1-2)+(weeks3-4)+weeks(5-6)	4	390.54	12.31	0.00000
age=(week1)+(week2)+(week3)+(weeks4-6)	5	398.88	20.65	0.00000
age=(weeks1-2)+(weeks3-6)	3	400.36	22.13	0.00000
age=(week1)+(week2)+(weeks3-6)	4	401.97	23.74	0.00000
age=(week1)+(weeks2-6)	3	411.07	32.84	0.00000
age=(weeks1-3)+(weeks4-6)	3	416.49	38.26	0.00000
age=all weeks	2	418.80	40.57	0.00000
<u>Covariate Model Comparison</u>				
age* + hen age (yearling or adult)	7	293.59	0.00	0.99999
age* (Null Model)	6	378.22	84.68	0.00000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (week1) + (week2) + (week3) + (week4) + (weeks5-6), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.

Table A-3. Estimates of greater sage-grouse (*Centrocercus urophasianus*) chick daily survival rates for analysis action 2 of non- and mixed broods, Parker Mountain, Utah, 2005-2006.

*Age	$\beta_i$ 's	SE	Non Brood-mixed		Brood-mixed	
			DSR	SE	DSR	SE
Week 1	0.030	0.010	0.970	0.009	0.982	0.011
Week 2	0.034	0.010	0.967	0.010	0.978	0.012
Week 3	0.012	0.003	0.989	0.003	1.000	0.007
Week 4	0.029	0.008	0.972	0.008	0.983	0.010
Week 5-6	0.018	0.005	0.983	0.005	0.994	0.008

DSR: daily survival rate for each week

SE: standard Error

\* the null model age structure (in weeks) was determined by QAIC<sub>c</sub> values in Table A-1.

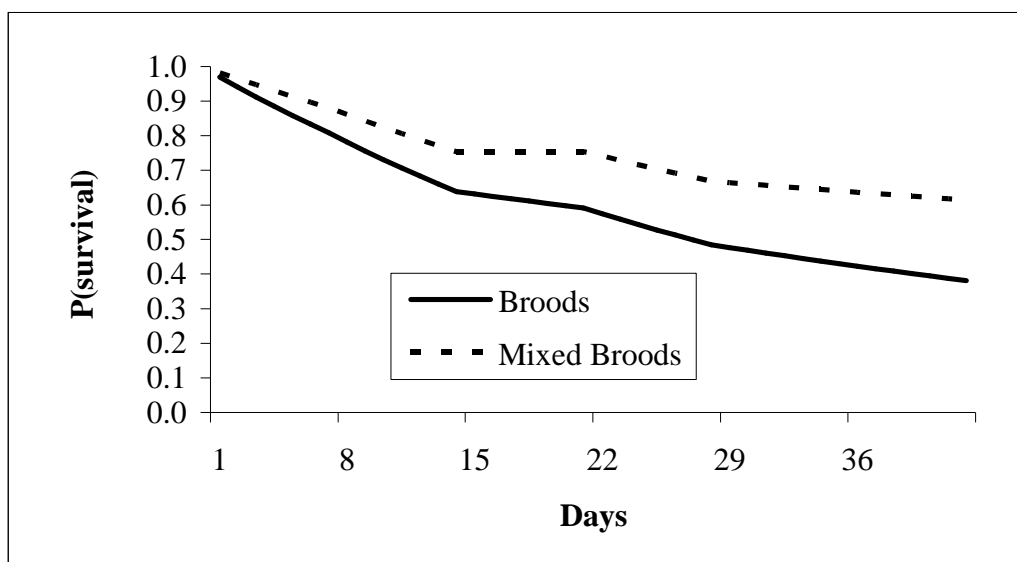


Figure A-1. Survivorship curve for greater sage-grouse (*Centrocercus urophasianus*) chicks with analysis action 2: where missing chicks are presumed mortalities (see Table A-3 for precision estimates), Parker Mountain, Utah, 2005-2006.

