

BREEDING ECOLOGY, SURVIVAL RATES, AND CAUSES OF MORTALITY  
OF HUNTED AND NONHUNTED GREATER SAGE-GROUSE  
IN CENTRAL MONTANA

by

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

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY  
Bozeman, Montana

November 2006

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## ACKNOWLEDGEMENTS

I extend sincere thanks to the many biologists (FWP, BLM, MSU, & UM) that contributed in innumerable ways to this project. Jay Newell mentored and teased me and was a positive force throughout. Jay Watson provided much technical ingenuity and was a nightlighting machine. Allison Puchniak-Begley trapped birds and befriended me at the beginning. At all hours of the night, Sean Stewart, Clair Simmons, Ray Mule', Gary Dusek, Dave Pac, and Tom Lehmke all trapped birds and provided comic relief. Charlie Eustace radio-tracked birds overwinter. Neil Anderson, Mark Atkinson, Jeff Herbert, Keith Aune, Kurt Alt, Rick Northrup, and Lydia Bailey provided logistical support, equipment, and expertise. Lee Burroughs and Dale Nixdorf assisted with trapping and/or tracking and provided landowner information and hunter data. Jay Parks made the habitat work possible.

I extend thanks and appreciation to my committee. Jay Rotella, my advisor, encouraged me to *always* be critical in my scientific thinking and doing, and his approach to mentoring was outstanding. Bob Garrott provided critical feedback and helped me improve my writing. Carl Wambolt was instrumental in getting the sagebrush-habitat work off the ground.

B. Sowell collaborated with the habitat work. V. Lane and J. Woodward conducted graduate research of sagebrush habitats. J. Woodward also monitored birds overwinter. B. Moynahan got me started with protocols and datasheets. H. Harrison made us movie stars. M. Richman, A. Anderson, S. Conner, D. Auerbach, D. Keto, M. Peters, M. Watrobka, K. Drake, and A. Torrick were the muscles of this project. S. Conner and D. Keto also conducted undergraduate research of artificial nests and sage-grouse males, respectively.

Finally, I extend a tremendous thanks to Brett Walker, who shared his enthusiasm for biology and hours and hours of sage-grouse shop talk, reviewed several versions of my thesis, cooked many meals, gave me hugs and encouragement, and walked with me.

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## ABSTRACT

Declines in productivity have been implicated in population declines for greater sage-grouse (*Centrocercus urophasianus*) in several areas, but there is considerable variation in reproductive effort, reproductive success and female survival, both temporally and spatially, and more data are needed. Despite declining populations, sage grouse are still legally harvested in most of their current range, including Montana, and uncertainty about how harvest impacts sage grouse vital rates remains. The reproductive activity, survival rates, and causes of mortality of hunted and nonhunted sage grouse females were monitored year round using radio-telemetry in central Montana during 2004 and 2005. Data on nest survival and brood survival were also collected. Nest survival was greater for renests, 0.56, than for first nests, 0.32. Brood survival to 30 days post-hatch was estimated as 0.79. Reproductive effort and reproductive success were higher in 2005. Female survival during the nesting season was constant, 0.94 monthly. Female survival during July of both years was similar on both sites, 0.99 to nearly 1.00, but survival was lower during August and declined between 2004 and 2005 from 0.94 to 0.84 on the hunted site and declined from 0.98 to 0.94 on the nonhunted site. This decline in survival between years in August was likely due to West Nile virus, as it was first detected in sage grouse in this area in August 2005. Female survival during the hunting season was lower for females that spent more days brood-rearing than those that spent few or no days brood rearing, and females on the hunted site had lower survival than females on the nonhunted site. However, lower survival rates on the hunted site could not be attributed to hunter kill, because no radio-marked females were bagged or reported by hunters and no evidence of hunter kill was observed. During the hunting season, monthly survival estimates ranged from 0.87 for hunted-site females that invested heavily in brood rearing to 0.99 for nonhunted-site females that invested little or no time in brood rearing. Overwinter survival was different between years, and monthly survival during winter 2004-05 was estimated as 0.98 and as 0.97 during winter 2005-06.

## CHAPTER ONE

## INTRODUCTION

Introduction to Thesis

Greater sage-grouse (*Centrocercus urophasianus*), hereafter sage grouse, populations have been declining throughout their historical range in western North America since the early 1900s (Hornaday 1916), with current abundance estimated at 1-31% of the numbers present prior to European settlement in the 1800s (United States Fish and Wildlife Service 2004). In addition to a dramatic decline in abundance, sage grouse distribution has contracted by as much as 44% (Schroeder et al. 2004).

Declines in productivity have been implicated in population declines in areas of Colorado, Idaho, Montana, Oregon, Wyoming, and Alberta (e.g., Crawford and Lutz 1985, Connelly and Braun 1997, Connelly et al. 2004, Aldridge 2005), but there is considerable variation in reproductive effort, reproductive success (productivity), and female survival (see Schroeder 1997, Schroeder et al. 1999 and Connelly et al. 2000a, 2004 for review), both temporally and spatially. Reproductive effort and reproductive success may be somewhat counterbalanced by opposite (or negatively covarying) levels of female survival, and this counterbalance may stabilize population growth rates. Therefore, it is important to study both reproduction and survival across years to obtain a more accurate picture of how vital rates influence fluctuations in populations.

Despite declining populations, sage grouse are still legally harvested in most of their current range, including Montana. Although there is currently a need to reduce

sources of mortality for sage grouse, harvest is also an incentive for conservation. Licensing fees provide revenue for management of harvestable population sizes, and hunting maintains public interest in game species. Uncertainty about how harvest impacts sage grouse vital rates remains. Thus far, published research investigating the effects of harvest on sage grouse vital rates has suggested that harvest mortality may not be compensatory (Johnson and Braun 1999, Connelly et al. 2000*b*, Connelly et al. 2003) or in contrast, has reported that hunting has little impact on populations (Wallestad 1975, Crawford 1982, Braun and Beck 1985). Further, harvest may impact sage grouse populations differently across their range, and thus, area-specific data on the impact of harvest, and the magnitude of this impact relative to other potential sources of mortality, are necessary for informed management.

Information from areas where sage grouse populations appear to be doing well (i.e., where abundance is relatively high) may be valuable to understanding range-wide declines and subsequently informing future research needs and management decisions. This study was designed with the following objectives: 1) to estimate nesting and re-nesting probabilities, nest survival, brood survival, and female survival for breeding sage grouse with relatively healthy, robust populations on two sites in central Montana, 2) to simultaneously compare survival rates during the hunting season and overwinter between adjacent hunted and nonhunted sites with similar landscape and population characteristics, 3) to evaluate factors other than hunting that influence survival during the hunting season, 4) to assess the relative importance of different sources of mortality on sage grouse during the hunting season and overwinter, and 5) to assess, to the extent possible, the influence of harvest on the sage grouse populations studied and to make

recommendations for future investigations about the effects of harvest on sage grouse.

Breeding ecology is the subject of Chapter 2, and Chapter 3 discusses my research on harvest and mortality causes.

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## CHAPTER TWO

## BREEDING ECOLOGY OF GREATER SAGE-GROUSE IN CENTRAL MONTANA

Introduction

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage grouse) populations have been declining throughout their historical range in western North America since the early 1900s (Hornaday 1916), with current abundance estimated at 1-31% of the numbers present prior to European settlement in the 1800s (United States Fish and Wildlife Service 2004). In addition to a dramatic decline in abundance, sage grouse distribution has contracted by as much as 44% (Schroeder et al. 2004). As of 1997, populations were considered secure in Idaho, Wyoming, Oregon, Nevada, and Montana (Connelly and Braun 1997). Currently, populations in Colorado, Utah, California, Washington, and Nevada are considered the most isolated (Connelly et al. 2004). Much of central Montana is still in relatively contiguous sagebrush-steppe habitat, supports relatively large numbers of sage grouse, and supports populations that appear to be relatively stable at the present time (Connelly et al. 2004, Montana Sage Grouse Work Group 2005). Declines in productivity have been implicated in population declines in areas of Colorado, Idaho, Montana, Oregon, Wyoming, and Alberta (e.g., Crawford and Lutz 1985, Connelly and Braun 1997, Connelly et al. 2004, Aldridge 2005), but there is considerable variation in reproductive effort, reproductive success (productivity), and female survival (see Schroeder 1997, Schroeder et al. 1999 and Connelly et al. 2000, 2004 for review), both temporally and spatially. Currently, there are few published

studies of sage grouse in Montana, especially since the 1970s, and information from areas where sage grouse populations appear to be doing well (i.e., where abundance is relatively high) may be valuable to understanding range-wide declines and informing local management decisions.

For many bird species, reproductive success is the key to population dynamics (Sæther and Bakke 2000) and may be an important factor affecting population size in grouse species (Bergerud 1988). Sage grouse have relatively high survival and low reproduction compared to other grouse species (see Connelly et al. 2000 for review). Thus, the sage grouse is not a “highly reproductive species,” according to the criteria of Sæther and Bakke (2000), but may be a “bet-hedging species” with higher reproductive effort, nest and brood survival, and reproductive success in occasional good breeding years or conditions. If so, there may be considerable variation in reproductive success (productivity) and female survival, both temporally and spatially, and understanding what contributes to good breeding years or conditions is critical for management.

Studies of grouse species have documented higher reproductive effort in areas that may represent better breeding conditions (sage grouse: Schroeder 1997, ptarmigan [*Lagopus* species]: Sandercock et al. 2005). Typically, sage grouse have low rates of nest and re-nest initiation compared to rates for other grouse species (Bergerud 1988). In a bet-hedging species, theory predicts that increases in reproductive effort will coincide with reduced survival (Bergerud and Gratson 1988). A recent sage grouse study in Montana reported higher annual survival during a year with low reproductive effort, a year that also had mild, dry weather (Moynahan et al. 2006). In that study however, in contrast to predictions regarding costs of breeding, survival during the breeding season

was reportedly higher for nesting females than for non-nesting females (Moynahan et al. 2006). Clearly, more recent and local information about sage grouse breeding ecology is needed to better understand factors that influence reproductive effort and female survival and to examine trade-offs between the two.

There are a number of factors that can affect survival of nests, broods, and females, including weather, predator communities, habitat characteristics, disease, and female quality. Weather and predator density and species composition may change greatly over time causing vital rates to vary temporally, both within and among years. Drought has been shown to affect population dynamics (Connelly and Braun 1997, Connelly et al. 2000, Moynahan et al. 2006). Cold wet weather in spring may negatively affect brood survival (Wallestad 1975), and West Nile virus (WNV) (Naugle et al. 2004, Walker et al. 2004, Naugle et al. 2005, Moynahan et al. 2006) has recently been documented to negatively affect female survival. Predator communities, habitat characteristics, food availability, and disease may also vary spatially and subsequently influence vital rates differently across their range. Habitat alteration and fragmentation are thought to be the leading cause of decline in abundance and distribution (see Connelly and Braun 1997, Schroeder et al. 1999, and Connelly et al. 2000 for review). Breeding success may improve with female age either because older females are more experienced and therefore more successful breeders or because older females are less likely to be of low quality than younger females (females of poor quality are expected to die at an earlier age). Thus, individual variation in female quality may also influence vital rates.

Due to limited recent data for sage grouse breeding ecology in Montana and evidence of a continued range-wide decline, this study was designed with the following

objective: to estimate nesting and re-nesting probabilities, nest survival, brood survival, and female survival for breeding sage grouse with relatively high abundance on two sites in central Montana. This research was part of a larger project investigating the effects of hunter harvest of birds on sage-grouse demography, and some of these reproductive data (e.g., reproductive effort) were used to evaluate sources of variation in hunting season and overwinter survival of female sage grouse (see Chapter 3). Relationships between habitat conditions and reproductive parameters and between habitat conditions and habitat use are reported elsewhere (Lane 2005, Woodward 2006).

### Study Area

I studied sage grouse within an approximately 3,000 km<sup>2</sup> area in Musselshell and Golden Valley Counties in central Montana from 2003-2005 (46° 26' to 46° 76' N, 108° 32' to 109 15' W) (Appendix A1). This area was primarily sagebrush-steppe (80%) interspersed with native prairie grasslands (<1%), ponderosa pine (<1%), and both dry-land and irrigated agriculture (14%) (Appendix A2). Soil taxonomy for this area is described in detail by Woodward (2006). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), western wheatgrass (*Agropyron smithii*), green needlegrass (*Stipa viridula*), and blue grama (*Bouteloua gracilis*) characterized the predominant upland habitat and cover type. Two habitat types dominated lowlands: 1) Plains silver sagebrush (*A. cana cana*) with western wheatgrass and 2) greasewood (*Sarcobatus vermiculatus*) with Gardner saltbrush (*Atriplex gardneri*), inland saltgrass (*Distichlis spicata*), and green needlegrass. Historical and current land uses include cattle and sheep grazing. Relatively little energy development (i.e., oil or gas) occurred within the core areas of the

study sites. Portions of land continued to be converted to dry and irrigated cropland, including enrollment in the federal Conservation Reserve Program (CRP), and land was treated to remove sagebrush. The 70-year precipitation average was 37 cm, but severe to extreme drought conditions persisted from 2000-2005 (Appendix B; National Oceanic and Atmospheric Administration [NOAA] 2006). Annual precipitation was 25 cm in 2004 and 46 cm in 2005, and average monthly temperature ranged from -7°C in January to 22°C in July (NOAA 2006). Elevation ranged from 800 to 1,500 m. The study area supported relatively abundant breeding populations of nonmigratory sage grouse. Peak attendance at 25 leks averaged 24 to 37 males per lek (range 5-76 males among 25 leks) from 2002-2005 (Appendix C, Montana Fish, Wildlife and Parks [FWP], unpublished data). A large proportion of land in this region was enrolled in FWP's Block Management Program, which facilitates hunting access on private lands, and the FWP Commission had the ability to close a large area to sage grouse hunting to conduct this study.

I defined one hunted site and one nonhunted site within the study area by trapping birds at four adjacent leks on the nonhunted site and five adjacent leks on the hunted site that collectively had high male attendance (150 to >200 males). About 80% of this site was a sagebrush cover type and was similar to the nonhunted site, 88%, and about 20% of the hunted site was converted to some type of agriculture which was higher than the nonhunted site, 8% (Appendix A2). Based on previous studies, I expected that most birds would remain within 5 km of the leks where they were trapped (Eng and Schladweiler 1972, Wallestad and Pyrah 1974, Wallestad and Schladweiler 1974, Wallestad 1975). Thus, for vegetation sampling and site descriptions, I defined each

study site as a “lek complex,” the area within overlapping 5-km radii around trapped leks (Appendix A1). The hunted site was 287 km<sup>2</sup> in area, of which 60% was privately owned, and 40% was publicly owned and managed by either the Bureau of Land Management (BLM) or the State of Montana. The nonhunted site was 262 km<sup>2</sup> in size and 94% privately owned. The remaining 6% was publicly owned and managed by either the BLM or the State of Montana.

### Methods

Sage grouse were captured at or near leks from late-March through mid-April, and again prior to the opening of the hunting season in September using either nighttime spotlighting and hoop-netting (Wakkinen et al. 1992) or rocket nets (Geisen et al. 1982). For each female captured, I recorded age (yearling or adult (Eng 1955, Crunden 1963) and applied an individually numbered aluminum leg band (National Band and Tag Company, Newport, Kentucky). In 2003, each female was also marked with a uniquely numbered white plastic tarsus band for resighting. Each yearling and adult female was outfitted with a necklace-type radio transmitter (Advanced Telemetry Systems®, Isanti, Minnesota, models A4080 and A4050 [Armstrup 1980]). These transmitters weighed about 22 or 16 grams (less than 2% of female body weight), included a mortality switch that triggered after either 4 or 12 hours without movement, had a life expectancy of 680 or 890 days, and initially had a detection range up to 10 km from the ground and up to 24 km from the air. The latter model had a 16:8 hour duty-cycle switch.

I monitored the status (alive or dead) and movements of radio-marked females to estimate survival and to determine timing and causes of mortality. I also monitored each

female's reproductive effort to estimate rates of nest and re-nest initiation, nest survival, and brood survival, and to include reproductive effort as a metric in survival analyses. This research was part of larger project investigating the effects of harvest on population dynamics of sage grouse, and these reproductive effort metrics were included in those analyses of female survival (see Chapter 3). I used telemetry homing techniques (Samuel and Fuller 1996) to locate females visually ("visual locations") and recorded their locations using a Global Positioning System (GPS) receiver. Locations were estimated ("estimated locations") using triangulation and a modified vehicle-mounted antenna system with a null-peak design (Brinkman et al. 2002). In 2003-2004,  $\geq 2$  bearings were plotted by hand on aerial photos (Natural Resources Conservation Service State Office, Bozeman, Montana). In 2005, bearings were measured using a digital compass attached to a vehicle-mounted antenna system (Cox et al. 2002), and locations were estimated using LOAS 3.0.4 software (Ecological Software Solutions, Sacramento, California). I conducted telemetry flights to search for birds I was unable to locate on the ground. I recorded aerial locations with a GPS receiver.

When a mortality signal was detected, carcasses were located as soon as possible in an attempt to identify the cause of mortality and to collect remains. If bones were crushed, if only feathers remained, or if mammalian scat or tracks were observed at the kill site, I classified cause of mortality as mammalian predation. I classified the cause of mortality as avian predation if bones and ligaments were stripped or if raptor mites were located near the carcass. If evidence for both avian and mammalian predation were observed, I classified the mortality as "scavenged." It is possible that birds died of causes other than predation and were subsequently scavenged prior to our examination of

remains. Intact or mostly intact carcasses, heads, bones, internal organs, and blood feathers collected from late July through 31 August were sent to the Wyoming State Veterinary Laboratory for West Nile virus (WNV) testing.

I attempted to monitor all females in all seasons; however, some females were never relocated. If a female was “lost” during a season but was found alive after the season, then she was treated as having been alive for the entire season in analyses. If a female was found dead after the season, then she was included as having died in the season in which she was lost. If a female was lost during a season, was never found again, and her transmitter was new, then she was included in the dataset as alive until lost, after which she was considered dead (White & Garrott 1990). I decided to include females as having died in this case, rather than assuming they lived and censoring them from the dataset, because most sage grouse females in our study area were highly site faithful and transmitter failure was uncommon. Most females that were lost for more than a couple of weeks were found the following spring. If a female with an old transmitter (past expected battery life or other indication of battery failure) was lost during a season and never found, then she was included as alive until lost, and then censored from the dataset (White & Garrott 1990). On old transmitters, the signal strength typically decreased or was erratic in intensity, or the quality of the signal changed (e.g., clear beep or chirp changed to thud or sounded like a drop of water in an empty bucket) prior to signal loss (C. O. Kochanny, Advanced Telemetry Systems, personal communication).

## Nesting

Visual locations were obtained for all females once per week throughout the nesting season. I attempted to visually locate females before they flushed. After females flushed, searches for nests were made within a 5-m radius of flush locations. If a female did not flush on her own accord on the first and second nest visit, they were flushed off nests to count the clutch and to float two eggs to estimate stage of incubation (Westerkov 1950). Females were not intentionally flushed off nests after either a second clutch count or after the eggs were floated. I modified our nest-searching protocol in 2005 after determining that flushing hens off nests during laying caused some hens to abandon nests. Instead, I estimated nest locations from a distance of 15-20 meters on the first visit to avoid disturbing females that may have still been laying, and I returned to the nest site after two or more days, flushed the female off the nest, and floated and counted the clutch.

I estimated clutch completion dates using the stage of incubation and clutch counts. I estimated initiation and hatch dates from the clutch completion date using a laying rate of 3 days for every two eggs and a 27-day incubation period (Schroeder et al. 1999). I attempted to visit each nest near the estimated hatch date. If a nest failed, I classified the failure as an abandonment (clutch intact and hen alive), predation (eggs missing or destroyed or hen dead), or other (e.g., plowed). I considered a nest successful if  $\geq 1$  eggs hatched, and hatch was confirmed by the presence of chicks with the hen or eggshells with detached membranes in or near the nest bowl.