Table A-4. Models for greater sage-grouse (*Centrocercus urophasianus*) chick survival across week age groups based on the analysis action where missing chicks were considered to have survived within their natural broods (analysis action 3), Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age = (week1)+(week2)+(week3)+(week4)+(weeks5-6)	6	131.87	0.00	0.99999
age = (week1)+(week2)+(week3)+(weeks4-6)	5	159.82	27.94	0.00000
age = (weeks1-2)+(weeks3-4)+(weeks5-6)	4	162.24	30.36	0.00000
age = (week1)+(week2)+(weeks3-6)	4	166.83	34.95	0.00000
age = (weeks1-2)+(weeks3-6)	3	174.97	43.09	0.00000
age = (week1)+(weeks2-6)	3	181.31	49.43	0.00000
age = (weeks1-3)+(weeks4-6)	3	213.45	81.57	0.00000
age = (weeks 1-6)	2	228.32	96.44	0.00000
<u>Covariate Model Comparison</u>				
age* + year (2005 or 2006)	7	85.62	0.00	0.99999
age* (Null Model)	6	131.87	46.26	0.00000
age* + brood type (regular or mixed)	7	160.13	74.51	0.00000
age* + hatch date (Julian days)	7	203.61	117.99	0.00000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (week1) + (week2) + (week3) + (week4) + (weeks5-6), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.

Table A-5. Estimates of greater sage-grouse (*Centrocercus urophasianus*) chick daily survival rates for analysis action 3 of non- and mixed broods, Parker Mountain, Utah, 2005-2006.

*Age	$\beta_i$ 's	SE	Non Brood-mixed		Brood-mixed	
			DSR	SE	DSR	SE
Week 1	0.034	0.012	0.966	0.012	0.974	0.011
Week 2	0.026	0.009	0.975	0.009	0.983	0.012
Week 3	0.008	0.003	0.992	0.003	1.000	0.007
Week 4	0.067	0.012	0.935	0.011	0.943	0.010
Week 5-6	0.015	0.005	0.985	0.005	0.993	0.008

DSR: Daily Survival Rate

SE: Standard Error

\* the null model age structure (in weeks) was determined by QAIC<sub>c</sub> values in Table A-4

Table A-6. Models assessing the impact of greater sage-grouse (*Centrocercus urophasianus*) brood hen age (restricted data set without mixed broods because hen age was not determined for broods that radio-marked chicks mixed to) on chick survival based on the analysis action where missing chicks are considered surviving within their original broods (analysis action 3), Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age=(week1)+(week2)+(week3)+(week4)+(week5-6)	6	152.86	0.00	0.99999
age=(week1)+(week2)+(week3)+(weeks4-6)	5	171.62	86.00	0.00000
age=(weeks1-2)+(weeks3-4)+weeks(5-6)	4	176.90	91.28	0.00000
age=(week1)+(week2)+(weeks3-6)	4	181.85	96.23	0.00000
age=(weeks1-2)+(weeks3-6)	3	182.88	97.27	0.00000
age=(week1)+(weeks2-6)	3	185.11	99.50	0.00000
age=all weeks	2	198.15	112.54	0.00000
age=(weeks1-3)+(weeks4-6)	3	198.83	113.22	0.00000
<u>Covariate Model Comparison</u>				
age* + hen age (yearling or adult)	7	41.31	0.00	0.99999
age* (Null Model)	6	152.86	111.60	0.00000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (week1) + (week2) + (week3) + (week4) + (weeks5-6), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.