### Brood-Rearing

For non-brood hens, estimated or visual locations were obtained once per week. For brood hens, I typically waited until chicks were  $\geq 1$  week old before obtaining a visual location to avoid separating chicks from the hen before the chicks could fly or thermoregulate. Then, once every other week, I visited the hen to count chicks, and on alternate weeks, locations were estimated. Chicks were flushed in an attempt to get a flush count, and I thoroughly searched within 5 m of the hen's flush location. At approximately 30 days post-hatch, daytime flush counts of brood hens were conducted to determine chick presence or absence. Sage grouse chicks are well camouflaged and often roost away from the hen during the day, making them difficult to detect (Huyer 2004). If no chicks were observed at the 30-day daytime visit, then females were visited at night because chicks typically roost with the hen at night. I considered a brood successful if  $\geq 1$  chick survived to 30 days post-hatch. If a female was observed with other breeding-aged birds within the first 2-3 weeks post-hatch, I assumed her brood did not survive. If a female was observed with other breeding-aged birds close to or at 30 days post-hatch, I classified brood fate as unknown due to the potential for brood mixing. After broods from radio-marked females reached 30 days of age, female survival was monitored once per week until the beginning of the hunting season.

### Data Analysis

I used an information-theoretic approach to evaluate the relative support for sets of candidate models describing competing hypotheses about nest, brood, and female

survival (Burnham and Anderson 2002). I used logistic regression and maximum-likelihood estimation in Program MARK (White and Burnham 1999) to obtain beta estimates, and for most models, I used the logit link to derive estimates of daily survival rates (DSR) for nests, broods, and females and to estimate the precision of those rates. I used the sine link when seasonal survival for a particular set of individuals was 100% because of convergence problems with the logit link function in such cases. In situations where all birds with a given covariate condition survived, e.g., 100% survival for all birds in an age class, I used the profile-likelihood function to estimate confidence intervals for estimates of DSR. I used the nest-survival data format and nest-survival estimation in Program MARK for nests, broods, and females. The number of encounter occasions used in these analyses are listed in Appendix D. I used this approach for female survival, because not all females were visited on the same date or in the same week, i.e., the visit schedule was ragged. The nest survival module does not require data on the specific timing of death, allows for the inclusion of females that were not tracked with the same intensity over time, and allows staggered entry and right-censoring. I also used logistic regression in the program R 2.3.1 software (R Foundation for Statistical Computing, Vienna, Austria) to conduct a goodness of fit test for brood-survival analysis (no such analogous procedure yet exists for data in a nest-survival format). I used Akaike's Information Criterion ( $AIC_c$ ) scores and AIC weights to evaluate all models (Burnham and Anderson 2002). Although I would have liked to estimate goodness-of-fit for models of other data sets and to estimate possible overdispersion in models of all datasets, such diagnostics are not available for these data types at this time.

While all analyses were conducted at the level of daily survival rates, survival estimates for nests, broods, and females were the product of all the daily survival rates for the relevant incubation period (28 days), brood-rearing period (30 days), month, or season length (Appendix D). I used the delta method and parametric bootstrap method to estimate associated variances (Seber 1982, Zhou 2002).

I included the following covariates in all candidate model sets (nest, brood, and female survival): *year* (0 = 2004, 1 = 2005), *site* (0 = nonhunted, 1 = hunted), and *female age* (0 = adult, 1 = yearling). Year was included as a surrogate for annual variation in other variables that were not measured, including weather, vegetation, and bird density. Survival may vary between sites due to intrinsic differences in ecological features, such as vegetation quality or quantity. I included female age, because age-specific variation in survival (Zablan et al. 2003) and age-specific reproductive success have been previously documented in sage grouse (Schroeder et al. 1999). For all adult female survival analyses, I delineated seasons (Appendix D) based on the biology of sage grouse and factors that may influence their survival at different times of year (e.g., reproductive effort, WNV, density, or weather), and then I conducted analyses for each season with replicate years. Covariates specific to nest survival, brood survival, or female survival are described in detail below.

Nesting Probability, Renesting Probability, and Reproductive Success Observed nesting probabilities were calculated as the proportion of females detected initiating at least one nest, and renesting probabilities were calculated as the proportion of females detected initiating a second nest given a failed first nest. I calculated these estimates for

yearlings and adults in both years. Renesting probabilities were also calculated excluding females that may have abandoned first nests due to investigator activity. It is likely that probabilities for both first nest and reneest initiation were underestimated, because some nests are missed. Reproductive success was calculated as the proportion of females that successfully raised a brood to 30 days from the total sample at the beginning of the nesting season and for which reproductive data were complete. Standard errors were calculated for a distribution of sample proportions ( $\sigma = \sqrt{(pq / N)}$ ). Females that died early in the season (by about 2 weeks) were excluded from nesting probabilities but were included in reproductive success calculations.

Nest Survival I included 22 models in our *a priori* candidate model set for nest survival. Nests were included in the analysis from the day found until either the day failed or the estimated or realized hatch date. I hypothesized that nest survival may increase as the season progresses (Klett and Johnson 1982). For example, nests and nesting hens in poor locations or with less vegetative cover are likely discovered and depredated earlier, leading to a pattern of higher DSR later in incubation. For this reason, I included *nest age* and *nest-age*<sup>2</sup> covariates which allowed for a linear or exponentially increasing or decreasing trend with increasing nest age. Finally, I predicted that renests would have higher survival than first nests (*nest attempt*: 0 = first nest, 1 = reneest), possibly due to the increase in vegetative cover at nests occurring later in the season (Bousquet 1996) or nest predator abundance, foraging behavior or predators switching to alternative food sources (Moynahan et al. in press).

Brood Survival I included eight models in our *a priori* candidate model set for brood survival. The brood survival analysis was conducted for a 29-day period, because I was unable to analyze the data at a finer time resolution due to uncertainty about timing of brood failure. Chicks were difficult to detect on day-time flush counts, and for some females, I did not observe a brood until the final 30-day nighttime brood count. Thus, assigning brood failure dates prior to 30 days was not possible. I included *year*, *site*, and *female age* as covariates in this analysis as discussed under *Data Analysis* above.

Female Survival I delineated seasons based on the biology of sage grouse and factors that may influence their survival at different times of year (Appendix D [e.g., WNV, density, or weather]), and then I conducted analyses for each season with replicate years. Female survival during the nesting season and late-summer are included in this chapter, and female survival during the hunting season and overwinter are included in Chapter 3. I included 34 *a priori* models in my candidate set for female survival during the nesting season. This season included the first day a nest was found and the last day a nest finished (hatched or failed) for each year. I predicted that female survival would increase over the season, because females at poor nest sites are likely to be detected and killed earlier in the season. For example, nests and nesting hens in poor locations or with less vegetative cover are likely discovered and depredated earlier, leading to a pattern of higher DSR later in incubation. For this reason, I included variables to represent within-season variation (*3 periods* and *trend3*). Period was represented by the first 22 days, second 22 days, and last 23 days of the season in 2004, and was represented by 21:22:40 days, respectively in 2005. More females renested in 2005, which extended the nesting

season. I included a model that allowed female survival to vary between years for the last period, because in 2005 this period was longer and represented the bulk of reneating in our dataset. I also included a term (*trend3*) that restricted survival to an increasing or decreasing trend over the three periods. I included *nesting status* with the expectation that nesting females would have lower survival while on nests than while off nests, and I classified each female as being on or off a nest (*nesting status*: 0 = not on nest, 1 = on nest) on each day of the nesting season. These data were subsequently used to evaluate whether females with higher reproductive effort had different survival probabilities than females with lower reproductive effort. Reproductive effort covariates included in analysis for female survival during late-summer are described in detail below. Because the precise date of nest failure and female death were unknown, failure and death were included during a “failure window.” For the *nesting status* covariate, when a nest failed and the female lived, I included half of the days during the failure window as on the nest and half as off the nest. When a nest failed and the female died, or a female died after the last nest visit and the nest was intact, I assumed the fate of the female and her nest were due to the same predator and included all days as on the nest during the failure window.

Fifty-nine *a priori* models were included in my model set for female survival during late summer. The late-summer season began after the last nest finished in each year and ended on 31 August, the day before sage grouse hunting season opened. I considered two different terms for within-season variation in survival during this season, the last two weeks of August and August, based on field observations of timing of mortality and initial detection of WNV. WNV was first detected in sage grouse in 2004 in both southeastern and north-central Montana but not in central Montana (Naugle et al.

2005). In 2005, carcasses collected in August from our area tested positive, so I included models to evaluate differences in survival during August between years.

I chose to include six covariates to evaluate the effect of reproductive effort during the late-summer season, because I did not know which covariate would best reflect potential reproductive costs. But, only one reproductive-effort term was considered per model, and I predicted that continuous reproductive effort covariates would better reflect this effect than categorical variables. For reproductive effort, the categorical covariates were *nest fate* (0 = failed, 1 = succeeded or equivalent number of days incubating a nest) and *brood fate* (0 = failed, 1 = succeeded), and the continuous covariates were *days laying*, *days incubating*, *days rearing*, and the sum of days laying, incubating, and rearing (summed reproductive effort [*SRE*]). *Nest fate*, *days laying*, and *days incubating* were included for the entire season, but *brood fate*, *days rearing*, and *SRE* were only included for August, after brood success was determined for all females. I calculated the number of days laying by multiplying the complete clutch size by a laying rate of 1.5 days per egg (Schroeder et al. 1999). I calculated the number of days incubating as the interval from the first to the last known day of incubation. I defined the last day of incubation as the expected hatch date for successful nests, and for failed nests, the last day was the date of the last nest visit plus one-half the failure window. Females whose nests failed but that had an equivalent number of days incubating as successful females (28 days) were considered “successful” for the reproductive effort covariate *nest fate* (*nest fate* = 1). I calculated the number of days rearing as the interval from the hatch date to the last day on which the female was known to have had chicks. The last day of brood rearing was 30 days for females that had successful broods, and for failed broods,

this was the last date on which a hen was confirmed with a brood plus one-half the failure window. Finally, for the *brood fate* term, females either had a successful brood at 30 days, or they failed. I included models that evaluated effects of reproductive effort between years, because reproductive effort, and subsequently, survival, may vary annually if there are good or bad years for reproduction (Rotella et al. 2003, Ruf et al. 2006).

### Results

Data were collected during a relatively dry year in 2004 and a relatively wet year in 2005 (Appendix B). Seventy-one females were captured and radio-marked in 2004, and 45 females were captured and radio-marked in 2005 (See Appendix E for 2003 field season). Only one female was never relocated after capture, and this bird was censored from the dataset. I used telemetry to determine the fates of 71 radio-marked females in 2004 and 102 radio-marked females in 2005. The 2004 sample included 11 females originally marked in 2003 and one female that had been recaptured and released without a collar in 2003. The 2005 sample included 51 females originally marked in 2004 and 7 originally marked in 2003. Individual birds that survived to the next study year continued to be monitored, and associated data were included in our analyses. In 2004, I was able to monitor all birds until they died or until the start of the fall hunting season. During the nesting season in 2005, two birds were lost, and I included data up until the time they were lost and considered them dead thereafter. Late in the summer in 2005, I lost contact with one other female with a radio-collar that had been losing signal strength, so I included data up until the time she was lost and then censored data thereafter.

During the nesting season, I monitored the survival of 69 females in 2004 and 96 females in 2005 and monitored the reproductive activity of all but two females in both years (67:94). Data were obtained for 182 nests and 73 broods.

Females began initiating nests between late March and early April in both years and were first observed on nests in mid-April in both years. The earliest known renests were found 6 May in 2004 and 25 April in 2005, and the last nests finished on 21 June in 2004 and 8 July in 2005. The nesting season was 17 days longer in 2005 due to greater renesting.

Reproductive effort was greater in 2005 (Table 2.1 and 2.2). Nesting probability increased from 72% to 88% for yearlings and increased from 85% to 100% for adults. Renesting probability increased from 0% to 46% for yearlings and increased from 18% to 63% for adults. Overall, renesting probability increased from 13% to 59%. When nests that were abandoned due to investigator activity were excluded from calculations of renesting probability (Table 2.2), renesting probability between 2004 and 2005 increased from 0% to 22% for yearlings, from 13% to 60% for adults, and from 9% to 53% overall. Thirty-eight of 41 renests detected occurred in 2005, and at least three females attempted a third nest in 2005. Although a higher proportion of nests were successful in the first year, reproductive success (the proportion of females that successfully raised a brood of the total sample of females at the beginning of the season) increased from 28% in 2004 to 43% in 2005. Average clutch sizes were similar between years, and for first nests, clutch size was 8.3 (SE = 0.98) for adults and 7.7 (SE = 1.39) for yearlings. For renests, clutch size was 7.8 (SE = 0.99) for adults and 6.75 (SE = 1.5) for yearlings. Most nests were

located under shrubs, sagebrush (91%) or greasewood (3%), and only 6% were located in some type of agriculture (CRP, crested wheatgrass, or alfalfa fields).

### Nest Survival

I included 167 nests from 104 individual females in our nest-survival analysis (Table 2.4). Nests located during the laying period (2004:  $n = 6$ , 2005:  $n = 19$ ) were included in our analysis, but most of these contained data for few days in the egg-laying state, i.e., clutches were nearly complete. Thus, I pooled data for egg-laying with those for the incubation stage. I excluded 13 nests that were abandoned due to investigator activity, one nest of unknown fate, and one nest that had already failed and for which the hen was found dead at the nest on the day it was found (Table 2.3). Causes of nest abandonment may have also included human and livestock activity or predator activity. One nest was destroyed when it was plowed under. Most failed nests were depredated, and 11 of these nest failures coincided with the death of the female (Table 2.3).

Table 2.1. Observed nesting probabilities  $\pm$  SE (proportion of females detected initiating at least one nest) and renesting probabilities  $\pm$  SE (proportion of females detected initiating a second nest given a failed first nest) for yearling and adult sage-grouse females, and reproductive success  $\pm$  SE (proportion of females that successfully raised a brood to 30 days from the total sample at the beginning of the nesting season and for which reproductive data were complete) in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Females that died early in the season (about 2 weeks into the season) were excluded from nesting probabilities but were included in reproductive success calculations.

Year	Nesting probability			Renesting probability			Reproductive success
	Yearlings	Adults	All ages	Yearlings	Adults	Both ages	Brooding
2004	0.720 $\pm$ 0.090	0.850 $\pm$ 0.056	0.800 $\pm$ 0.050	0.000 $\pm$ 0.000	0.176 $\pm$ 0.092	0.130 $\pm$ 0.070	0.284 $\pm$ 0.055
2005	0.882 $\pm$ 0.078	1.000 $\pm$ 0.0	0.978 $\pm$ 0.016	0.462 $\pm$ 0.138	0.630 $\pm$ 0.071	0.593 $\pm$ 0.064	0.430 $\pm$ 0.052
Both	0.786 $\pm$ 0.063	0.947 $\pm$ 0.021	0.903 $\pm$ 0.024	0.316 $\pm$ 0.107	0.508 $\pm$ 0.063	0.463 $\pm$ 0.055	0.369 $\pm$ 0.038

Table 2.2. Observed renesting probabilities  $\pm$  SE for yearlings and adults excluding females that may have abandoned first nests due to investigator activity for sage grouse in Musselshell and Golden Valley counties, Montana during 2004-05.

Year	Renesting probability		
	Yearlings	Adults	Both ages
2004	0.000 $\pm$ 0.000	0.125 $\pm$ 0.083	0.0915 $\pm$ 0.064
2005	0.222 $\pm$ 0.139	0.595 $\pm$ 0.076	0.529 $\pm$ 0.070
Both	0.143 $\pm$ 0.094	0.466 $\pm$ 0.065	0.403 $\pm$ 0.058

Table 2.3. Number, fate and apparent causes of failure of sage-grouse nests in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. First nests and renests are listed for yearling and adults females as # successful/total number. For causes of failure listed as “Hen died” the clutch was still intact.

Year	Yearlings		Adults		Cause of failure				
	First nests	Renests	First nests	Renests	Predator	Abandoned	Abandoned (investigator)	Hen died	Plowed
2004	9/18	0/0	16/34	1/3	25	0	2	2	0
2005	3/15	2/6	22/73	20/32	64	3	11	0	1
Both	12/33	2/6	38/107	21/35	89	3	13	2	1

In our nest-survival analysis, five models were within 2 AIC<sub>c</sub> units of the best model and these provided support for including the following covariates: *nest attempt*, *year*, and *site* (Table 2.5). Both the best model ( $\Delta\text{AIC}_c = 0$ ) and all other models within 2 AIC<sub>c</sub> units of the best model included *nest attempt* (summed AIC<sub>c</sub> weight, summed  $w_i = 0.906$ ). The estimated coefficient for *nest attempt* was quite stable across all six models. Renesting attempts had higher DSRs than did first nest attempts. From the best model, estimated DSR for first nest attempts was 0.960 (SE = 0.004) and for renests was 0.980 (SE = 0.005; Table 2.6). For a 28-day incubation period, the nest survival estimate derived from the best-supported model including only *nest attempt* was higher for renests,  $\hat{S}_{\text{renests}} = 0.563$ , (SE = 0.081, 95% CI: 0.404 to 0.721), than for first nests,  $\hat{S}_{\text{first nests}} = 0.320$ , (SE = 0.041, 95% CI: 0.239 to 0.401). Models containing *year* and *site* also received some support, but the coefficients for these covariates were less precisely estimated and 95% confidence intervals overlapped zero ( $\hat{\beta}_{2005} = -0.327$ , SE = 0.240, 95% CI: -0.797 to 0.143,  $\hat{\beta}_{\text{hunted site}} = 0.215$ , SE = 0.211, 95% CI: -0.199 to 0.630).

Table 2.4. Sample sizes included in survival analysis of sage grouse nests, broods, and females during nesting and late-summer listed by year, site, total, and number of individual females in Musselshell (hunted site) and Golden Valley (nonhunted site) counties, Montana during 2004-05.

Category	2004		2005		Total	Individual females
	Hunted	Nonhunted	Hunted	Nonhunted		
Nests	34	19	61	53	167	104
Broods	18	8	27	20	73	62
Nesting season	39	30	50	46	165	117
Late-summer	37	36	43	35	151	106

Table 2.5. *A priori* models of Daily Survival Rate (DSR) for sage grouse nests in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Models were ranked by differences in  $AIC_c$  values, and *nest attempt*, the covariate shown in **bold type**, received the highest summed model weight.

Model	# Parameters	$\Delta AIC_c$	$AIC_c$ weight
<b>Nest Attempt</b>	2	0.000	0.260
Year + <b>Nest Attempt</b>	3	0.088	0.249
Site + <b>Nest Attempt</b>	3	0.976	0.160
<b>Nest Attempt</b> + Nest Age	3	1.879	0.102
<b>Nest Attempt</b> + Female Age	3	1.990	0.096
<b>Nest Attempt</b> + Nest Age + Nest Age <sup>2</sup>	4	3.768	0.040
Constant	1	5.136	0.020
Site	2	5.853	0.014
Year	2	6.889	0.008
Female Age	2	7.009	0.008
Nest Age	2	7.079	0.008
Site + Nest Age	3	7.716	0.005
Year + Site	3	7.746	0.005
Site + Nest Age	3	7.825	0.005
Year + Female Age	3	8.667	0.003
Year + Nest Age	3	8.859	0.003
Nest Age + Nest Age <sup>2</sup>	3	8.872	0.003
Female Age + Nest Age	3	8.955	0.003
Year * Site	4	9.202	0.003
Site + Nest Age + Nest Age <sup>2</sup>	4	9.584	0.002
Year + Nest Age + Nest Age <sup>2</sup>	4	10.609	0.001
Female Age + Nest Age + Nest Age <sup>2</sup>	4	10.752	0.001

Table 2.6. Maximum-likelihood (logit-link) estimates of beta parameters from competing Daily Survival Rate (DSR) models for sage-grouse nests in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Model	Parameter label	Estimate	SE	95% Confidence Interval	
				Lower	Upper
Nest Attempt	Intercept	3.182	0.116	2.955	3.409
	Renest Attempt	0.694	0.278	0.149	1.239

### Brood Survival

I obtained information for survival of 73 broods from 62 individual females in our brood-survival analysis; 11 females produced a brood in both years (Table 2.4). I did not determine fate for one brood, because I did not visit that female at night. I included

information from this brood from hatch until the last day it was observed alive and then censored it from the dataset. In both years, first nest attempts hatched in early in mid-May, and all broods were expected to reach 30 days post-hatch by late July or early August. When modeling brood-survival data, a goodness-of-fit test failed to reject the null hypothesis that the global model (*year + site + female age*) fit the data ( $P = 0.68$ ).