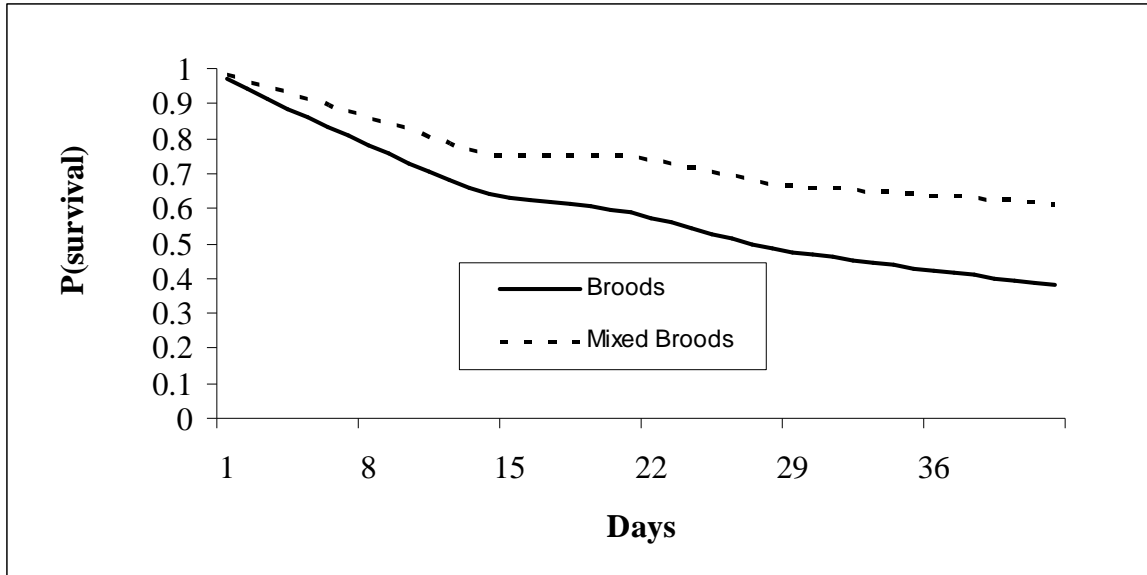


Figure A-2. Survivorship curve greater sage-grouse (*Centrocercus urophasianus*) chicks with analysis action 3: missing chicks were presumed to survive within their original broods (see Table A-5 for precision estimates), Parker Mountain, Utah, 2005-2006.

## APPENDIX B: VEGETATION ANALYSIS

**INTRODUCTION**

Several studies suggest that vegetation characteristics may be linked to sage-grouse chick survival (Aldridge 2005, Aldridge and Boyce 2007, and Gregg 2005). During the chick monitoring period we sampled vegetation at brood sites weekly. We used the brood hen's location as the central point for sampling. We used the line-intercept for shrub cover (Canfield 1941), and Daubenmire frames to measure herbaceous cover (Daubenmire 1959). We place 4 10-meter transects (starting at a random direction) 90 degrees apart. Line-intercept measurements were taken along each transect and Daubenmire frames were placed every 2.5m along each transect (n = 4 per transect). No random locations were sampled for comparison.

We used vegetation-based covariates (shrub, grass, and forb cover and height) to assess the relationship between habitat and chick survival. Because we did not sample the vegetation each time we monitored a brood, only chick survival periods following vegetation sampling were used in the survival analysis. By chance, restricting the dataset this way, survival periods where missing chicks were involved were excluded. Thus, alternative analysis actions to account for missing chicks (Appendix A) were precluded. By far, the null model was our top model in all vegetation-related survival analyses (Table B-1). Therefore we found no significant relationships between vegetation parameters and chick survival.

In addition to analyzing the relationship between vegetation and chick survival, we assessed the relationship between habitat and insect abundance. Data for arthropod abundance was collected using methods described in the main text. We used linear



regression in R (R version 2.8.0, Copyright © 2008, The R Foundation for Statistical Computing) to evaluate this relationship. For arthropod parameters we used Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, ants, miscellaneous, and total abundance. For vegetation parameters we considered shrub, forb, and grass cover and heights. When variables did not meet assumptions of normality we transformed them accordingly. No significant relationships were revealed during this analysis ( $P > 0.05$  or very low  $r^2$  values). Therefore, we found no relationship between habitat and arthropod abundance in our study.