Although an intercept-only model (i.e., brood survival constant across all covariate conditions) was the best supported model in our analysis ( $\Delta AIC_c = 0$ ), a model that estimated different survival rates by year also received substantial support ( $\Delta AIC_c = 0.390$ ) (Table 2.7). Models including *site* and *female age* were also supported, but the coefficients were not precisely estimated ( $\hat{\beta}_{\text{hunted site}} = -0.525$ , SE = 0.594, 95% CI: -1.689 to 0.638;  $\hat{\beta}_{\text{female age}} = 0.798$ , SE = 0.791, 95% CI: -0.751 to 2.348). Using the constant model, 79% (SE = 0.002, 95% CI: 0.698 to 0.890) of broods survived to 30 days post-hatch. Using the model including only *year*, 71% (SE = 0.092, 95% CI: 0.527 to 0.889) of broods survived to 30 days post-hatch in 2004, and 84% (SE = 0.055, 95% CI: 0.732 to 0.949) of broods survived to 30 days post-hatch in 2005.

Table 2.7. *A priori* models of Daily Survival Rate (DSR) ranked by differences in  $AIC_c$  values for sage-grouse broods in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Model	# Parameters	$\Delta AIC_c$	$AIC_c$ weight
Constant	1	0.000	0.232
Year	2	0.390	0.191
Site	2	1.170	0.129
Year + Female Age	3	1.210	0.127
Female Age	2	1.570	0.106
Year + Site	3	1.700	0.099
Year * Site	4	2.750	0.058
Site + Female Age	3	2.760	0.058

### Female Survival and Causes of Mortality

For 28 of 35 females that died, the cause of mortality was determined from evidence at the kill site, by necropsy, or by lab tests (Table 2.8). Known causes of female mortality included predation, vehicle and power line collisions, and WNV. Most of the birds that died were likely killed by mammals or raptors. There was evidence of both mammalian and avian predators at the kill site for at least three carcasses, and I classified these as scavenged. One automobile collision was confirmed as the cause of death because it was reported to us, and one female was found alive near a road with a broken wing. In 2004, I sent three samples to the lab for WNV testing, and none tested positive. In 2005, I sent in remains from nine radio-marked females and one unmarked female, and of these, eight were testable and two radio-marked females and the unmarked female tested positive for WNV.

Nesting-Season Survival I estimated female survival during the nesting season, which I defined as extending from the day the first incubating nests were found in mid-April until the last nests of each year were completed in late June in 2004 or early July in 2005. I included 117 individuals in the analysis, and 48 females were included in both years (Table 2.4). In 2005, two females were lost and were never relocated. I censored data for a third female after her radio-necklace fell off; she was later confirmed alive on her nest.

An intercept-only model (constant survival across all covariate conditions) received the most support from the data ( $\Delta AIC_c = 0$ ), but 13 other models including temporal variation (within season patterns and *year*), *female age*, *nesting status*, and *site*

also received some support (Table 2.9 and 2.10). From the constant-survival model, I estimated female survival during the nesting season for 2004, which was 68 days in length, as 0.867 (SE = 0.025, 95% CI: 0.818 to 0.917) and for 2005, which was 85 days in length, as 0.837 (SE = 0.030, 95% CI: 0.777 to 0.896). Monthly survival during the nesting season was estimated as 0.939 (SE = 0.012, 95% CI: 0.915 to 0.963). Within-season variation in survival was supported in several models (trend, periods, and date-trend models) and summed  $w_i$  was 60%. In the trend model ( $\Delta AIC_c = 0.24$ ), estimated survival increased across the nesting season (Table 2.10). The third best model, which allowed survival to differ among three different portions of the season and to vary between years during the third period, indicated that survival was similar in the first two periods of both years and increased more during the third period in 2004, in which all females survived, than in 2005 (Table 2.10).

Table 2.8. Number of mortalities listed by year and site for each season and suspected causes of mortality by season for sage grouse females in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Numbers separated by “/” indicate the number of females that were scavenged out of total number of females for which the cause of mortality was unknown.

Season	2004		2005		Total	Suspected cause of death			
	Hunted	Nonhunted	Hunted	Nonhunted		Depredated	WNv	Collision	Scavenged/ Unknown
Nesting	4	3	5	10	22	16	0	1	2/5
Late-summer	4	0	6	3	13	8	2	1	1/2

A model including *nesting status* ( $\Delta AIC_c = 0.75$ ) suggested that females had a lower probability of survival while on nests ( $\hat{DSR} = 0.997$ , SE = 0.001, 95% CI: 0.994 to 0.999) than while off nests ( $\hat{DSR} = 0.998$ , SE = 0.001, 95% CI: 0.997 to 0.999), but this difference was not precisely estimated. The probability of a female surviving until nest completion was 0.922 (SE = 0.025), while the probability of survival for females that were not on nests for the same duration was 0.952 (SE = 0.013). Effects of *site*, *year*, and *female age* were also in top models, but the estimated coefficients for these coefficients were imprecise and 95% confidence intervals widely overlapped zero.

Table 2.9. *A priori* models of Daily Survival Rate (DSR) for sage grouse females during the nesting season in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Models were ranked by differences in  $AIC_c$  values, and covariates in **bold type** represent seasonal variation which received the highest summed model weight.

Model	# Parameters	$\Delta AIC_c$	$AIC_c$ weight
Constant	1	0.000	0.079
<b>Trend3</b>	2	0.242	0.070
<b>Period 1 + Period 2 + Year * 3rd period</b>	4	0.522	0.061
Nesting Status	2	0.753	0.054
<b>Date Trend</b>	2	1.008	0.048
Site	2	1.157	0.044
Year + <b>Trend3</b>	3	1.218	0.043
Year	2	1.254	0.042
<b>3 Periods</b>	3	1.419	0.039
<b>Trend3</b> + Site	3	1.427	0.039
<b>Trend3</b> + Nesting Status	3	1.593	0.036
Site + Nesting Status	3	1.801	0.032
Female Age	2	1.917	0.030
Year + <b>Date Trend</b>	3	1.945	0.030
Year + Nesting Status	3	2.090	0.028
<b>Trend3</b> + Female Age	3	2.179	0.027
<b>Date Trend</b> + Site	3	2.185	0.027
<b>Date Trend</b> + Nesting Status	3	2.207	0.026
Year + 3 Periods	4	2.291	0.025
Year + Site	3	2.447	0.023
Nesting Status + Female Age	3	2.596	0.020
<b>3 Periods</b> + Site	4	2.604	0.022

Table 2.9. Continued.

<b>3 Periods</b> + Nesting Status	4	2.904	0.019
<b>Date Trend</b> + Female Age	3	2.946	0.018
<b>Date Trend</b> + <b>Date Trend</b> <sup>2</sup>	3	2.965	0.018
Year + Female Age	3	3.021	0.018
Site + Female Age	3	3.054	0.017
3 Periods + Female Age	4	3.360	0.015
Year + <b>Date Trend</b> + <b>Date Trend</b> <sup>2</sup>	4	3.833	0.012
Year * Nesting Status	4	3.907	0.011
Year * Site	4	4.080	0.010
<b>Date Trend</b> + <b>Date Trend</b> <sup>2</sup> + Site	4	4.139	0.010
<b>Date Trend</b> + <b>Date Trend</b> <sup>2</sup> + Nesting Status	4	4.208	0.010
Year * Female Age	4	4.224	0.010
<b>Date Trend</b> + <b>Date Trend</b> <sup>2</sup> + Female Age	4	4.905	0.007

Table 2.10. Maximum-likelihood (logit-link) estimates of beta parameters from competing Daily Survival Rate (DSR) models for sage grouse females during the nesting season in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Model	Parameter label	Estimate	SE	95% Confidence Interval	
				Lower	Upper
Constant <sup>†</sup>	Intercept	1.479	0.009	1.461	1.498
Trend3	Intercept	5.502	0.518	4.487	6.516
	Trend	0.335	0.254	-0.163	0.833
Period 1 + Period 2 + Year*Period 3 <sup>†</sup>	Period 1	1.469	0.018	1.435	1.504
	Period 2	1.463	0.018	1.428	1.499
	2004 Period 3	1.571	0.048	1.476	1.666
	2005 Period 3	1.489	0.018	1.453	1.524
Nesting Status	Intercept	6.337	0.268	5.812	6.863
	On Nest	-0.498	0.437	-1.355	0.358
Date Trend	Intercept	5.833	0.378	5.092	6.574
	Date Trend	0.009	0.009	-0.009	0.028
Site	Nonhunted Site	5.977	0.278	5.433	6.522
	Hunted Site	0.376	0.410	-0.428	1.180

<sup>†</sup> The sin link  $[(\sin(\chi \times \beta) + 1)/2]$  was used to derive estimates of daily survival rates (DSR) and to estimate the precision of those rates for these models, e.g.,  $(\sin(1.48) + 1)/2 = 0.998$ .

Late-Summer Survival This season began after nest completion, late June in 2004 and early July in 2005, and extended until 31 August, the day before the hunting season opened. The late-summer season was longer in 2004 than in 2005 due to greater

renewing in 2005. I included 106 individuals in our analysis of female survival during late summer, and 45 females were included in both years (Table 2.4). In 2004, one female that was lost in July died between July and October, and was included as having died during the late-summer season in our analyses. One radio-transmitter expired in late summer in 2005.

The best model ( $\Delta AIC_c = 0$ ) provided support for our prediction that survival would be higher in August 2004 than it would be in August 2005, when WNV was first detected in sage grouse in our area (Table 2.11 and 2.12). The best model also estimated a lower survival rate for females on the hunted site than on the nonhunted site (Table 2.12). The summed  $w_i$  for models including *Year\*August* was 0.54, whereas summed  $w_i$  for models including *August*, *year*, and *site* were 0.97, 0.61, and 0.30, respectively. Models including *female age*, *reproductive effort*, and seasonal variation terms were not supported.

Based on the estimated coefficients from the best model, survival estimates on both sites were high and similar in July for both years, 0.99 (Table 2.13). However, survival during August declined from 0.938 (SE = 0.037) in 2004 to 0.838 (SE = 0.054) on the hunted site and from 0.978 (SE = 0.017) to 0.941 (SE = 0.035) on the nonhunted site (Table 2.13).

Table 2.11. *A priori* models of Daily Survival Rate (DSR) for sage-grouse females during late summer in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Models were ranked by differences in AIC<sub>c</sub> values, and the “\*” symbol indicates an interaction between covariates. The *Year \* August* term in **bold type** had the highest summed model weight.

Model	# Parameters	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weight
<b>Year * August</b> + Site	4	0.000	0.164
August + Site	3	0.579	0.123
<b>Year * August</b>	3	1.107	0.094
August	2	1.830	0.066
Year + August	3	2.136	0.056
<b>Year * August</b> + Nest Fate	4	2.285	0.052
<b>Year * August</b> + Days Incubating	4	2.391	0.050
<b>Year * August</b> + August * SRE	4	2.784	0.041
<b>Year * August</b> + August * Days Rearing	4	3.015	0.036
<b>Year * August</b> + August * Brood Fate	4	3.081	0.035
<b>Year * August</b> + Female Age	4	3.089	0.035
<b>Year * August</b> + Days Laying	4	3.109	0.035
August + Days Laying	3	3.418	0.030
August + Nest Fate	3	3.521	0.028
August + Female Age	3	3.578	0.027
August + Days Incubating	3	3.728	0.025
August * Brood Fate	3	3.804	0.024
August * Days Rearing	3	3.831	0.024
August * SRE	3	3.831	0.024
Year * Site	4	7.880	0.003
Last 1/2 August + Site	3	8.314	0.003
Year + Site	3	8.496	0.002
Site	2	9.060	0.002
Year + Last 1/2 August	3	9.127	0.002
Year	2	9.377	0.002
Last 1/2 August	2	9.484	0.001
Constant	1	9.963	0.001
Year * Days Incubating + Site	5	10.363	0.001
Site + Nest Fate	3	10.549	0.001
Year + Nest Fate	3	10.706	0.001
Site + Days Laying	3	10.760	0.001
Site + Days Incubating	3	10.844	0.001
Year + Days Incubating	3	10.844	0.001
Site + Female Age	3	10.881	0.001
Last 1/2 August + Days Laying	3	10.921	0.001
Year * Days Incubating	4	11.019	0.001
Year * Nest Fate + Site	5	11.088	0.001
Last 1/2 August + Female Age	3	11.207	0.001
Last 1/2 August + Nest Fate	3	11.250	0.001
Days Laying	2	11.310	0.001
Year + Female Age	3	11.344	0.001

Table 2.11. Continued.

Year + Days Laying	3	11.354	0.001
Last 1/2 August + Last 1/2 Aug * Days Rearing	3	11.368	0.001
Last 1/2 August + Days Incubating	3	11.432	0.001
Last 1/2 August + last 1/2 Aug * Brood Fate	3	11.446	0.001
Last 1/2 August + SRE	3	11.485	0.001
Female Age	2	11.691	0.000
Nest Fate	2	11.767	0.000
Days Incubating	2	11.932	0.000
Year * Nest Fate	4	12.189	0.000
Year * Days Laying + Site	5	12.299	0.000
Year * Days Incubating + Female Age	5	12.745	0.000
Year * Female Age	4	12.998	0.000
Year * Days Laying	4	13.042	0.000
Days Laying + Female Age	3	13.244	0.000
Nest Fate + Female Age	3	13.395	0.000
Days Incubating + Female Age	3	13.573	0.000
Year * Nest Fate + Female Age	5	13.985	0.000
Year * Days Laying + Female Age	5	15.020	0.000

Table 2.12. Covariate coefficient estimates, standard errors, and 95% confidence intervals for the best approximating model of late-summer survival of sage grouse females in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Parameter	Estimate	Std. error	95% Confidence Intervals	
			Lower	Upper
July 2004 & 2005	8.981	1.124	6.779	11.184
August 2004	-1.752	1.193	-4.091	0.587
August 2005	-2.773	1.050	-4.832	-0.715
Hunted site	-1.074	0.659	-2.366	0.218

Table 2.13. Monthly survival estimates  $\pm$ SE during late summer from the best approximating model for sage grouse females in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Month & Year(s)	Study site	$\hat{S}$	Std. error	95% Confidence Intervals	
				Lower	Upper
July 2004 & 2005	Hunted	0.989	0.011	0.968	1.0
July 2004 & 2005	Nonhunted	0.996	0.004	0.988	1.0
August 2004	Hunted	0.938	0.037	0.866	1.0
August 2004	Nonhunted	0.978	0.017	0.946	1.0
August 2005	Hunted	0.838	0.054	0.733	0.944
August 2005	Nonhunted	0.941	0.035	0.874	1.0

## Discussion

My research documented differences in reproductive effort, re-nest survival, brood survival, and reproductive success between a relatively dry year in 2004 and a relatively wet year in 2005 (Appendix B). Increases in nesting and re-nesting probability, higher survival of re-nests, and higher brood success may have been due to increased precipitation and a subsequent increase in grass and forb abundance in 2005 (Woodward 2006). This increase may have provided better nutrition for females and chicks, better cover at late-season nests, and better cover for chicks.

### Reproductive Effort

Females initiated first nests between late March and early April, which was one to three weeks earlier than initiation dates reported by other studies in Montana (Wallestad 1975, Moynahan et al. in press). Average clutch sizes were comparable to studies from other parts of their range (see Schroeder et al. 1999 and Connelly et al. 2000 for review, Moynahan et al. in press). Probabilities of nest initiation (0.72 to 1.0) and re-nest initiation (0.0 to 0.63) were also within ranges recently reported for north-central Montana (0.62 to 1.0 nesting probability and 0.0 to 0.56 re-nesting probability [Moynahan et al. in press]). Re-nesting probabilities vary temporally and across the species range (5-87% [see Schroeder et al. 1999 for review]), but few studies have reported re-nesting probabilities higher than those reported here. In California, re-nesting probability was reported as 63% (Popham and Gutiérrez 2003), and for north-central Washington re-nesting was reported at 87% (Schroeder 1997). As in numerous other studies, I

documented higher nesting probability (Gregg 1991, Connelly et al. 1993, Holloran 2005, Moynahan et al. in press) and higher reneating probability (see Schroeder et al. 1999 for review, Gregg et al. 2006, Moynahan et al. in press) for adults than for yearlings.

### Nest Survival

For both years combined, maximum-likelihood estimates of nest survival for a 28-day incubation period were 0.32 for first nests and 0.56 for renests. This pattern, higher survival estimates for renests than first nests, is consistent with numerous other studies (Aldridge and Brigham 2001, Hall 2001, Moynahan et al. in press). If DSR during laying is assumed to be the same as that for the incubation period, an assumption I was unable to evaluate, the estimates from the best model would estimate nest survival for a 41-day nesting period (13 days of egg laying [clutch size = 8] + 28 days of incubation) as 0.18 (SE = 0.04) for first nests and as 0.43 (SE = 0.09) for renests.

Nest survival estimates for a 28-day incubation period for north-central Montana ranged from 0.24 to 0.32 for early-season nests and 0.28 to 0.42 for late-season nests (Moynahan et al. in press). All other previously published studies reported apparent nest success estimates, a method that is known to produce estimates that are biased high (Mayfield 1961, 1975). Further, some of these studies utilized methods such as nest searching to locate nests (e.g., Batterson and Morse 1948, Bean 1941, Keller et al. 1941, Patterson 1952) rather than working with radio-marked females. Nest searching can result in nest success estimates that are biased high if the sample of nests found is not representative of the total population, e.g., if un-modeled heterogeneity among nest fates exists, bias occurs because successful nests survive longer and are more likely to be

detected by investigators. Estimates from studies utilizing methods different from this study ranged widely, from 15-86% (see Schroeder et al. 1999 for review, Aldridge and Brigham 2001, Popham and Gutiérrez 2003, Holloran et al. 2005), and although they overlap my estimates, they should not be directly compared with the maximum-likelihood estimates obtained in this study. Excluding studies based on nest searching, nest-success estimates ranged from 15-72%. Apparent nest success rates for this study were 0.39 for first nests and 0.59 for renests, which were biased high by 22% (first nests) and 5% (renests) compared to maximum-likelihood estimates. Moynahan et al. (in press) also demonstrated that apparent nest success estimates could be biased high by 8% to 91% of the maximum-likelihood estimates. Due to the variability in bias of apparent nest success estimates, future studies should utilize modern methods (e.g., maximum-likelihood estimates) for analyzing nest-survival data so that estimates are more accurate and comparisons can be made over time and between areas.

The survival of renests observed on our study is relatively high and may actually be an underestimate given that some first nests were likely renests. Schroeder (1997) suggested that as much as 29% of the nesting period (laying) is not monitored, because most nests go undetected prior to incubation. However, the methods I used for classifying nests as renests are similar to those used in other studies, and therefore, estimates are comparable. Most renesting (38/41 renests) occurred in 2005, and high renest survival relative to first nests may be attributable to both warmer temperatures later in the nesting season in both years and to a bloom of yellow sweet clover (*Melilotus officinale*) in 2005, an introduced biennial forb, that increased concealment around many late-season nests (i.e., renests). Other Montana studies of greater sage-grouse (Moynahan

et al. in press) and plains sharp-tailed grouse (*Tympanuchus phasianellus jamesi* [Bousquet 1996]) have also observed higher nest survival in years that coincided with abundant yellow sweet clover.

Forb abundance may be a key factor influencing year-to-year variation in reproductive effort and success. Forbs represent 18 to 50% of the diet of prelaying females, increase the nutrient value of the diet in spring (Barnett and Crawford 1994), and may be important for prelaying body condition (Barnett and Crawford 1994, Gregg et al. 2006, Pyle and Crawford 1996). Gregg et al. (2006) documented higher plasma protein in females that renested than those that did not, and in ruffed grouse (*Bonasa umbellus*), increases in dietary protein increased clutch size, clutch mass, and chick viability (Beckerton and Middleton 1982). Woodward (2006) documented a 2.5 fold increase in forbs from 2004 to 2005 at this study area. Other studies have suggested a similar relationship between forb availability and probability of renesting (Barnett and Crawford 1994, Schroeder 1997). I suspect that a higher proportion of forbs comprised the diets of prelaying females in 2005, the year with higher nesting and renesting probabilities, and that this increase in reproductive effort was probably due to better nutritional condition of females.

Land-management practices that maintain forb availability and abundance may be critical for stabilizing or increasing production. Further, it would be useful to know which other factors encourage females to invest in reproduction. Reproductive effort may be influenced not only by forb abundance and female age or experience but could also be influenced by investment in reproduction in the preceding year or snow depth during winter.

### Brood Survival

Point estimates of brood survival to 30-days post-hatch were higher in 2004 (71%) than in 2005 (84%), but estimates were too imprecise to allow confidence in measures of annual variation. Brood survival for both years combined was 79%. These brood-survival estimates suggest less annual variation than estimates published elsewhere. These estimates were within the range reported for north-central Montana (21-76% [Moynahan 2005]) and were similar to apparent brood-survival estimates reported for a study conducted adjacent to our area thirty years prior to this study (44-77% [Wallestad 1975]). The brood-survival estimates I observed were higher than estimates for Washington (0.36 to 0.52 [Sveum 1995]), but were within the range of estimates for Wyoming, (0.33 to 1.0 [Heath et al. 1998, Holloran 2005, Slater 2003]), but these studies used a different period length for calculating brood survival. However, two features are noteworthy: 1) most chicks die early in brood-rearing and so estimates from periods of different lengths may provide more reasonable comparisons than might be expected if survival were not high and relatively constant after the first few weeks of the brood-rearing period, and 2) I visited females at night to determine whether or not they had broods, which improved our brood-detection probability. Thus, except for a study in Alberta that reported 0.63 brood survival to 30 days post-hatch for radio-marked chicks (Aldridge 2005), reports from other studies are likely underestimates of brood survival. Chick survival is thought to be limiting population growth in Alberta, but the estimates in my study are higher than those of Aldridge (2005) which suggests that brood-rearing conditions are more favorable in central Montana. The increase in brood survival that I

observed from 2004 to 2005 may have been attributable to the increase in grass and forbs, including the bloom of yellow sweet clover, which provided better cover and food availability for chicks. This annual variation may also have been related to changes in insect abundance.

Due to low probability of detecting all chicks, I was not able to estimate chick survival, which makes drawing conclusions about productivity difficult. Brood survival estimates provide crude estimates of actual chick survival. Brood survival overestimates chick survival (Aldridge 2005), and therefore, brood-survival estimates must be viewed cautiously as measures of productivity. However, obtaining reliable estimates of chick survival will require new technology, innovative observation methods, or evidence that radio-marking chicks at hatch does not affect their survival. Because most hens with chicks tend not to flush at night, even with investigators approaching to within  $\leq 10$  m, the risk of increased mortality due to nighttime disturbance is low. I expect chick survival to continue to be a difficult parameter to estimate. Researchers should estimate chick survival by counting chicks at night to increase detectability, and conducting multiple counts to allow estimation of detection probability. In this way, more accurate estimates of both chick survival and production could be obtained. We may then be able to learn more about timing and causes of chick mortality and more accurately model sage grouse population dynamics and estimate population growth.

Because renests had a higher probability of success than first nests, and most renests occurred in 2005, and because brood survival may have been slightly higher in 2005, reproductive success was 50% greater in 2005 (0.43) than in 2004 (0.28). I report reproductive success as the proportion of females that successfully raised a brood to 30

days old. Reproductive success was previously reported at 50% for a Washington study, a study that also observed extremely high reneating probabilities (0.87 [Schroeder 1997]). Typically, studies have reported “reproductive success” as the proportion of females that successfully hatch at least one chick, which has ranged from 15% to 70% (see Schroeder et al. 1999 for review) and during this study, was 39% in 2004 and 50% in 2005.

### Female Survival

Few published studies of sage-grouse females report seasonal-survival estimates (Connelly et al. 2004); most report annual estimates. Some report survival from spring through fall or suggest that overwinter survival is high (Robertson 1991, Wik 2002, Hausleitner 2003, Zablan 2003). More studies are needed that evaluate seasonal differences in survival. Where available, I discuss our seasonal estimates in relation to other studies. I discuss the results of this study in relation to annual estimates from other studies in Chapter 3.

Nesting-Season Survival Our results indicate that female survival during the nesting seasons was constant across all covariate conditions. The constant-survival model estimated monthly female survival rate as 0.94, which was near the high end of the range of estimates reported for north-central Montana during the nesting season (0.75 to 0.99 [Moynahan et al. 2006]) and was within the range of estimates for a recent study in Colorado (0.91 to 0.99 [Hausleitner 2003]). I did not observe age-specific variation in female survival. However, there was considerable model selection uncertainty, and models including both within and among year variation, *site*, and *nesting status* received some support. Although I discuss each of these effects with regard to our predictions

below, I cannot make strong inferences about these effects due to model-selection uncertainty and lack of precision in these estimates.

Within-season variation was supported in the second and third best models. The trend model, which allowed survival to differ across the season as an increasing or decreasing trend, indicated that survival may have increased steadily across the season. The period model, which allowed survival to differ among three different portions of the season and to vary between years during the third period, indicated that survival may have been similar in the first two periods of both years and increased more in the third period during 2004 than in 2005. Biologically, the last period represented different female activity between years. Because re-nest initiation was low in 2004, the last period was shorter and few females incubated nests far into the last period ( $n = 4$ ). In 2005, because re-nesting was high, the last period was 17 days longer and many females were still incubating re-nests during the late period ( $n = 30$ ). This within- and among-year variation in survival during the nesting season may represent differences in survival for females on early versus late-season nests (first nests versus re-nests) or differences in survival between nesting and non-nesting females. Increased cover at nest sites later in the season may decrease probability of detection by predators and increase a female's probability of survival, or females with low quality nest sites may be detected by predators earlier and the remaining females would be those at better nest sites conferring higher probability of female survival.

As predicted, my results suggest that survival was lower for female sage grouse while incubating nests than while off nests. A model including *nesting status* received some support from the data. Additionally, a model including the *year \* period 3* term,

which supported lowered survival during the last period of the nesting season in 2005 than in 2004, may also lend support to this prediction. More females were still incubating nests during the last period in 2005 than in 2004, and female survival was lower during the last period in 2005 than in 2004.

This finding, that females have lower survival while incubating, contrasts with those of a recent study in north-central Montana, in which nesting females were reported to have higher survival than non-nesting females (Moynahan et al. 2006). However, while *nesting status* of females was used to address the same prediction, *nesting status* was represented differently in my analysis than in Moynahan et al. (2006). I included the term for each day of the nesting season (*nesting status*: 0 = off nest, 1 = on nest) for each female to evaluate the risk of incubating a nest. In the north-central Montana study, *nesting status* defined nesting females as those for which a nest was detected and non-nesting females were defined as those for which no nest was detected (0 = no nest detected, 1 = nest detected) and was used to evaluate the same risk. This pattern may be misleading in three ways. First, females may die before their nests are detected and would therefore go undetected as nesting females. Second, the timing of death, if early in the season, reduces the probability of finding a female on a nest. Third, as pointed out by Moynahan et al. (2006), with the covariate constructed as nesters versus non-nesters, it may better reflect a difference, such as body condition, between females that choose to nest and those that do not, rather than the risk associated with incubating a nest. When I included the same categorical variable of whether or not a female was detected on a nest, the results were the same as Moynahan et al. (2006), and a model with only this term was the best supported in that model set. However, during my study, I did not detect a nest

for 20 females, and of those 20, five died. But, all five either died within the first two to three weeks of the nesting season, and they may have been nesting but nests went undetected, and they were not as likely to be detected on a nest compared to other females, given timing of death.

During the nesting season, female survival was lower on the nonhunted site, 80%, than on the hunted site, 86%, but the estimates were too imprecise to allow us to be very confident of the exact level of site variation. Although this site difference is consistent with the hypothesis for compensation for the effect of hunting (higher survival of birds at reduced breeding densities [Nichols et al. 1984]), I did not collect data on bird densities. It is more likely that this difference in female survival between sites was due to factors unrelated to hunting, such as differences in habitat quality or predator communities between sites.

Late-Summer Survival In contrast to the nesting season, survival was lower on the hunted site than on the nonhunted site later in the summer. Differences in female survival between sites during this season may also be due to landscape-scale factors, such as differences in the quality of sagebrush habitat or predator communities between sites. West Nile virus was first detected in sage grouse in summer 2003 in both north-central and southeastern Montana but was not detected in this study area in central Montana until August 2005. West Nile virus was likely a major contributor to the decrease in survival observed in this study between August 2004 (0.94 to 0.98) and August 2005 (0.84 to 0.94). The range of monthly survival estimates for July and August (0.84 to nearly 1.0) in this study was wider and lower than estimates reported for north-central Montana for

the same time period (0.92 to 0.97 [Moynahan et al. 2006]), but the range was not as low or wide as estimates reported for southeastern Montana (0.45 to 0.89 [Naugle et al. 2004]). It is important to continue to monitor the prevalence and effects of WNV on sage grouse.

West Nile virus was only detected in three out of eight testable samples in 2005, which included one unmarked female, and in 2004 tests of remains from three females were negative. Infection with WNV has resulted in 100% mortality in laboratory studies of sage grouse (Clark et al. 2006). Most of the remains that were tested from this study only included bone fragments or molting feathers, which are not ideal for WNV screening (Walker et al. 2004), and infection and mortality due to WNV may have been higher than detected in 2005 or may have gone undetected in this area in 2004. Precipitation was greater in 2005 than 2004, which may have contributed to increased mosquito production and higher infection rates that may have subsequently increased our probability of detecting WNV in 2005. Alternatively or additionally, heat stress during late summer, reductions in availability of water, or the timing of molt may have also contributed to the decrease in survival during August.

### Future Research

Central Montana represents some of the most intact, contiguous sagebrush habitat within current greater sage-grouse range in Montana (Montana Sage Grouse Working Group 2005), and like Wyoming, Idaho, Nevada, and Oregon, Montana supports relatively abundant numbers of sage grouse compared to the rest of their range (Connelly et al. 2004). Currently, no published population model exists for integrating such a

combination of vital rates together in a way that allows me to estimate population growth rate. But, lek counts do suggest that the rates are such that large numbers are being sustained (Appendix C). Of course, available data do not allow me to consider the possible role of immigration in the population's dynamics, and data on exchange of individuals with surrounding populations would also be useful.

Variation in reproductive effort and success and high survival of renests has important implications for management. Managing sagebrush habitats to maintain forb availability and abundance may be critical for stabilizing or increasing production. However, variation in reproductive effort and success if accompanied by negatively covarying female survival may stabilize population growth. If there is a reproductive cost to survival, then the age structure of females in the population may be different during a spring following a year of high reproductive investment. Adult females are important to the population, because they are more likely to nest and reneest. Therefore, reproductive success may be lower during a spring following a year of high reproductive investment. The cost of reproduction to female survival immediately following the breeding season is considered in the Chapter 3. In future studies, it would be helpful to consider how investment in reproduction affects future fecundity and survival. Future studies should also directly assess how habitat characteristics influence reproductive effort, nest survival, brood survival, and female survival; this may be the subject of a collaborative effort between my project and the habitat projects conducted in conjunction with my project in the near future.

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## CHAPTER THREE.

FALL AND WINTER SURVIVAL RATES AND CAUSES OF MORTALITY  
AMONG HUNTED AND NONHUNTED GREATER SAGE-GROUSE  
IN CENTRAL MONTANAIntroduction

Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage grouse) populations have been declining throughout their historical range in western North America since the early 1900s (Hornaday 1916), with current abundance estimated at 1-31% of the numbers present prior to European settlement in the 1800s (United States Fish and Wildlife Service 2004). In addition to a dramatic decline in abundance, sage grouse distribution has contracted by as much as 44% (Schroeder et al. 2004). Historically, the largest populations existed in Colorado, Idaho, Oregon, Wyoming, and Montana (Connelly and Braun 1997). Much of central Montana is still in relatively contiguous sagebrush-steppe habitat, supports relatively large numbers of sage grouse, and supports populations that appear to be relatively stable (Connelly et al. 2004, Montana Sage Grouse Work Group 2005).

There are a number of possible factors contributing to sage grouse population declines, including energy development (see Connelly et al. 2000a for review, Holloran 2005), West Nile virus (Naugle et al. 2004), weather (Connelly and Braun 1997, Connelly et al. 2000a, Moynahan et al. 2006), predation (Batterson and Morse 1948), habitat alteration (natural and human-caused), pesticide and herbicide use, and harvest (see Connelly and Braun 1997, Schroeder et al. 1999, and Connelly et al. 2000a for

review). Despite increasing concerns, sage grouse are still legally harvested in most of their current range, including Montana. Direct investigation of how harvest affects population vital rates and population growth, and the magnitude of harvest effects relative to other sources of mortality, is needed for informed management of harvested species (Nichols and Johnson 1989), especially species that are declining. Further, because harvest is regulated by state governments, it is a valuable management action that can be directly manipulated.

The realized effect of harvest on natural mortality and population growth for a given species depends on the magnitude and timing of density-dependent natural mortality and the existence of reproductive compensation (Nichols et al. 1984). If harvest reduces densities, survival probability may increase for the remaining individuals after harvest if density-dependent mortality occurs at some time later in the annual cycle. A subsequent reduction in nonhunting density-dependent mortality may directly compensate for at least part of the hunting loss. Alternatively, if hunting reduces densities below some biological threshold level necessary for survival (inverse density dependence), survival probability may decrease for the remaining individuals (Courchamp et al. 1999). If harvest reduces breeding densities and a population has density-dependent reproduction, then indirect compensation may occur through increases in reproductive success or recruitment. The management question becomes, at different levels of harvest and at varying population densities, what is a population's demographic response? Ideally, this question would be addressed by applying a range of harvest levels randomly to multiple, replicated sites with varying population densities and habitat qualities and by conducting investigations at landscape scales adequate to detect

dispersal. However, assessing population responses across densities for diverse harvest levels is often prohibitively difficult, and many studies have relied on a variety of constrained research designs, including comparing fall population numbers to spring breeding numbers, comparing fall numbers to annual mortality rates, evaluating the magnitude of harvest mortality relative to other sources of mortality, comparing annual survival rates and kill rates, and comparing survival between hunted and nonhunted populations.

Several investigations of harvest effects in upland game birds have compared survival rates and causes of mortality between hunted and nonhunted radio-marked populations (Smith and Willebrand 1999, Pedersen et al. 2003, McAuley et al. 2005). In two studies of willow ptarmigan, no evidence or weak evidence for compensation was found, but those populations did not decline (Smith and Willebrand 1999, Pedersen et al. 2003). Stable population size in those studies was attributed to immigration of juveniles, not compensation, and suggested that as the study area expanded evidence for compensation would grow weaker (Smith and Willebrand 1999, Pedersen et al. 2003). In woodcock, 36% of the total mortality was attributed to hunting, and researchers concluded that harvest was not reducing survival (McAuley et al. 2005).

Uncertainty about how harvest impacts sage grouse vital rates remains. Thus far, published research investigating the effects of harvest on sage grouse vital rates has suggested that harvest mortality may not be compensatory (Johnson and Braun 1999, Connelly et al. 2000*b*, Connelly et al. 2003) or in contrast, has reported that hunting has little impact on populations (Wallestad 1975, Crawford 1982, Braun and Beck 1985). Because population size or density may influence survival (Anderson and Burnham 1976,

Caswell et al. 1985, Nichols et al. 1984, Krementz et al. 1988, Nichols and Johnson 1989, Sedinger and Rextad 1994, Sedinger and Rotella 2005), it is sometimes difficult to draw strong conclusions about the effects of hunting with some study designs. For example, a major limitation of some harvest studies in both waterfowl and upland game birds has been the historical pattern of manipulating harvest regulations in response to changes in population size which makes it difficult to ascertain the effect on survival (Anderson and Burnham 1976, Caswell et al. 1985, Krementz et al. 1988). Further, some study designs have led to divergent interpretation of results (Connelly et al. 2003, Reese et al. 2005, Sedinger and Rotella 2005). Harvest may impact sage grouse populations very differently across their range, and thus, area-specific data on the impact of harvest, and the magnitude of this impact relative to other potential sources of mortality, are necessary for informed management.

Other factors influence mortality. Greater reproductive effort (i.e., reneating or days brood rearing) may reduce probability of survival or overall fecundity (this trade-off is the cost of reproduction) as documented in long-lived sea birds in variable and harsh environments (Reid 1987, Jacobsen et al. 1995, Erikstad et al. 1997, 1998, Golet et al. 1998). Previous research has suggested this cost of reproduction may also exist for sage grouse (Bergerud and Gratson 1988, Moynahan et al. 2006). Age-specific variation in survival (Zablan et al. 2003) and age-specific reproductive success have been previously documented in sage grouse (Schroeder et al. 1999). Habitat alteration and fragmentation are thought to be the leading cause of decline in abundance and distribution (see Connelly and Braun 1997, Schroeder et al. 1999, and Connelly et al. 2000a for review), and drought may also affect populations (Connelly and Braun 1997, Connelly et al. 2000a,

Moynahan et al. 2006). Differences in predator communities may also impact survival (Connelly et al. 2000a). Severe winter weather (Moynahan et al. 2006) and West Nile virus (WNV [Naugle et al. 2004, Walker et al. 2004, Naugle et al. 2005, Moynahan et al. 2006]) have recently been documented to negatively affect survival. Harvest theory indicates that direct compensation should occur following harvest, therefore it is necessary to consider survival during winter.

Due to uncertainty about the impact of harvest on vital rates and uncertainty about the relative importance of harvest compared to other sources of mortality, we designed a case study with the following objectives: 1) simultaneously compare survival rates during the hunting season and overwinter between adjacent hunted and nonhunted sites with similar landscape and population characteristics, 2) evaluate nonhunting factors influencing survival during the hunting season, 3) assess the relative importance of different mortality factors on sage grouse overwinter, and 4) assess, to the extent possible, the importance of harvest to the sage grouse populations studied and to make recommendations for future investigations about the effects of harvest on sage grouse.

### Study Area

I studied sage grouse within approximately 3,000 km<sup>2</sup> in Musselshell and Golden Valley Counties in central Montana from 2003-2005 (46° 26' to 46° 76' N, 108° 32' to 109 15' W) (Appendix A1). This area was primarily sagebrush-steppe (80%) interspersed with native prairie grasslands (<1%), ponderosa pine (<1%), and both dry and irrigated agriculture (14%) (Appendix A2). Soil taxonomy is described in detail by Woodward (2006). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*),

western wheatgrass (*Agropyron smithii*), green needlegrass (*Stipa viridula*), and blue grama (*Bouteloua gracilis*) characterized the predominant habitat and cover type. Two habitat types dominated lowlands: 1) plains silver sagebrush (*A. cana cana*) with western wheatgrass and 2) greasewood (*Sarcobatus vermiculatus*) with Gardner saltbrush (*Atriplex gardneri*), inland saltgrass (*Distichlis spicata*), and green needlegrass.