Table B-1. Models for greater sage-grouse (*Centrocercus urophasianus*) chick survival based on vegetation measurements at brood sites (this dataset was restricted to only those survival periods immediately following vegetation sampling at brood sites), Parker Mountain, Utah, 2005-2006.

Model	K	QAIC <sub>c</sub>	$\Delta_i$	$w_i$
<u>Null Model Determination</u>				
age = (week1)+(week2)+(week3)+(week4)+(weeks5-6)	6	-74.37	0.00	0.99999
age = (week1)+(week2)+(week3)+(weeks4-6)	5	-10.32	64.05	0.00000
age = (weeks1-3)+(weeks4-6)	3	8.9	83.27	0.00000
age = (weeks1-2)+(weeks3-4)+(weeks5-6)	4	39.73	114.10	0.00000
age = (week1)+(week2)+(weeks3-6)	4	41.81	116.18	0.00000
age = (week1)+(weeks2-6)	3	50.34	124.71	0.00000
age = (weeks1-2)+(weeks3-6)	3	58.03	132.40	0.00000
age = (weeks1-6)	2	104.17	178.54	0.00000
<u>Vegetation Model Selection</u>				
age (NULL)	6	-74.37	0.00	0.99999
age* + forb height	7	-11.73	62.64	0.00000
age* + shrub height	7	41.8	116.17	0.00000
age* + grass height	7	42.15	116.52	0.00000
age* + forb cover + forb height	8	50.3	124.67	0.00000
age* + forb cover + grass cover	8	62.31	136.68	0.00000
age* + grass cover + grass height	8	75.04	149.41	0.00000
age* + shrub cover + shrub height	8	76	150.37	0.00000
age* + shrub type	9	86.12	160.49	0.00000
age* + shrub cover	7	87.94	162.31	0.00000
age* + forb cover + forb height + grass cover + grass height	10	97.49	171.86	0.00000
age* + grass cover	7	105.17	179.54	0.00000
age* + forb height + grass height	8	111.14	185.51	0.00000
age* + forb cover	7	137.92	212.29	0.00000
age* + All Vegetation Covariates	15	243.29	317.66	0.00000

K: the number of parameters used in each model.

QAIC<sub>c</sub> : quasi-likelihood version of Akaike's Information Criterion.

$\Delta_i$  : QAIC<sub>c</sub> difference between a model (i.e., model *i*) and the best performing model (i.e., model with the lowest QAIC<sub>c</sub> among the set of models examined).

$w_i$ : Akaike model weight. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC<sub>c</sub> values can be drastically different; even amongst the top few models. Thus, model weights can be highly skewed towards the top model.

\* The best model of age = (week1) + (week2) + (week3) + (week4) + (weeks5-6), which is shown in the null model determination. The null model once determined is then used to test for the importance of covariate structure in the modeling process.

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## CURRICULUM VITAE

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**Objective**

To obtain a research, extension, and teaching position that allows me to 1) continue to conduct quality applied research for wildlife conservation, 2) provide outreach to public and private interests for wildlife conservation and planning, and 3) to work with students to facilitate learning and mentoring in natural resource education.

**Education**

Sep. 2005 – Present

**Utah State University**

*Logan, Utah*

Ph. D. Candidate – Wildlife Biology

Dissertation: Greater Sage-grouse Juvenile Ecology and Population Dynamics, Parker Mountain, Utah

Mar. 2002 – Sep. 2005

**Utah State University**

*Logan, Utah*

M.S. – Wildlife Biology

Thesis: Greater Sage-grouse Reproductive Ecology and Response to Experimental Management of Mountain Big Sagebrush on Parker Mountain, Utah, 2006