Historical and current land uses include cattle and sheep grazing. Relatively little energy development (i.e., oil or gas) occurred within the core areas of the study sites. Portions of land continued to be converted to dry and irrigated cropland, including enrollment in the federal Conservation Reserve Program (CRP), and land was treated to remove sagebrush. The 70-year precipitation average was 37 cm, but severe to extreme drought conditions persisted from 2000-2005 (Appendix B). Annual precipitation was 25 cm in 2004 and 46 in 2005, and average monthly temperature ranged from -7°C in January to 22°C in July (National Oceanic and Atmospheric Administration [NOAA] 2006). Elevation ranged from 800 to 1,500 m. The study area supported relatively abundant breeding populations of nonmigratory sage grouse. Peak attendance at 25 leks averaged 24 to 37 males per lek (range 5-76 males among 25 leks) from 2002-2005 (Appendix C, Montana Fish, Wildlife and Parks [FWP], unpublished data). A large proportion of land in this region was enrolled in FWP's Block Management Program, which facilitates hunting access on private lands, and the FWP Commission had the ability to close a large area to sage grouse hunting to conduct this study.

I defined one hunted site and one nonhunted site within the study area by trapping birds at four (nonhunted) to five (hunted) adjacent leks that collectively had high male attendance. About 40% of the hunted site was a sagebrush cover type, similar to the

nonhunted site, and about 10% of the hunted site was converted to some type of agriculture which was slightly higher than the nonhunted site, 4% (Appendix A2). I expected that most birds would remain within 5 km of the leks where they were trapped (Eng and Schladweiler 1972, Wallestad and Pyrah 1974, Wallestad and Schladweiler 1974, Wallestad 1975). Thus, for vegetation sampling and site descriptions, I defined each study site as a “lek complex,” the area within overlapping 5-km-radii around trapped leks (Appendix A1).

The hunted site was 287 km<sup>2</sup> in area, of which 60% was privately owned, and 40% was publicly owned and managed by either the Bureau of Land Management (BLM) or the State of Montana. Hunters could access all public lands directly from county roads and highways or from private lands enrolled in FWP’s Block Management Program. The combination of private lands in Block Management and public lands yielded a minimum of 200 km<sup>2</sup> (70% of the hunted site) open and accessible for sage grouse hunting. The 2003-2004 hunting regulations permitted a 3 bird daily bag and 6 bird possession limit, while 2005 regulations reduced the daily bag to 2 birds and 4 bird possession limit. The sage grouse hunting season extended from 1 September to 1 November in all years. In 2003, the last year that harvest information was available from hunter telephone surveys, sage grouse harvest was 81% below the long-term average (1967-2002) in this region (FWP, unpublished data). However, I expected this area to have more hunting pressure for upland birds compared to other areas in the state. The hunted site was 80 km north of Billings, Montana (population 90,000). I placed wing barrels and signs informing hunters about the study at hunter sign-in boxes across the site.

The nonhunted site was 262 km<sup>2</sup> in size and 94% privately owned. The remaining 6% was publicly owned and managed by either the BLM or the State of Montana. For this study, 1,176 km<sup>2</sup> were experimentally closed to sage grouse hunting from 2002-2005, including areas surrounding the nonhunted study site (Appendix A1). I placed signs around the boundary identifying the area as closed to sage grouse hunting just prior to the start of the sage grouse hunting season, and the closure was announced in annual upland game bird hunting regulations.

### Methods

I captured sage grouse at or near leks from late-March through mid-April, and again prior to the opening of the hunting season in September, using either nighttime spotlighting and hoop-netting (Wakkinen et al. 1992) or rocket nets (Geisen et al. 1982). Monte Carlo simulations indicated a sample size of 25 adult female birds per site was adequate to detect a difference of  $\geq 5\%$  in survival between hunted and nonhunted site birds, which I considered biologically meaningful. I expected some females to die over the summer, so I increased our target number of radio-marked females to 30 for each site in each spring. For each female captured, I recorded age (yearling or adult [Eng 1955, Crunden 1963]) and applied an individually numbered aluminum leg band (National Band and Tag Company, Newport, Kentucky). In 2003, I also marked females with a uniquely numbered white plastic tarsus band for resighting. I outfitted each yearling and adult female with a necklace-type radio transmitter (Advanced Telemetry Systems®, Isanti, Minnesota, models A4080 and A4050 [Armstrup 1980]). These transmitters weighed about 22 or 16 grams (less than 2% of female body weight), included a mortality

switch that triggered after either 4 or 12 hours without movement, had a life expectancy of 680 or 890 days, and initially had a detection range up to 10 km from the ground and up to 24 km from the air. The latter model had a 16:8 hour duty-cycle switch.

I monitored the status (alive or dead) and movements of radio-marked females to estimate survival, determine timing and causes of mortality, and to assess availability of marked birds to hunters. I also monitored each female's reproductive effort for inclusion as a covariate in survival analyses (see Chapter 2 for details). I used telemetry homing techniques (Samuel and Fuller 1996) to locate females visually ("visual locations") and recorded locations using a Global Positioning System (GPS) receiver. Locations were estimated ("estimated locations") using biangulation and a modified vehicle-mounted antenna system with a null-peak design (Brinkman et al. 2002). In 2003-2004,  $\geq 2$  bearings were plotted by hand on aerial photos (Natural Resources Conservation Service State Office, Bozeman, Montana). In 2005, bearings were measured using a digital compass attached to a vehicle-mounted antenna system (Cox et al. 2002), and locations were estimated using LOAS 3.0.4 software (Ecological Software Solutions, Sacramento, California). I conducted telemetry flights to search for birds that were not located on the ground. I recorded aerial locations with a GPS receiver.

When a mortality signal was detected, I located the carcass as soon as possible in an attempt to identify the cause of mortality and to collect remains. If bones were crushed, if only feathers remained, or if predator scats or tracks were observed at the kill site, I classified cause of mortality as mammalian predation. I classified the cause of mortality as avian predation if bones and ligaments were stripped or if raptor mutes were located near the carcass. If evidence for both avian and mammalian predation were

observed, I reported “scavenged.” It is possible that birds died of causes other than predation and were subsequently scavenged prior to our examination of remains. Therefore, I could not rule out the possibility of crippling losses due to hunting. In 2005, carcasses collected during the hunting season were x-rayed for shotgun pellets. Intact or mostly intact carcasses, heads, bones, internal organs, and blood feathers collected 1 September through mid September 2004 and 1 September through early November 2005 were sent to the Wyoming State Veterinary Laboratory for West Nile virus (WNV) testing.

I attempted to monitor all females in all seasons, however, some females were never relocated. If a female was “lost” during a season but was found alive after the season, then she was treated as having been alive for the entire season in analyses. If a female was found dead after the season, then she was included as having died in the season in which she was lost. If a female was lost during a season, was never found again, and her transmitter was new, then she was included in the dataset as alive until lost, after which she was considered dead (White & Garrott 1990). I decided to include females as having died in this case, rather than assuming they lived and censoring them from the dataset, because most sage grouse females in our study area were highly site faithful and transmitter failure was uncommon. Most females that were lost for more than a couple of weeks were found the following spring. If a female with an old transmitter (past expected battery life or other indication of battery failure) was lost during a season and never found, then she was included as alive until lost, and then censored from the dataset (White & Garrott 1990). On old transmitters, the signal strength typically decreased or was erratic in intensity, or the quality of the signal

changed (e.g., clear beep or chirp changed to thud or sounded like a drop of water in an empty bucket) prior to signal loss (C. O. Kochanny, Advanced Telemetry Systems, personal communication).

### Nesting and Brood-Rearing

This research was part of larger project investigating the breeding ecology of sage grouse, and the methods specific to data collection during the breeding and late-summer seasons, how covariates were constructed or coded, and the methods for analyses of these data are detailed in Chapter 2. Some of these metrics were included as covariates in fall and winter female survival analyses.

### Hunting Season

During the hunting season, I obtained  $\geq 1$  observed location, estimated location, or both, per week for each bird on both hunted and nonhunted sites. Because I expected hunter activity to be greatest on weekends, I also checked status (live or dead) of radio-marked birds on the hunted site on Mondays. Estimated locations were digitized using ArcView 3.3 software (ESRI, Redlands, California) and LOAS. For nonhunted-site females, I documented whether the location was inside or outside the area closed to hunting. I conducted telemetry flights immediately before and after the hunting season to locate any missing females and to determine female status (live or dead) to accurately document whether mortalities occurred before, during, or after the hunting season.

### Overwinter

In winter 2004-2005, females were visually located about twice per month from mid-December through early March by telemetry homing on the ground, and telemetry flights were conducted in mid-January and late March. In winter 2005-2006, females were visually located approximately once every two weeks by telemetry homing from mid-December to early March, and flights were conducted in early January and early April.

### Data Analysis

I used an information-theoretic approach to evaluate the relative support for sets of candidate models describing competing hypotheses about female survival (Burnham and Anderson 1998). I used logistic regression and maximum-likelihood estimation in Program MARK (White and Burnham 1999) to obtain beta estimates, and for most models, I used the logit link to derive estimates of daily survival rates (DSR) for females and to estimate the precision of those rates. I used the sine link when seasonal survival for a particular set of individuals was 100% because of convergence problems with the logit-link function in such cases. I used the nest-survival data format and nest-survival estimation in Program MARK for females. The number of encounter occasions used in these analyses are listed in Appendix D. I used this approach for female survival, because not all females were visited on the same date or in the same week, i.e., the visit schedule was ragged. The nest survival module does not require entry of specific timing of death, allows for the inclusion of females that were not tracked with the same intensity over time, and allows staggered entry and right-censoring. I used Akaike's Information

Criterion scores adjusted for sample size ( $AIC_c$ ) and  $AIC_c$  weights to evaluate all models (Burnham and Anderson 2002). Diagnostics to examine goodness-of-fit and overdispersion are not yet available for these types of data.

Survival estimates for females were the product of all the daily survival rates for the relevant period, month, or season length (Appendix D). Annual survival of females was the product of all seasonal survival rates. I used the delta and parametric bootstrap methods to estimate associated variances (Seber 1982, Zhou 2002).

I delineated seasons based on the biology of sage grouse and factors likely to influence their survival at different times of year (Appendix D [e.g., WNV, hunting, density, or weather]), and then I conducted analyses for both the hunting season and overwinter with replicate years. I included the following covariates in both hunting-season and overwinter candidate model sets and my predictions were the same for both seasons: *year* (0 = 2004, 1 = 2005), within season variation (periods and trends within seasons), *site* (0 = nonhunted, 1 = hunted), *female age* (0 = adult, 1 = yearling), and the cost of reproduction. Year was included as a surrogate for annual variation in other variables that were not measured, including weather, vegetation, and bird density. Survival may vary between sites, due to a direct or indirect effect of hunting or intrinsic differences between sites in other ecological features, such as vegetation quality or quantity. I included female age, because age-specific variation in survival (Zablan et al. 2003) and age-specific reproductive success have been previously documented in sage grouse (Schroeder et al. 1999). The following categorical covariates represented the cost of reproduction: *nest fate* (0 = failed, 1 = succeeded or equivalent number of days incubating a nest), and *brood fate* (0 = failed, 1 = succeeded), and the following

continuous covariates also represented the cost of reproduction: *days laying*, *days incubating*, *days rearing*, and summed reproductive effort (*SRE*). Chapter 2 detailed how these covariates were measured. I chose to include six covariates to evaluate the effect of reproductive effort, because I did not know which covariates would best reflect any potential reproductive cost. But, only one reproductive-effort term was considered per model, and I predicted that continuous reproductive effort covariates would better reflect this effect than categorical variables. I included models that evaluated effects of reproductive effort between years, because reproductive effort, and subsequently, survival, may vary annually (i.e., good or bad reproduction years) (Rotella et al. 2003, Ruf et al. 2006). Covariates specific to female survival within the hunting season and overwinter are described in detail below.

Hunting-Season Survival I included 106 *a priori* models in our candidate model list for female survival during the hunting season. This was essentially about 25 core models, because to create this model set, eight covariate terms (*site*, *female age* and six terms representing reproductive effort) were added to each temporal covariate (e.g., *year*, *trend 3*, and *weekends*) and because six reproductive effort terms were included as stand alone models and individually in conjunction with *site* and *female age*. I divided the hunting season into three time periods (first 20 days, second 20 days, and last 21 days) and included models that restricted female survival to a trend over the three periods to evaluate seasonal variation in hunting pressure and subsequently, female survival. I considered these periods for the hunted site only and for both sites combined, but I was primarily interested in testing hypotheses about how a hunted population's survival might

vary with changes in hunting pressure throughout the hunting season and did not expect a nonhunted population to experience the same variation. I predicted that hunting pressure may be higher at the beginning of the season when the sage grouse hunting season opens and/or when pronghorn (*Antilocapra americana*) hunting season opens in mid-October if hunters opportunistically hunt sage grouse while scouting or hunting pronghorn (FWP, unpublished data). Hunting pressure may decrease over the season as hunter interest declines or as bag limits are met, or hunting pressure may increase during pronghorn or white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) hunting seasons. I suspected that there may be more hunter activity on weekends or when hunting seasons open, so I included models that considered weekends separately from week days and that considered opening weekends for sage grouse, pronghorn, white-tailed deer, and mule deer on the hunted site. Hunting regulations changed between years, so I included models allowing survival to vary between sites and between years on the hunted site only to account for potential changes in hunting pressure and subsequently, survival. I investigated the effect of WNV during the hunting season by considering 1 September until about 1 week following the first hard frost (21 September) separately from the rest of the season. Hard frosts typically kill or induce hibernation in mosquitoes known to transmit WNV in sagebrush habitats of the west (G. Johnson, personal communication).

Overwinter Survival I included 68 a priori models in our candidate set for female survival during winter. This season began on 2 November, the day after sage grouse hunting closed, and ended 14 April 2005 and 8 April 2006. I included *date trend* and

*date trend*<sup>2</sup> in our analysis to represent within season variation in survival, because female survival may be lower earlier in the season if females in poorer body condition die early or winter weather may result in such within-season variation in survival. I also considered the lekking season separately (15 Mar to 14 April) in our models, as females may be at greater risk of predation when visiting leks.

## Results

I collected data during a relatively dry year in 2004 and a relatively wet year in 2005 (Appendix B). I captured and radio-marked 71 females in 2004 and 45 females in 2005 (see Appendix E for 2003 field season). Only one female was never relocated after capture, and data for this bird was censored from the dataset. I used telemetry to determine the fates of 71 radio-marked females in 2004 and 102 radio-marked females in 2005. The 2004 sample included 11 females originally marked in 2003 and one female that had been recaptured and released without a collar in 2003. The 2005 sample included 51 females originally marked in 2004 and 7 originally marked in 2003. Individual birds that survived to the next study year continued to be monitored, and associated data were included in our analyses.

### Hunting-Season Survival

I included 93 females in our analysis of female survival during the hunting season (Table 3.1). Twenty-eight females were included in both years. Birds that were known to have left the area closed to hunting in Golden Valley county for more than one location were censored from the dataset for the nonhunted site (10 in 2004 and 11 in 2005). I lost

contact with one nonhunted-site female after 15 September 2004, and I suspected that her transmitter failed and used all data up until the time she was lost and then censored data thereafter. In 2005, one hunted-site female was lost, and I used all data up until the time she was lost and considered her dead thereafter.

For 15 of 30 females that died, the cause of mortality could be determined (Table 3.2). Known causes of female mortality included predation, vehicle and power line collisions, drowning in stock tanks, and WNV. Most of the birds that died were likely killed by mammals or raptors. Eleven of the 93 females included in this analysis died during the hunting season (Table 3.2). The causes of mortality were difficult to assess due to potential scavenging of carcasses, but I classified seven mortalities as depredated, one as a probable collision (soft tissue hemorrhaging with no other indication of cause of death), two as scavenged (evidence of both mammalian and avian predators at kill site), one as an unknown (only the transmitter was recovered). Remains of two females were x-rayed to test for presence of shotgun pellets that would indicate hunter kill or crippling loss, but I did not find any pellets. I did not find evidence for hunter-killed birds, and no radio-marked birds were reported or returned as hunter killed in any year. In 2005, I collected remains from eight radio-marked females for WNV testing at the Wyoming State Veterinary Laboratory (Laramie, Wyoming), and of these, two were tested and neither was positive.

Table 3.1. Sample sizes included in survival analysis of sage grouse females for fall and winter listed by year, site, total, and individual females in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Season	2004		2005		Total	Individual females
	Hunted	Nonhunted	Hunted	Nonhunted		
Hunting	33	26	36	26	121	93
Winter	30	34	27	32	123	94

Table 3.2. Number of female sage grouse mortalities listed by year and site for each season and suspected causes of mortality by season in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Numbers separated by “/” indicate the number of carcasses that were scavenged out of total number of unknown mortalities.

Season	2004		2005		Total	Suspected cause of death			
	Hunted	Nonhunted	Hunted	Nonhunted		Depredated	WNv	Collision	Scavenged/ Unknown
Hunting	3	0	5	3	11	7	0	1	2/3
Winter	4	1	5	9	19	6	0	1	1/12

Results of model selection indicated that the following covariates were important to consider: *days rearing*, *site*, and seasonal variation (for the hunted site only) (Table 3.3). In accordance with our prediction, there was clear support for a reproductive cost to survival on both study sites: *days rearing* was in the top model and the second best model within 2  $AIC_c$  units of the best model (summed  $w_i = 0.475$ ). The estimated coefficient for the effect of *days rearing* was negative and the 95% confidence interval included only negative values (Table 3.4).

There was some evidence that survival rate was lower on the hunted site (Table 3.4). An effect of *site* was present in the top three models ( $\Delta AIC_c < 2.097$ ). Summed model weight (summed  $w_i$ ) for models including an effect of *site* was 0.648. In the top model, the estimated survival rate for a given level of *days rearing* was always higher on the nonhunted site than on the hunted site, but confidence intervals were widely overlapping for survival estimates from the two sites (Figure 3.4).

I found evidence of a negative trend in survival rate on the hunted site as the hunting season progressed (Table 3.4, summed  $w_i = 0.350$ ). While this negative trend was represented in the top two models in our set, there was little support for the second best model ( $\Delta AIC_c = 1.833$ ); this model, which was a simple generalization of the best model, could not have been more than 2.002  $AIC_c$  units worse than the best model. The structure of the top two models only differed in that the second best model included an additional intercept term, which allowed for the survival estimates to be different between the two study sites at the beginning of the hunting season. However, the confidence intervals for intercept terms in the second best model overlapped almost

entirely (i.e., the intercepts were the same [Table 3.5]), and thus the top two models are essentially the same and produce similar survival estimates.

The reproductive-effort term *brood fate* (categorical variable) was in the third best model, but *brood fate* is a categorical representation of *days rearing* and  $\Delta\text{AIC}_c = 2.097$ . Other reproductive effort terms did not appear to affect female survival ( $\Delta\text{AIC}_c \geq 3.560$ ), nor did female age ( $\Delta\text{AIC}_c \geq 4.984$ ). There was no support for models including an effect of either opening weekends ( $\Delta\text{AIC}_c \geq 4.992$ ) or weekends ( $\Delta\text{AIC}_c \geq 7.610$ ) on hunted-site survival. There was no support for models that allowed survival to decrease during the window when WNV infection was still a possibility (until approximately 21 September;  $\Delta\text{AIC}_c \geq 4.473$ ), and there was no support for models that included seasonal variation in survival on the nonhunted site ( $\Delta\text{AIC}_c \geq 3.710$ ).

Based on the best model, I concluded that female survival on both sites during the hunting season was greater for females that spent little or no time brood rearing than for those females that raised a brood to 30 days, and survival was higher for females on the nonhunted site than on the hunted site (Figure 3.4). For females that raised a brood to 30 days, seasonal survival on the nonhunted site was estimated as 0.898 (95% CI: 0.746 to 0.926), and seasonal survival on the hunted site was estimated as 0.753 (95% CI: 0.553 to 0.864). Survival was similar for females on either site that spent little or no time brood rearing ( $\hat{S}_{\text{Nonhunted}} = 0.981$ , 95% CI: 0.992 to 0.996;  $\hat{S}_{\text{Hunted}} = 0.951$ , 95% CI: 0.827 to 0.986). The average number of days spent rearing a brood for hunted-site females was 14.0 days, for nonhunted-site females was 13.4 days, and for females on both sites was 13.7. Seasonal survival for hunted-site females with the average number of days spent

brood rearing was estimated as 0.895, and for nonhunted-site females was estimated as 0.959. Monthly survival estimates ranged from 87% for hunted-site females that spent 30 days brood rearing to 99% for nonhunted site females with few to no days brood rearing.

Table 3.3. *A priori* models of Daily Survival Rate (DSR) for sage grouse females during the hunting season in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Models were ranked by differences in AIC<sub>c</sub> values, and the covariate *days rearing* in **bold type** received the highest summed model weight.

Model	# Parameters	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weight
Nonhunted + Hunted * Trend3 + <b>Days Rearing</b>	3	0.000	0.170
Nonhunted + Hunted + Hunted * Trend3 + <b>Days Rearing</b>	4	1.833	0.068
Nonhunted + Hunted * Trend3 + Brood Fate	3	2.097	0.060
Year * <b>Days Rearing</b>	4	2.988	0.038
<b>Days Rearing</b>	2	2.991	0.038
Year + <b>Days Rearing</b>	3	3.064	0.037
Site + <b>Days Rearing</b>	3	3.546	0.029
Nonhunted + Hunted * Trend3 + SRE	3	3.560	0.029
Year + Nonhunted + Hunted * Trend3	3	3.584	0.028
Nonhunted + Hunted * 3 Periods + <b>Days Rearing</b>	5	3.790	0.026
Nonhunted + Hunted + Hunted * Trend3 + Brood Fate	4	3.951	0.024
Nonhunted + Hunted * Trend3 + Nest Fate	3	4.288	0.020
Trend3 + <b>Days Rearing</b>	3	4.473	0.018
Nonhunted + Hunted * Trend3	2	4.486	0.018
Year * Nest Fate	4	4.688	0.016
WNv + <b>Days Rearing</b>	3	4.812	0.015
Year + Brood Fate	3	4.984	0.014
<b>Days Rearing</b> + Female Age	3	4.984	0.014
Nonhunted Site + Hunted Site * Opening Weekends + <b>Days Rearing</b>	4	4.992	0.014
Brood Fate	2	5.045	0.014
Nonhunted + Hunted + Hunted * Trend3 + SRE	4	5.392	0.011
Nonhunted + Hunted * Trend3 + Days Incubating	3	5.411	0.011
Year + Nonhunted + Hunted+ Hunted * Trend3	4	5.461	0.011
Site + Brood Fate	3	5.550	0.011
Nonhunted + Hunted * 3 Periods + Brood Fate	5	5.911	0.009
Nonhunted + Hunted + Hunted * Trend3 + Nest Fate	4	6.101	0.008
Year * SRE	4	6.109	0.008
Year * WNv	3	6.136	0.008
SRE	2	6.214	0.008
3 Periods + <b>Days Rearing</b>	4	6.217	0.008
Year	2	6.346	0.007
Nonhunted + Hunted * Trend3 + Female Age	3	6.374	0.007
Nonhunted + Hunted + Hunted * Trend3	3	6.381	0.007
Nonhunted + Hunted * Trend3 + Days Laying	3	6.398	0.007
Trend3 + Brood Fate	3	6.555	0.006
Year + SRE	3	6.566	0.006
Year + Nest Fate	3	6.609	0.006

Table 3.3. Continued.

Year * Site sin	4	6.613	0.006
Year * Brood Fate	4	6.850	0.006
Year + Site	3	6.850	0.006
Nest Fate	2	6.863	0.006
WNv + Brood Fate	3	6.878	0.005
Site + SRE	3	6.896	0.005
Nonhunted Site + Hunted Site * Opening Weekends + Brood Fate	4	7.000	0.005
Brood Fate + Female Age	3	7.024	0.005
Nonhunted + Hunted + Hunted * Trend3 + Days Incubating	4	7.260	0.005
Year * Days Incubating	4	7.301	0.004
Nonhunted + Hunted * 3 Periods + SRE	5	7.358	0.004
Constant	1	7.423	0.004
Year + Nonhunted + Hunted * 3 Periods	5	7.432	0.004
Nonhunted Site + Hunted Site * Weekends vs. Weekdays	3	7.610	0.004
Site + Nest Fate	3	7.626	0.004
Trend3 + SRE	3	7.743	0.004
Year + Days Laying	3	7.760	0.004
Site	2	7.796	0.003
Year + Days Incubating	3	7.863	0.003
Year + Trend3	3	7.896	0.003
WNv + SRE	3	8.054	0.003
Days Incubating	2	8.057	0.003
Nonhunted + Hunted * 3 Periods + Nest Fate	5	8.067	0.003
Year + WNv	3	8.192	0.003
SRE + Female Age	3	8.210	0.003
Nonhunted + Hunted+ Hunted * Trend3 + Female Age	4	8.257	0.003
3 Periods + Brood Fates	4	8.304	0.003
Year + Nonhunted Site + Hunted Site * Opening Weekends	4	8.306	0.003
Year + Female Age	3	8.308	0.003
Nonhunted + Hunted + Hunted * Trend3 + Days Laying	4	8.310	0.003
Nonhunted + Hunted * 3 Periods	4	8.350	0.003
Nonhunted Site + Hunted Site * Opening Weekends + SRE	4	8.360	0.003
Trend3 + Nest Fate	3	8.392	0.003
Site + Days Incubating	3	8.698	0.002
WNv + Nest Fate	3	8.704	0.002
Nest Fate + Female Age	3	8.858	0.002
Year * Hunted Site	3	8.965	0.002
Trend3	2	8.978	0.002
Nonhunted Site + Hunted Site * Opening Weekends + Nest Fate	4	9.091	0.002
Female Age	2	9.212	0.002
Nonhunted + Hunted * 3 Periods + Days Incubating	5	9.228	0.002
Nonhunted Site + Hunted Site * Opening Weekends	3	9.265	0.002
WNv	2	9.273	0.002
Year * Days Laying	4	9.347	0.002
Days Laying	2	9.422	0.002
3 Periods + SRE	4	9.502	0.001
Trend3 + Days Incubating	3	9.608	0.001

Table 3.3. Continued.

Site + WNv	3	9.647	0.001
Year + 3 Periods	4	9.667	0.001
Site + Female Age	3	9.675	0.001
Site + Days Laying	3	9.732	0.001
WNv + Days Incubating	3	9.907	0.001
Days Incubating + Female Age	3	10.052	0.001
3 Periods + Nest Fate	4	10.147	0.001
Nonhunted Site + Hunted Site * Opening Weekends + Days Incubating	4	10.168	0.001
Nonhunted + Hunted * 3 Periods + Female Age	5	10.225	0.001
Nonhunted + Hunted * 3 Periods + Days Laying	5	10.279	0.001
Year * Female Age	4	10.305	0.001
3 Periods	3	10.744	0.001
Trend3 + Female Age	3	10.765	0.001
Trend3 + Days Laying	3	10.978	0.001
WNv + Female Age	3	11.062	0.001
Nonhunted Site + Hunted Site * Opening Weekends + Female Age	4	11.144	0.001
Days Laying + Female Age	3	11.168	0.001
Nonhunted Site + Hunted Site * Opening Weekends + Days Laying	4	11.202	0.001
WNv + Days Laying	3	11.273	0.001
3 Periods + Days Incubating	4	11.370	0.001
3 Periods + Female Age	4	12.529	0.000
3 Periods + Days Laying	4	12.744	0.000

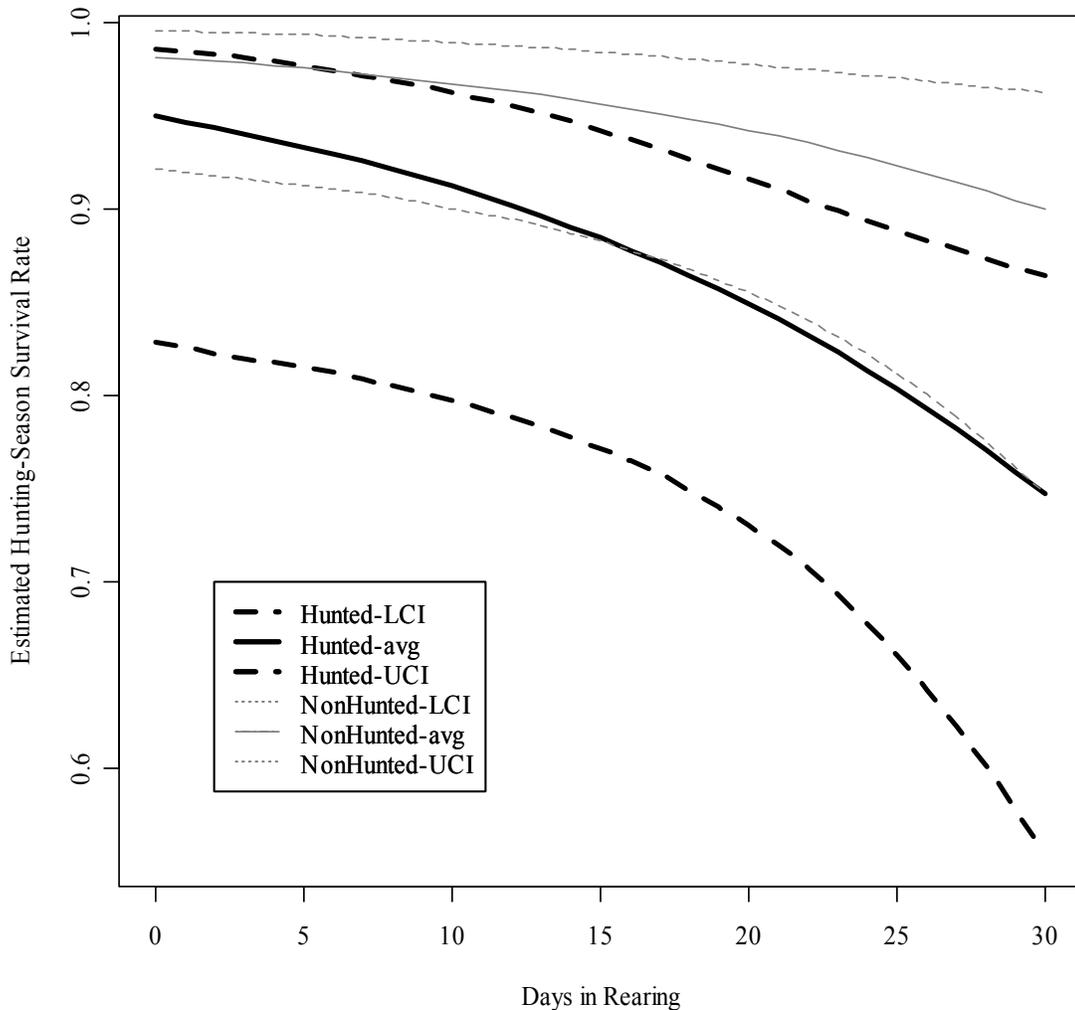
Table 3.4. Parameter estimates, standard errors, and 95% confidence intervals for the best approximating model, *Nonhunted + Hunted \* Trend3 + Days Rearing* (single intercept model), of hunting-season survival of sage grouse females in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Parameter	Estimate	Std. error	95% Confidence Intervals	
			Lower	Upper
Intercept	8.084	0.751	6.612	9.557
Trend3 * Hunted Site	-0.779	0.346	-1.458	-0.101
Days Rearing	-0.058	0.025	-0.107	-0.009

Table 3.5. Parameter estimates, standard errors, and 95% confidence intervals for the second best approximating model, *Nonhunted + Hunted + Hunted \* Trend3 + Days Rearing* (a model with two intercepts), of hunting season survival of sage grouse females in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Parameter	Estimate	Std. error	95% Confidence Intervals	
			Lower	Upper
Intercept: Nonhunted	7.952	0.802	6.379	9.524
Intercept: Hunted	8.378	1.076	6.269	10.487
Trend3 * Hunted Site	-0.939	0.538	-1.994	0.117
Days Rearing	-0.058	0.025	-0.108	-0.009

Figure 3.1. Hunting-season survival estimates (61 days) for sage grouse females by number of days spent rearing a brood for a hunted and nonhunted population in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Estimates of hunting-season survival rate are based on estimates from the best model, and the averages and 95% CI values were obtained using parametric bootstrapping.



### Overwinter Survival

The overwinter period extended from the end of hunting season on 1 November to 14 April 2005 and 8 April 2006. I included 94 individuals in our analysis of female

survival overwinter, and 29 females were included in both years (Table 3.1). Two females were lost overwinter, one in each year, were never relocated, and were included as having died in the analysis. One female with a transmitter with a very weak signal was lost later in the winter in 2005-06, and I included all data up until the time she was lost and then censored data thereafter.

Nineteen females included in this analysis died overwinter (Table 3.2). I classified six as depredated, one as a collision (bruising and no other damage), one as scavenged (evidence of both mammalian and avian predators at kill site), and 11 as unknowns. The higher incidence of unknown cause of mortality overwinter was likely due to a reduction in monitoring intensity. By the time a visit was made, all portions of the carcass were probably consumed by scavengers and only the collar remained.

Results of model selection strongly indicated that survival rate varied by year and that the probability of surviving overwinter was higher in 2004-2005 than in 2005-2006. Year was in all the best models for female survival overwinter (Table 3.6; summed  $w_i = 0.85$ ), and the estimated difference in survival between years was stable across models. A number of models that added a single covariate to a model containing *year* were within 2  $AIC_c$  units of the best model, but none of the coefficients associated with the additional covariates in these models were precisely estimated: 95% confidence intervals broadly overlapped zero in all cases. The  $AIC_c$  values may at first glance indicate support. However, these models, which were simple generalizations of the best model, could not have been more than 2.007  $AIC_c$  units worse than the best model, and all were at least 1.622  $AIC_c$  units more than the best model. Thus, the support for inclusion of these

covariates was weak. There was no support for an effect of reproductive effort, *site*, *lekking*, *female age*, or within-season variation in models without the *year* term.

The best-supported model estimated female survival as 0.905 (SE = 0.037, 95% CI: 0.833 to 0.977) in the first winter (164 days) and 0.743 (SE = 0.057, 95% CI: 0.631 to 0.855) in the second winter (158 days). Monthly survival during winter 2004-05 was estimated at 0.982 (SE = 0.007, 95% CI: 0.968 to 0.996) and during winter 2005-06 was estimated at 0.967 (SE = 0.014, 95% CI: 0.918 to 0.972).

Annual survival estimates ranged from 38% for hunted-site females that invested heavily (30 days) in brood rearing in 2005 to 75% for nonhunted-site females that invested little (0 days) in brood rearing in 2004 (Table 3.7). Corresponding mean life span ( $1/[-\ln(\text{annual } \hat{S})]$ ) was calculated as one year for hunted-site females that invested heavily in brood rearing in 2005 and was 3.5 years for nonhunted females that invested little in brood rearing in 2004 (Table 3.7).

Table 3.6. *A priori* models of Daily Survival Rate (DSR) for sage grouse females overwinter in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. Models were ranked by differences in  $AIC_c$  values, and the covariate *year* in **bold type** received the highest summed model weight of all covariates.

Model	# Parameters	$\Delta AIC_c$	$AIC_c$ weight
<b>Year</b>	2	0.000	0.131
<b>Year</b> + Days Laying	3	1.622	0.058
<b>Year</b> + Brood Fate	3	1.773	0.054
<b>Year</b> + Days Rearing	3	1.837	0.052
<b>Year</b> + SRE	3	1.902	0.050
<b>Year</b> + Female Age	3	1.926	0.050
<b>Year</b> + Nest Fate	3	1.968	0.049
<b>Year</b> + Site	3	1.977	0.049
<b>Year</b> + Lekking	3	1.986	0.048
<b>Year</b> + Days Incubating	3	1.990	0.048
<b>Year</b> + Date Trend	3	1.993	0.048
Year * Site	4	2.781	0.032
Year * Brood Fate	4	2.962	0.030
Year * Days Rearing	4	3.334	0.025

Table 3.6. Continued.

Year * Days Laying	4	3.601	0.022
Year * SRE	4	3.822	0.019
Year * Nest Fate	4	3.879	0.019
Year * Days Incubating	4	3.924	0.018
<b>Year</b> + Date Trend + Date Trend <sup>2</sup>	4	3.994	0.018
Constant	1	4.178	0.016
Days Incubating	2	5.181	0.010
Nest Fate	2	5.479	0.008
Female Age	2	5.497	0.008
SRE	2	5.793	0.007
Days Laying	2	5.978	0.007
Date Trend	2	6.111	0.006
Days Rearing	2	6.152	0.006
Site	2	6.158	0.006
Brood Fate	2	6.161	0.006
Lekking	2	6.171	0.006
Days Incubating + Female Age	3	6.912	0.004
Nest Fate + Female Age	3	7.051	0.004
Date Trend + Days Incubating	3	7.129	0.004
Lekking + Days Incubating	3	7.179	0.004
Site + Days Incubating	3	7.182	0.004
SRE + Female Age	3	7.345	0.003
Date Trend + Nest Fate	3	7.422	0.003
Date Trend + Female Age	3	7.440	0.003
Days Laying + Female Age	3	7.472	0.003
Lekking + Nest Fate	3	7.476	0.003
Site + Nest Fate	3	7.478	0.003
Lekking + Female Age	3	7.493	0.003
Site + Female Age	3	7.494	0.003
Days Rearing + Female Age	3	7.495	0.003
Brood Fate+ Female Age	3	7.497	0.003
Date Trend + SRE	3	7.733	0.003
Site + SRE	3	7.784	0.003
Lekking + SRE	3	7.789	0.003
Date Trend + Days Laying	3	7.918	0.002
Lekking + Days Laying	3	7.974	0.002
Site + Days Laying	3	7.976	0.002
Date Trend + Days Rearing	3	8.085	0.002
Date Trend + Site	3	8.091	0.002
Date Trend + Brood Fate	3	8.094	0.002
Date Trend + Date Trend <sup>2</sup>	3	8.094	0.002
Site + Days Rearing	3	8.129	0.002
Site + Brood Fate	3	8.139	0.002
Lekking + Days Rearing	3	8.145	0.002
Lekking + Site	3	8.151	0.002
Lekking + Brood Fate	3	8.154	0.002
Date Trend + Date Trend <sup>2</sup> + Days Incubating	4	9.118	0.001

Table 3.6. Continued.

Date Trend + Date Trend <sup>2</sup> + Nest Fate	4	9.409	0.001
Date Trend + Date Trend <sup>2</sup> + Female Age	4	9.426	0.001
Date Trend + Date Trend <sup>2</sup> + SRE	4	9.720	0.001
Date Trend + Date Trend <sup>2</sup> + Days Laying	4	9.904	0.001
Date Trend + Date Trend <sup>2</sup> + Days Rearing	4	10.072	0.001
Date Trend + Date Trend <sup>2</sup> + Site	4	10.075	0.001
Date Trend + Date Trend <sup>2</sup> + Brood Fate	4	10.079	0.001

Table 3.7. Summary of survival estimates from the best-supported models for each season, annual survival estimates, and mean life span according to year, site, and number of days spent rearing a brood for sage grouse females in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05. The lowest and highest annual survival estimates are in **bold type**.