Sep. 1998 – May 2001

**Utah State University**

*Logan, Utah*

B.S. – Wildlife Biology

Sep. 1993 – Sep. 1998

**Ricks College**

*Rexburg, Idaho*

Associates Degree – Natural Resource emphasis

## Awards and Honors

Spring 1988	Eagle Scout
June 1993	Honor Roll
December 1997	Honor Roll
September 1999	Department of Fisheries and Wildlife Scholarship
May 2001	Dean's Honor Roll
February 2009	USU CNR Graduate Research Assistant of the Year

## Professional Experience

2002 – Present	Graduate Research Assistant (M.S. and Ph. D.) Utah State University Parker Mountain Sage-grouse Project
2008 – 2009	Program and Volunteer Coordinator Utah State University Extension and Utah Division of Wildlife Resources Sage and Columbian Sharptailed Grouse Lek Search Program
2004	Sage-grouse Lek Data Technician Western Association of Fish and Wildlife Agencies Sage and Columbian Sharptailed Grouse Technical Committee Range-wide Sage-grouse Conservation Assessment (2004)
2001 – 2002	Environmental Scientist Entranco Inc., Salt Lake City Biological Environmental Consultant
1999 – 2000	Biological Technician Utah Division of Wildlife Resources State-wide Banding Crew, Partners in Flight Program

## Professional Skills

- Extensive experience with telemetric techniques (both ground and aerial) for sage-grouse research
- Extensive experience locating sage-grouse nests using telemetry and binoculars
- Extensive experience in monitoring breeding surveys (lek counts) of native grouse
- Extensive experience in locating new or previously unknown lek sites

- Extensive experience trapping, handling, and radio-marking sage-grouse
- Experience in trapping, handling, and characterizing passerine birds using mist-nets
- Statistical analysis package experience: SAS, R, DISTANCE, and MARK
- Population Modeling (matrix modeling)
- Data collection, storage, and manipulation: Excel and Access
- Vegetation monitoring experience in sagebrush ecosystems
- GPS and GIS spatial manipulation and analysis experience
- Scientific document preparation (agency and peer-review publications)
- Experience in refereeing scientific literature for peer-review publication
- Experience collaboration within community-based conservation teams, including federal, state, and private interests
- Experience with sportsman organizations
- Experience with preparation of outreach materials
- Experience with determining sex and age characteristics of sage-grouse from harvested wing samples
- Experience procuring and coordinating volunteer efforts for wildlife projects
- Experience supervising multiple technicians for a research project
- Training and experience in wetland delineation
- Driving 4x4 trucks and ATVs in adverse climate and terrain for field research
- Experience using pointing dogs for upland game field research
- Experience purchasing and maintenance of field equipment, including vehicles

#### **Equipment used and maintained**

- multiple types of telemetry antennae
- scanners and receivers (Telonics and ICOM)
- radio-collars for sage-grouse
- 4x4 truck and ATV
- GPS units (Garmin and Trimble)
- Sage-grouse trapping equipment
- vegetation monitoring equipment
- field notebooks and data sheets
- computer
- binoculars and spotting scopes

## Volunteer Activities

- 2005-2008 *Vice President/Board Member, Utah Chukar and Wildlife Foundation.* The UCWF is a non-profit organization dedicated to improving habitat and upland game populations on public lands throughout the state of Utah.
- 2008 *Utah Upland Game Advisory Committee Chair, Utah Division of Wildlife Resources.* The UGAC works in association with the UDWR upland game program advising the program coordinator on upland game issues throughout the state.
- 2005 – present *Forest Grouse Committee Chair, Utah Chukar and Wildlife Foundation.* The forest grouse committee within UCWF is committed to gathering information on forest grouse populations and promoting hunting of forest grouse.
- 2007 – 2008 *Volunteer Instructor, 4-H Wildlife Habitat Evaluation Program (WHEP).* I instructed 4-H members (Oklahoma and Utah teams) in sage-grouse habitat and conservation issues in preparation for WHEP competition.
- 2004 – 2008 *Utah Division of Wildlife Resources (UDWR) Youth Chukar and Pheasant Hunts.* I helped guide qualified youth hunters during the UDWR youth hunts to help promote recruitment of teenagers into outdoor related activities such as hunting.