Year	Site	Days rearing	Season				Annual	Mean life span
			Nesting	Late-summer	Hunting	Overwinter		
2004	Hunted	0	0.87	0.92	0.95	0.91	0.69	2.68
2004	Hunted	30	0.87	0.92	0.75	0.91	0.55	1.65
<b>2004</b>	<b>Nonhunted</b>	<b>0</b>	0.87	0.97	0.98	0.91	<b>0.75</b>	<b>3.47</b>
2004	Nonhunted	30	0.87	0.97	0.90	0.91	0.69	2.65
2005	Hunted	0	0.84	0.83	0.95	0.73	0.48	1.37
<b>2005</b>	<b>Hunted</b>	<b>30</b>	0.84	0.83	0.75	0.73	<b>0.38</b>	<b>1.04</b>
2005	Nonhunted	0	0.84	0.94	0.98	0.73	0.56	1.75
2005	Nonhunted	30	0.84	0.94	0.90	0.73	0.52	1.51

## Discussion

### Hunting-Season Survival

The most striking findings of my research were that I did not find any evidence that radio-marked birds were killed by hunters on the hunted site and that the best model supported both a difference in survival between sites and a cost of reproduction. Females with higher reproductive effort had lower survival at both sites. Survival was lower for hunted-site females compared to nonhunted-site females, which could be taken as evidence of a hunting effect. But, as is discussed below, the cause of this difference in

survival between sites is unclear, and the difference may be unrelated to site-specific hunting activity.

Point estimates for female survival during the hunting season were lowest for females on the hunted site (0.75 to 0.95) compared to females on the nonhunted site (0.90 to 0.98), but I could not attribute this difference to hunter kill. However, I was unable to rule out the possibility that survival rate was lower on the hunted site due to crippling losses or hunter kills that went unreported (see below for discussion of causes of mortality). Hunters did report killing some non-radiomarked birds on the area, and for a larger sample of male and female birds on the hunted area that were leg-banded but not radio-marked ( $n = 218$  [FWP, unpublished data]), five sage grouse were reported as hunter bagged during 2002-2005. This yields a band-return rate of 2.3%, which is an underestimate because some of the banded-only sample died during the course of the study. For that reason, the lack of hunter-killed radio-marked birds on the hunted site probably resulted from low hunting pressure and abundant sage grouse rather than hunters failing to report harvest of radio-marked birds. In 2003, the last year that harvest information is available from hunter telephone surveys, the sage grouse harvest was 82% below the long-term average (1967-2002 [FWP, unpublished data]), suggesting that harvest rates may have been relatively low.

This difference in survival between the hunted and nonhunted sites may have been due to site-level differences in features such as land ownership and land-use, habitat, disease, disturbance, predators, or a combination thereof. For example, survival rate was also lower on the hunted site than on the nonhunted site during late summer (see Chapter 2). Additionally, a greater proportion of the hunted site (40%) was publicly

owned than the nonhunted site (6%), and this difference in land ownership may represent differences in land-use. Moreover, there was a negative trend in survival on the hunted site during the hunting season, which was opposite to my predictions that 1) survival rate on the hunted site would be lowest early in the hunting season and 2) that due to an expected decrease in hunting pressure over the hunting season, survival rate would increase as the season progressed. However, this negative trend in survival on the hunted site during the hunting season was consistent with my predictions that 1) survival rate on the hunted site would be lower after the pronghorn hunting season opens and 2) that due to an expected increase in hunting pressure over the hunting season, survival rate would decrease as the hunting season progressed. But again, no evidence for hunter kill of radio-marked birds was observed. One possible explanation for the decreasing survival trend has to do with activity patterns of pronghorn hunters. Based on personal observations during field work, I suspect that higher hunter activity in the area both before (scouting) and during the pronghorn hunting season, which begins in mid-October and ends in early November, may be responsible. Such activity may have caused increased disturbance of birds and mortality due to other causes (e.g., road kill or increased exposure to predators). Differences in the levels of pronghorn-hunter activity between the two sites may help explain differences in survival rates between the two sites. Pronghorn were more abundant on the hunted site (FWP, unpublished data), pronghorn hunting pressure was greater on the hunted site (J. A. Newell, personal communication), and the hunted site was more readily accessible to hunters due to the availability of self-permitting for access to BMA's at sign-in boxes on that site. The

nonhunted site required written permission from FWP for access to BMA's during the pronghorn season.

It was not possible to determine the cause of death for all birds. At least two birds were scavenged, and for another female, only a radio collar was retrieved. Two females were known to be alive at the beginning of the hunting season, and then they were never detected again, despite intensive efforts to locate them, which included repeated telemetry flights. It is possible that those two females were hunter killed, and were either removed from the study area or had their collars destroyed. However, birds were lost and never relocated in all seasons and at the nonhunted study site as well; thus, it is not readily apparent that these missing birds were necessarily killed by hunters. For six of the eight females that died during the hunting season on the hunted site, evidence indicated that depredation was the cause of death, and two out of the eight were scavenged. However, it is possible that any of these birds were crippled by hunters and later scavenged. I did inform hunters about the study and intensively monitor the status (live or dead) of hunted-site birds during the hunting season, and thus, it seems unlikely that all of these birds were killed by hunters, yet went unreported. The best estimate for harvest rate of the radio-marked population from this study is zero. Connelly et al. (2000a) suggested that harvest should be  $\leq 10\%$  of the fall population, and the proportion of the hunted-site radio-marked females that died from all causes during the hunting season in this study was 0.12. I documented other human-related sources of mortality of radio-marked birds besides hunting. Necropsy indicated some type of collision (power line or automobile) for an intact carcass (nonhunted site), and one radio-marked female was found dead in a stock tank with seven other unmarked sage grouse during the

hunting season in 2003 (hunted site). Previously, nine unmarked birds had been found dead in the same stock tank. In addition to these human-related sources of mortality, I also documented a trade-off between reproductive effort and female survival.

Another notable result from this study was the strong evidence for survival costs of reproduction immediately following the breeding season. Reproductive costs were evident for females at both hunted and nonhunted sites. I estimated lower survival rates for females that spent more days brood-rearing (0.75 to 0.90) than those that spent few or no days brood rearing (0.95 to 0.98). High reproductive effort may negatively affect body condition and subsequent survival or fecundity (e.g., Reid 1987, Jacobsen et al. 1995, Erikstad et al. 1997, 1998, Cam et al. 1998, Golet et al. 1998, and Rotella et al. 2003). To my knowledge, no other sage grouse study has addressed the cost of reproduction at the seasonal level, besides the breeding season, by specifically including reproductive effort as a mechanism in analyses. But, other sage grouse studies have suggested a negative correlation between annual survival and reproductive effort (see section on overwinter survival below). Other avian studies have documented that brood rearing poses an energetic cost to the female by decreasing the amount of time spent foraging, which reduces body condition, and subsequently decreases her probability of survival post-brood-rearing (Golet et al. 1998, Roff 2002). Females may also be more susceptible to predation if foraging with a brood reduces vigilance or increases detectability to predators, or if females actively protect broods from predators (Schroeder et al. 1999). I did not actively monitor brood presence or absence beyond 30 days, but other studies have observed females with chicks for an average of 120 days (range: 93-170 days [T. R. Thompson, personal communication]). If brood vigilance continued

through the hunting season, this vigilance may also contribute to lower survival. Further, previous research has speculated that predators may switch to more abundant prey and mortality may increase in more productive years (Moynahan 2005).

The reproductive-effort term in the best-supported models in my analysis was *days rearing*. At first consideration, one might expect that *SRE* (summed reproductive effort) would be more representative, and therefore in better-supported models than *days rearing*. However, I think that *days rearing* was in better-supported models because rearing a brood is more taxing energetically than either laying eggs or incubating nests. Broods move around, are attended and protected by the hen, and probably put her at a greater risk to predation and reduce foraging time. In contrast, during early laying females only spend about an hour a day at the nest site (Griner 1939). With data from this study, females could be on equal footing with *SRE* scores composed of different days of activity, i.e., females could have similar *SRE* but the majority of that sum could come from days laying and incubating and very little from days rearing. Given that we do not know what the energetic costs are for the various stages of breeding, there is uncertainty about which part of the process is most taxing and therefore best reflects reproductive effort. The results of this research suggest that the number of days a female spends rearing a brood may represent reproductive effort well.

In this study, the range of monthly survival estimates for the hunting season, 0.87 for hunted-site females that spent 30 days brood rearing to 0.99 for nonhunted-site females with few to no days brood rearing, were within the range of rates reported for north-central Montana (0.82 to 0.98 [Moynahan et al. 2006]) and northwest Colorado (0.96 [Hausleitner 2004]) during the hunting season. However, the topic has not been

well studied and merits further attention. The costs of breeding to survival rate detected here indicate that population growth rates may not vary as much as we might suspect if we only were to examine reproductive data across years. That is, reproductive effort and reproductive success may be highly variable (see Schroeder et al. 1999 and Connelly et al. 2000a for review) but counterbalanced by opposite (or negatively covarying) levels of female survival. This is not to say that populations are not expected to fluctuate, rather population fluctuations may not be as extreme as they would be in the absence of reproductive costs.

### Overwinter Survival

I did not detect a difference in survival between sites overwinter, although winter is when we would expect to observe a possible compensatory response (survival rates higher on hunted site) if hunting had caused a biologically significant decline in the density of birds (Nichols et al. 1984). I did, however, detect a difference in survival rates between years. Survival rate during winter was lower on our study in 2005-06 (0.74) than in 2004-05 (0.91). Monthly estimates of survival rate ranged from 0.97 to 0.98 and were within the range of rates reported for north-central Montana overwinter (0.91 to 0.99 [Moynahan et al. 2006]) and northwest Colorado (0.97 to 0.99 [Hausleitner 2004]). There was no dramatic difference in weather between winters during this study, and thus, I do not think that the difference observed was due to differences in snow depths or temperatures (NOAA 2006).

The difference in overwinter survival between years may have been due to annual differences in reproductive effort, although I did not detect an effect for reproductive

effort in our analysis. Overall, females invested more heavily in reproduction in 2005 than in 2004, and perhaps all females were in relatively worse body condition and at a greater risk of dying. A trade-off between annual survival and reproductive effort has been suggested in other grouse studies. Bergerud and Gratson (1988) suggested that there is a negative correlation between reneating and annual survival of female sage grouse, and a recent study in north-central Montana noted that annual female survival was higher in a year with low reproductive effort, which coincided with mild, dry weather (Moynahan 2005). In contrast, sage grouse in north-central Washington, which had higher reproductive effort than reported for other regions, did not experience reduced survival rates (Schroeder 1997).

#### Seasonal and Annual Survival Summary

Our results demonstrated that year, season, site, and reproductive effort all contributed to variation in survival of female sage grouse. Although age-specific variation in survival has previously been documented, this was not supported with our data, but this may have been due to the small sample size of yearlings, particularly in 2005. Between years, precipitation, reproductive effort (nesting and reneating probability, season length), and WNV mortality increased, and female survival decreased between years during late-summer and winter. The range of monthly survival estimates (84-100%) and annual survival estimates (38-75%) reported here were similar to rates recently reported for north-central Montana (75-99% monthly, 25-96% annually [Moynahan et al. 2006]) and northwestern Colorado (91-99% monthly, 48-78% annually [Hausleitner 2004]) and also varied more on a seasonal and annual basis than what has

previously been reported (see Connelly et al. 2000a, 2004 for review). Collectively, previous studies have reported annual survival rates from 35 to 85% (see Schroeder et al. 1999 and Connelly et al. 2000a, 2004 for review). A 1970s study adjacent to my study area reported annual survival rates of 35% for yearling females and 40% for adult females (Wallestad 1975). Annual female survival estimates ranged from 48-78% in Colorado (Hauleitner 2004), 48-75% in Idaho, 67-78% in Wyoming, 57% in Alberta, and 37% in Utah (see Connelly et al. 2004 for review).

Overall, the *average* monthly probability of survival in my study was highest in winter (97-98%) and lower during all other seasons: nesting (94%), late-summer (95%), and hunting season (95%), which is consistent with previous findings. Survival was constant (94% monthly) during the nesting season, but there was within-season variation in survival during the late summer (84 to nearly 100%), hunting season (87-99%), and overwinter (97-98%). Few published studies have considered survival at the seasonal level. Based on these results, the most critical period for adult female survival occurred from August through October. During August, this was likely due to WNV, and during the hunting season was attributable to both reproductive costs and a site effect. Winter did not appear to be a critical period, but 2004 and 2005 were both mild winters in this area. Annual survival was lowest for hunted-site females that invested heavily (30 days) in brood rearing in 2005 (39%) and was highest for nonhunted-site females that invested little (0 days) in brood rearing in 2004 (75%).

### Future Research

The work reported here represents a case study that generates hypotheses and predictions that can only be properly evaluated by replicated studies. Although survival was lower on a hunted site, the evidence does not indicate hunting mortality, and therefore, I cannot attribute this mortality to hunting and cannot draw conclusions about whether or not sage grouse compensate for harvest. However, harvest appears to be low in central Montana and appears to have little impact on the population, especially relative to other mortality causes that were identified. Harvest may impact sage grouse populations very differently across their range, and thus, area-specific data on the impact of harvest, and the magnitude of this impact relative to other potential sources of mortality, are necessary for informed management. To truly understand why survival rates during fall and winter vary in space and time will require replicate study sites across a range of conditions for habitat, weather, and hunting pressure. Differences in female survival between sites during this study may have been due to other landscape-scale characteristics besides differences in hunting activity, such as differences in the quality of sagebrush habitat or predator communities between sites. It may be informative to use available GIS data to consider the effect of fragmentation in future studies.

To learn how sage grouse populations respond to harvest, future research may need to have both a low kill rate (low or 0) and a series of experimentally controlled sites with a range of kill rates. Ideally, several experimental kill rates would be implemented, across a range of population densities, because we expect populations to respond differently to varying levels of harvest and expect different responses based on density.

Some level of harvest may be compensatory, but regardless, for most populations at some level or threshold, harvest will be additive to natural mortality, and it would be helpful for managers to know (1) what that harvest rate is for populations at varying densities, and (2) what factors influence harvest rate (e.g., distance to human population centers, land-ownership patterns, hunting regulations, etc.). In addition, to address potential cross-seasonal effects of harvest, either direct compensation through improved survival of remaining individuals or indirectly via reproductive compensation, some monitoring of bird density is necessary. However, as stated previously, harvest studies are notoriously difficult to conduct, and researchers frequently rely on constrained study designs. It would be informative to conduct harvest studies of a limited design across their range, in areas where sage grouse populations or sage grouse habitat are different, in an effort to understand how harvest may influence population vital rates and growth differently under these varying conditions. Replicated studies will broaden our understanding and strengthen our inferences on this topic.

My results indicate costs of reproduction to survival. The costs detected here were expressed immediately following the reproductive season during the hunting season. However, it is possible that there are also less-immediate costs to survival. Survival probability may be reduced in future years, or there may be reproductive costs to future fecundity. Breeding probabilities and reneating probabilities may be reduced in years subsequent to years of high reproductive effort (e.g., Jacobsen et al. 1995, Golet et al. 1998). Lifetime reproductive output is a balance of current reproduction and future survival and reproduction (Williams 1966), and a number of factors, such as age, body condition, and environmental variation, may influence reproductive effort, reproductive

success, and reproductive costs. Determining how, or if, these factors influence reproduction and survival is essential to understanding life-history strategies (Roff 2002) and to distinguishing between reproductive costs and other sources of mortality. To properly investigate reproductive costs, individuals with known reproductive histories will have to be studied in multiple years.

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## CHAPTER FOUR

## CONCLUSION TO THESIS

Extended Abstract

Breeding ecology, survival rates, and mortality causes of hunted and nonhunted greater sage-grouse (*Centrocercus urophasianus*), hereafter sage grouse, were studied in central Montana in 2004 and 2005. Sage grouse populations have been declining throughout their historical range in western North America since the early 1900s, with current abundance estimated at 1-31% of the numbers present prior to European settlement in the 1800s. In addition to a dramatic decline in abundance, sage grouse distribution has contracted by as much as 44%. Declines in productivity have been implicated in population declines in several areas, but there is considerable variation in reproductive effort, reproductive success (productivity) and female survival, both temporally and spatially. Reproductive success may be an important factor affecting population size. Moreover, despite declining populations, sage grouse are still legally harvested in most of their current range, including Montana, and uncertainty about how harvest impacts sage grouse vital rates remains. Information on productivity and impacts of harvest mortality from areas where sage grouse populations are doing well may be valuable to understanding range-wide declines and subsequently informing management decisions. I conducted a two-year case study examining productivity and hunting-season mortality in central Montana, where sage grouse abundance is relatively high and sagebrush habitat is relatively contiguous. I collected data during a relatively dry year in

2004 and a relatively wet year in 2005. I used telemetry to determine fates of 71 radio-marked females in 2004 and 102 radio-marked females in 2005. I relocated birds every week from the beginning of nest incubation in mid April until the close of the hunting season on 2 November in 2004 and 2005. Females were monitored twice per month from mid-December through early March. I monitored the reproductive activity of 67 females in 2004 and 96 females in 2005. I collected data for 182 nests and 73 broods of radio-marked females. Nests were initiated between late March and early April in both years, and the earliest known renests were found in late April to early May. Nests were located under sagebrush (91% [*Artemisia tridentata wyomingensis*]), greasewood (3% [*Sarcobatus vermiculatus*]), or in agriculture fields (6% [CRP, crested wheat, or alfalfa]). Nest survival was greater for renests,  $\hat{S} = 0.563$ , (SE = 0.081), than for first nests,  $\hat{S} = 0.320$ , (SE = 0.041). In both years, first nest attempts hatched in mid-May, and all broods were expected to reach 30 days old by late July or early August. Our best supported model for brood survival was an intercept-only model, and from this model brood survival to 30 days of age was estimated at 0.794 (SE = 0.002). A model that estimated different brood survival rates between years also received substantial support and estimated brood survival to 30 days of age at 0.708 (SE = 0.092) in 2004 and at 0.841 (SE = 0.055) in 2005. Reproductive effort (nesting probability and renesting probability) and reproductive success (the proportion of females that successfully raised a brood out of the total sample at the beginning of the nesting season) were higher in 2005. Increases in nesting and renesting probabilities and higher renest and brood survival may have been due to increased precipitation and a subsequent increase in grass and forb abundance in 2005. This increase may have provided better cover at late-season nests, better cover for

chicks, and better nutrition for females and chicks. Known causes of female mortality included predation, vehicle and power line collision, drowning in stock tanks, and West Nile virus (WNV). Female survival was constant during the nesting season, and I estimated a monthly survival rate of  $\hat{S} = 0.939$  (SE = 0.012). Survival estimates were similar on both sites for females in July of both years  $\hat{S} : 0.989$  to  $0.996$  (SE: 0.004 to 0.011), but survival in August declined between 2004 and 2005, from  $\hat{S} = 0.938$  (SE = 0.037) to  $\hat{S} = 0.838$  (SE = 0.054) on the hunted site and from  $\hat{S} = 0.978$  (SE = 0.017) to  $\hat{S} = 0.941$  (SE = 0.035) on the nonhunted site. This decline in survival between years in August was likely due to an increase in WNV, which was first detected in sage grouse in this area in August 2005. Two important effects were supported in our best model for female survival during the hunting season: a site effect and reproductive cost. During the hunting season, monthly survival estimates ranged from  $\hat{S} = 0.872$  for hunted-site females that invested heavily in brood rearing to  $\hat{S} = 0.991$  for nonhunted-site females that invested little or no time in brood rearing. Female survival during the hunting season was lower for females on the hunted site than on the nonhunted site, but I could not attribute this difference to hunter kill. However, I also was unable to rule out the possibility that survival was lower on the hunted site due to crippling losses or hunter kills that went unreported. This difference in survival between the hunted and nonhunted sites may have been due to site-level differences in factors that were not measured, including habitat, disease, disturbance, or predators. During the hunting season, hunted and nonhunted site females that spent more days brood-rearing had lower estimated

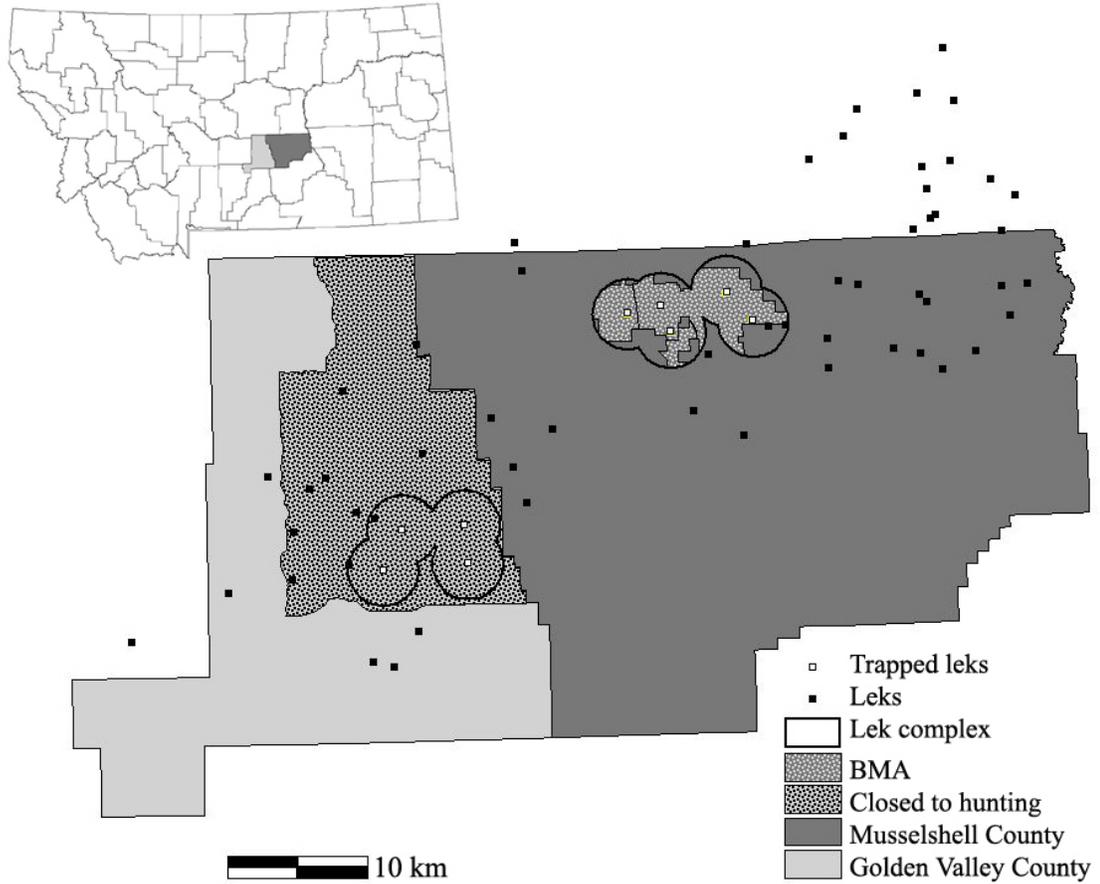
survival than those that spent few or no days brood rearing. I suspect that high reproductive effort negatively affected body condition and subsequent survival of females. Monthly survival was estimated as  $\hat{S} = 0.982$  (SE = 0.007) during winter 2004-05 and as  $\hat{S} = 0.967$  (SE = 0.014) during winter 2005-06. There was no dramatic difference in weather between winters, and thus, I do not think that the difference observed was due to differences in snow depth or temperature. A trade-off between annual survival and reproductive effort has been suggested in other grouse studies. Although I did not detect an effect of reproductive effort on winter survival, the difference in overwinter survival between years may have been due to annual differences in reproductive effort. Overall, females invested more heavily in reproduction in 2005 than in 2004, and winter survival was reduced in 2005-06. Annual survival ranged from 39% for hunted-site females that invested heavily (30 days) in brood rearing in 2005 to 75% for nonhunted-site females that invested little (0 days) in brood rearing in 2004. Future studies of sage grouse breeding ecology should directly address how habitat characteristics influence reproductive effort and reproductive-survival trade-offs. Replicated studies of survival rates and causes of mortality for sage grouse are needed both in this area of Montana and throughout the species' range. Harvest may impact sage grouse populations very differently across their range, and thus, area-specific data on the impact of harvest, and the magnitude of this impact relative to other potential sources of mortality, are necessary for informed management.

APPENDICES

APPENDIX A:

MAP AND COVER TYPES OF STUDY AREA IN CENTRAL MONTANA.

Appendix A1. Trapped lek complexes and leks in and surrounding the study area. Block Management Areas (BMA) in Musselshell county and the area closed to hunting in Golden Valley county, Montana, 2002-2005. Inset in upper left corner shows all counties of Montana with Musselshell and Golden Valley counties shown in gray.



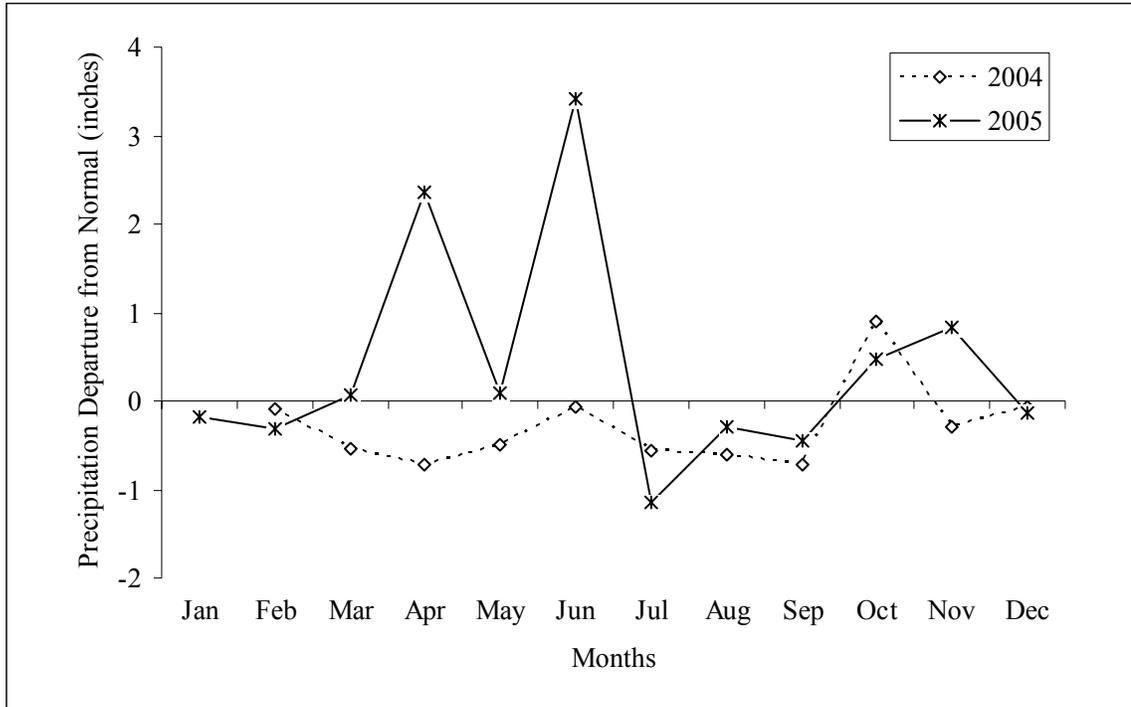
Appendix A2. Vegetation cover types for hunted study site (Musselshell county) and nonhunted study site (Golden Valley county), in central Montana 2003.

Cover type	Musselshell County		Golden Valley County	
	km <sup>2</sup>	%	km <sup>2</sup>	%
Sagebrush	226.2	0.79	231.1	0.88
Urban	0.3	0.00	0.0	0.00
Agriculture	56.8	0.20	20.0	0.08
Riparian	4.6	0.02	7.8	0.03
Pine	0.0	0.00	2.3	0.01
Total	287.9	100.00	261.3	100.00

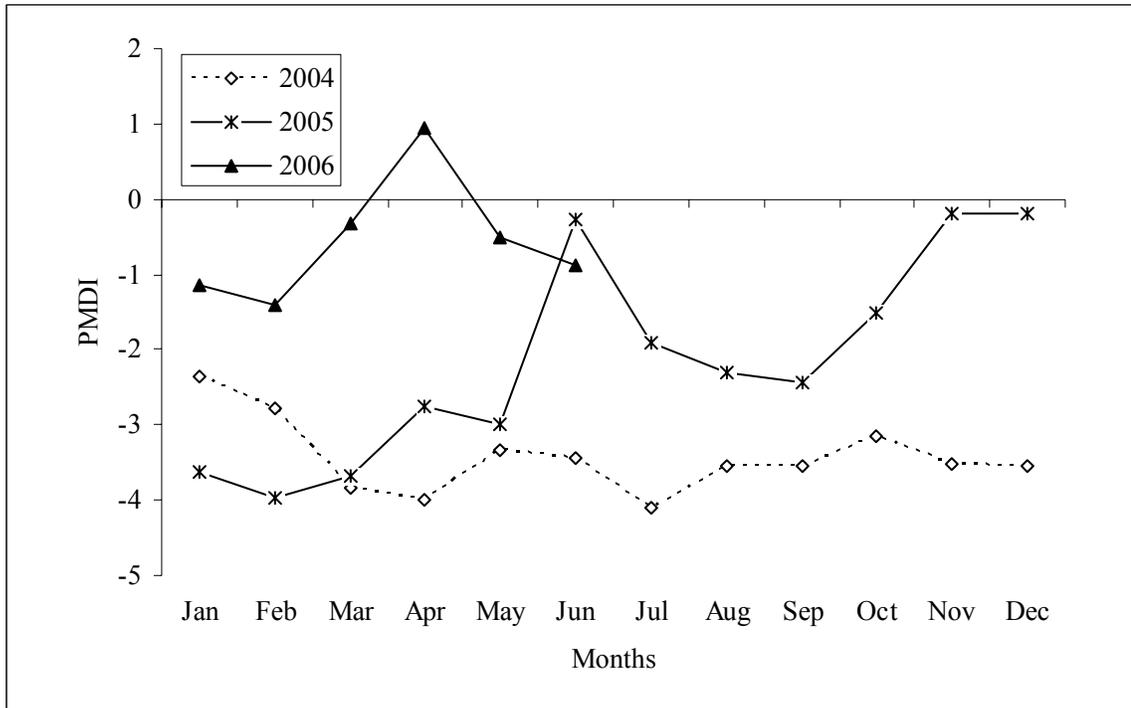
APPENDIX B:

PRECIPITATION AND PALMER DROUGHT SEVERITY INDEX  
FOR CENTRAL MONTANA.

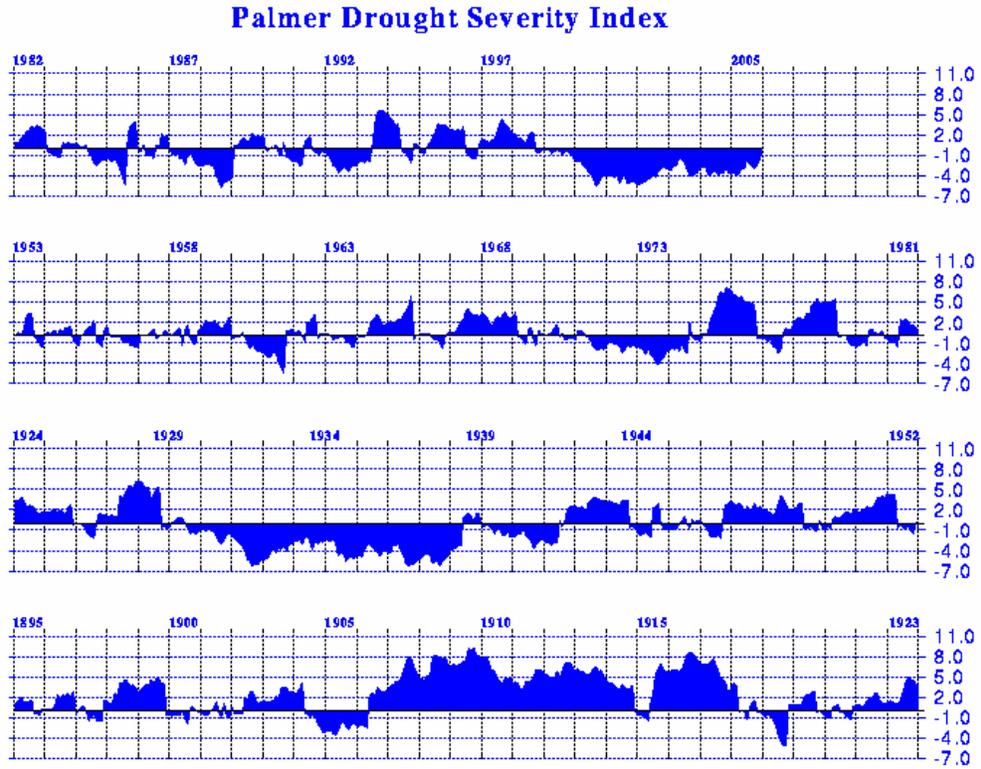
Appendix B1. Precipitation (inches) departure from normal for Roundup, Montana (Musselshell County) during 2004-2005 (National Oceanic and Atmospheric Administration [NOAA] 2006). Data were incomplete for January 2004.



Appendix B2. Modified Palmer Drought Severity Index (PMDI) for central Montana during a relatively dry period (2004) and wet period (2005). Negative PMDI values represent drought conditions whereas more positive values represent relatively mesic conditions (NOAA 2006). Data were incomplete after July 2006.



Appendix B3. Palmer Drought Severity Index (average monthly variation in precipitation) for central Montana, 1895-2005. Negative PMDI values represent drought conditions whereas more positive values represent relatively mesic conditions (NOAA 2006).



**Montana - Division 04: 1895-2005 (Monthly Averages)**

APPENDIX C:

UNPUBLISHED GREATER SAGE-GROUSE LEK COUNT DATA  
IN MUSSELSHELL AND GOLDEN VALLEY COUNTIES FROM  
MONTANA FISH, WILDLIFE AND PARKS, 1993-2005.

Appendix C1. Unpublished counts of male sage grouse at leks known to exist from Montana Fish, Wildlife, and Parks Region 5, 1993-2005.

County	Lek	Year												
		1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
Musselshell	SG-24	19	20	21	7	18	25	22	25	25	16	26	33	23
	SG-25	10	10	22	21	16	20	19	26	14	8	6	11	9
	SG-27	4	2	0	2	0	2	3	0	0	0	0	0	0
	SG-29	16	25	31	40	21	39	31	106	81	69	58	30	43
	SG-31	49	23	26	24	22	26	16	24	35	22	24	22	33
	Devil's Basin 1			41	44	23	57	47	52	65	43	62	52	37
	Schmeckel's			8	12	11	26	26	39	23	19	29	20	34
	Adolph BLM				3	7	9	14	24	24	22	23	13	11
	Devil's Basin 2							29	51	51	25	45	24	53
	Graves 2								37	33	20	15	8	6
	Crooked Creek 2								37	31	25	20	22	15
	Eagle Post										10	30	23	41
Nirvana										14	11	7	10	
Golden Valley	SG-2	29	19	19	22	30	32	49	92	69	54	71	76	64
	SG-5	52	22	32	39	32	44	78	102	104	60	64	73	58
	SG-9	31	23	12	27	46	33	38	45	65	35	32	59	34
	SG-11	22	17	27	19	31	27	42	42	50	41	39	19	20
	SG-17	39	21	21	34	7	27	22	41	34	18	23	17	38
	SG-39	30	27	32	21	30	22	39	54	52	50	41	53	55
	SG-43	39	25	16	11	35	25	40	88	77	47	52	47	39
	SG-45	5	0	5	6	8	12	16	14	18	16	27	17	9
	SG-34	21	20	22	21	12	22	24	8	12	9	14	7	7
	SG-2s	11	8	11	15	6	0	0	0	1	0	0	0	0
	SG-36	22	10	11	8	16	15	21	33	35	31	35	50	38
	Barber N.								21	23	16	16	13	8
	Lone Pine										11	11	9	5
	C-Lek										19	25	43	32

Appendix C2. Unpublished lek count data for leks known to exist and periodically counted for Montana Fish, Wildlife, and Parks Region 5, 1997-2005.

County	Lek	Year								
		1997	1998	1999	2000	2001	2002	2003	2004	2005
Musselshell	4- Mile 2	5	8	-	15	26	-	-	-	-
	Devil's Pocket	-	-	14	14	-	-	-	-	16
	Getchell Coulee	-	-	-	-	10	-	-	-	-
	Howard Coulee 2	-	-	-	7	37	-	-	-	-
	Jones Creek 1	-	-	30	-	-	-	-	-	-
	Keggy Coulee	-	-	34	43	55	-	-	-	-
	Little Wall	-	-	-	15	-	2	-	-	-
	Mclean Coulee	-	-	-	-	4	-	-	-	-
	N. Willow Creek 1	7	-	-	20	-	-	-	-	-
	N. Willow Creek 2	-	-	-	-	25	-	-	-	-
	Ridge Road	-	-	-	-	3	-	-	-	-
	Sand Creek	-	-	-	20	10	4	-	-	7
	Sand Creek 2	-	-	-	-	31	-	-	-	-
	Temp 2	-	-	-	3	6	-	-	-	-
	Temp 3	-	-	-	-	2	-	-	-	-
	Wilson Coulee	-	-	-	-	3	-	-	-	-
Lost Wacker	-	-	-	-	-	-	-	15	28	
Totals		12	8	78	137	212	6	0	15	51
Golden Valley	Lek									
	Lone Pine	-	-	5	†	†	†	-	-	-
	Temp 7	-	-	-	-	-	7	-	-	-
	Temp 8	-	-	-	-	-	3	-	0	0
	Cushman	-	-	-	-	-	-	-	-	16
	Farm Ground	-	-	-	-	-	-	-	-	6
	Plateau	-	-	-	-	-	-	-	-	18
	Sika	-	-	-	-	-	-	-	-	17
Totals		0	0	5	0	0	10	0	0	57
Both Counties	Grand Total	12	8	83	137	212	16	0	15	108

† See Appendix C1.

APPENDIX D:

SEASONS FOR SURVIVAL ANALYSES IN  
CENTRAL MONTANA DURING 2004-05.

Appendix D1. Dates of seasons, number of encounter occasions, and season length for each season in each year for survival analyses of female sage grouse in Musselshell (hunted) and Golden Valley (nonhunted) counties, Montana during 2004-05.

Season	2004			2005		
	Dates	Num. occasions	Length (days)	Dates	Num. occasions	Length (days)
Nesting	15 Apr - 21 Jun	67	68	16 Apr - 8 Jul	83	84
Late-summer	22 Jun - 31 Aug	70	71	9 Jul - 31 Aug	53	54
Hunting	1 Sept - 1 Nov	61	62	1 Sept - 1 Nov	61	62
Overwinter	2 Nov - 14 Apr	163	164	2 Nov - 8 Apr	157	158

APPENDIX E:

2003 FIELD SEASON.

Appendix E1. I decided to omit the 2003 data that were collected for this study for three reasons. First, during the 2003 field season, there was a problem with the fit of the radio-collars on female sage grouse. As soon as we realized that there was a problem we immediately attempted to recapture all radio-collared females to assess their body condition. If we determined that a female was in poor or questionable body condition, we removed the radio-collar and released the female without a collar. If we decided the female was in good body condition, we re-fit the collar and released her. Second, we did capture females during late summer in 2003 on the hunted site. However, the majority of these females were captured in harvested wheat fields (“stubble” fields) and half of the newly marked sample died soon after capture. We suspect that this had something to do with either body condition (and lower probability of survival) and susceptibility to capture by investigators or that females in stubble fields had a lower probability of survival compared to their counterparts. Regardless, the sample may not have been random. Third, on the nonhunted site, only two radio-marked females were alive at the beginning of the hunting season, and one of those was outside the area that was closed to hunting, reducing our sample size to one for that site in that year.