## Teaching Experience

- 2003 *Grade School.* Salt Lake County School District, SLC, Utah. I taught 4<sup>th</sup> and 5<sup>th</sup> graders about sage-grouse ecology and use of telemetry in research.
- 2004 *Junior High School.* Wayne County Junior High, Bicknell, Utah, Utah State University Extension program. I have taught groups of junior high school kids about sagebrush ecology, and related wildlife species, along with telemetry techniques used in research.
- 2003 – 2004 *High School.* Copper Hills High School, West Jordan, Utah, Continuing to Higher Education Program. I was invited to lecture in a high school biology class on wildlife

science, sagebrush and sage-grouse ecology, general research methods, and graduate school experience.

2003 – 2009

*University Level.* Utah State University, Logan, Utah. I have been invited to give guest lectures in introductory wildlife classes on sage-grouse ecology and management issues on multiple occasions. I have led several field trips discussing land management practices for sagebrush systems for undergraduate and graduate courses. I also helped team teach a semester-based class on sagebrush and sage-grouse monitoring techniques.

2009

*University Level.* Utah State University, Logan, Utah. I helped teach undergraduate and graduate students Upland Game Ecology and Management topics in an Avian Ecology and Management course. I covered topics of general introduction to upland game, population principles and management, and habitat principles and management.

## **Presentations**

Dahlgren, D. K., and T. A. Messmer. 2003. Parker Mountain sage-grouse and rangeland Manipulation. Presented at the Utah State Chapter of the Society for Range Management Conference, Provo, Utah.

Dahlgren, D. K., and T. A. Messmer. 2003. Parker Mountain Greater Sage-grouse, Sagebrush Treatments, and Rabbit Herbivory. Presented at the Utah State Chapter of the Wildlife Society Meetings, Logan, Utah.

Dahlgren, D. K., and T. A. Messmer. 2004. Manipulation of Sage-grouse Brood-rearing Habitat and Lagomorph Herbivory. Presented at the Western Association of Wildlife Agencies Sage and Columbian Sharptailed Grouse Technical Committee meeting, Winatchee, Washington.

Dahlgren, D. K., and T. A. Messmer. 2005. Manipulation of sage-grouse brood-rearing habitat. Presented at the 2005 Berryman Institute Symposium, Logan, Utah.

Dahlgren, D. K., R. Chi, and T. A. Messmer. 2006. Greater sage-grouse response to sagebrush management in Utah. Presented at the Western Association of Wildlife Agencies Sage and Columbian Sharptailed Grouse Technical Committee meeting, Rapid City, South Dakota.



Dahlgren, D. K., R. Chi, and T. A. Messmer. 2007. Greater sage-grouse response to sagebrush management in Utah. Presented at the Society for Range Management meetings, Reno, Nevada.

Dahlgren, D. K., and T. A. Messmer. 2007. General methods: sage-grouse research. Presented at the Utah Sage-grouse Summit Meeting, Utah State University Extension and Utah Division of Wildlife Resources, Salt Lake City, Utah.

Dahlgren, D. K., E. Thacker, M. Guttery, and T. A. Messmer. 2007. Use of Bird-dogs in Prairie Grouse Research. Presented at the Prairie Grouse Technical Committee meetings, Chamberlain, South Dakota.

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Dahlgren, D., D. Elmore, and T.A. Messmer 2004. Community-based conservation programs in Utah: Parker Mountain Annual Report. Utah State University Extension, Logan. 30pp.

Dahlgren, D., D. Elmore, and T.A. Messmer 2003. Community-based conservation programs in Utah: Parker Mountain Annual Report. Utah State University Extension, Logan. 25pp.

## **Reviewed Manuscripts for the Following Journals:**

Journal of Wildlife Management  
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## **References**

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