# ECOLOGY OF GREATER SAGE-GROUSE IN THE DAKOTAS

**BY**

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This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that conclusions reached by the candidate are necessarily the conclusions of the major department.

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# DEDICATION

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# ABSTRACT

## ECOLOGY OF GREATER SAGE-GROUSE IN THE DAKOTAS

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Greater sage-grouse (*Centrocercus urophasianus*) populations and the sagebrush (*Artemisia* spp.) communities that they rely on have dramatically declined from historic levels. Moreover, information regarding sage-grouse annual life-history requirements at the eastern-most extension of sagebrush steppe communities is lacking. Understanding the ecology of sage-grouse in this region is essential for developing management strategies and to ensure future viability of populations in the Dakotas. This dissertation addresses factors that influence sage-grouse survival, winter habitat use, seasonal movements, and brood breakup based on research conducted from 2005-2007 in southwest North Dakota and from 2006-2008 in northwest South Dakota. Identifying critical periods of survival in sage-grouse during their annual life-cycle is important to support biologically based management actions. I evaluated factors influencing survival of 219 breeding-age (≥1 year of age) and juvenile (≥10 weeks of age) radio-marked sage-grouse using known-fate models in program MARK. I evaluated factors influencing annual (1 Mar – 28 Feb) and seasonal survival during five periods that reflected the chronology of their life-cycle in this region including: breeding (1 March – 15 April), nesting (16 April – 15 June), early brood-rearing (16 June – 15 July), late brood-rearing

(16 July – 31 October), and winter (1 November – 28 February). Survival was generally high except during the late-brood rearing period when there was high mortality (>50%) related to West Nile outbreaks and predation. Low recruitment compounded by the negative effects of West Nile virus may limit the sustainability of the low density sage-grouse population in this region. I also evaluated factors influencing sage-grouse winter habitat use in North Dakota 2005-06 and 2006-07 and in South Dakota 2006-07 and 2007-08. I used conditional logistic regression to test competing models of winter habitat use at used (*n* = 340) and 250 (*n* = 340) and 500 m (*n* = 340) dependent random sites from 124 radio-marked sage-grouse. Percent sagebrush canopy cover was the primary factor influencing winter habitat use in this region. Habitat used by sage-grouse was characterized by 7.6% higher sagebrush canopy cover than at random sites. My results indicated that sagebrush canopy cover (15%) and sagebrush height (20 cm) meet their winter habitat requirements during mild winters. Management should focus on avoiding additional loss of sagebrush habitat, identifying areas of critical winter habitat, and implementing management actions based on causal mechanisms (e.g., soil moisture, precipitation) that affect sagebrush community structure in this region. Movement behavior of sage-grouse varies by region and may be affected by the configuration of seasonal habitats. I documented movements of sage-grouse in the Dakotas during all aspects of their life-cycle to evaluate the timing and frequency of sage-grouse migration, estimating migratory and non-migratory sage-grouse survival, evaluating seasonal distribution and core seasonal ranges, and estimating the timing and distance of natal dispersal by juvenile sage-grouse. I collected 6,072 locations from 219 (97 females, 54

males, 68 juvenile) radio-marked sage-grouse, documented 89 seasonal migrations (21 in ND, 68 in SD) and 158 instances of non-migratory behavior (73 in ND, 85 in SD) during eight migration periods. Sage-grouse populations in this region exhibited mixed migration strategies with most (58%) birds considered resident. Average distance moved by migratory sage-grouse between breeding/nesting and summer range was 11.1 and 9.6 km, summer and winter range was 11.8 and 16.8 km, and winter and breeding range was 6.5 and 15.8 km in North Dakota and South Dakota, respectively. Timing of spring migration coincided with abandonment of leks by males and age of chicks (i.e., 3-4 weeks) for females. Timing of migration from summer to winter and winter to breeding ranges was less obvious, as movements were gradual and occurred over several months. Survival of migratory sage-grouse differed in North Dakota ($P = 0.03$) and was similar in South Dakota ($P = 0.50$) to non-migratory sage-grouse and did not differ among males ($P = 0.88$) and females ($P = 0.84$). Median date of natal dispersal of juveniles ($n = 11$) was 7 January (range = 15 October to 15 April) with a median dispersal distance of 11.7 km that was similar between females and males ($P = 0.13$) and between study areas ($P = 0.24$). Evidence of migration in this population indicates that highly interspersed seasonal habitats may not completely regulate migration. Mild winter weather, tradition, and behavioral plasticity may have influenced migration rate. Because of recent population declines, management of sage-grouse in this region may need to focus on maintaining or increasing population sizes to prevent loss of gene flow because sage-grouse rarely migrated outside the study areas and emigration rates appear to be low. I captured and relocated 29 radio-marked broods of sage-grouse to identify movement patterns, timing, and juvenile survival associated with brood breakup during 2005-2006 in North Dakota and 2006-2007 in South Dakota, respectively. Median date of brood breakup was 4 October (range = 17 Jul – 8 Nov) when juveniles reached a median age of 134 days (range = 38–173). Timing of brood breakup was independent of gender, juvenile age, brood female age, or study area. Brood breakup was usually initiated by the female and juveniles dispersed within days of the female abandoning the brood. Survival of juveniles from 10 weeks of age to 1 March was lower ($P < 0.01$) for orphaned juveniles (31.8 ± 0.10%) compared to juveniles (72.2 ± 0.11%) from broods that stayed with the female until brood breakup. Mortality to sage-grouse brood females before brood breakup appears to be additive to the survival of juveniles when population densities are low.

# TABLE OF CONTENTS

Page

## LIST OF TABLES

Table

# LIST OF FIGURES

Figure

# LIST OF APPENDICES

Appendix

# CHAPTER 1

# INTRODUCTION

The distribution and abundance of greater sage-grouse (*Centrocercus urophasianus*) populations and the sagebrush (*Artemisia* spp) communities they occupy have declined throughout most of their range since the onset of European settlement. Sage-grouse were once prevalent in at least 13 states and 3 provinces of Canada and presently occupy 11 states and 2 provinces and their distribution has decreased by 45% across North America (Schroeder et al. 2004). Populations have declined range-wide by 3.5% per year from 1965 to 1985 and 0.4% per year from 1986 to 2003 (Connelly et al. 2004). Because sage-grouse are dependent upon sagebrush to maintain their life-history needs (Patterson 1952), loss of sagebrush communities have been detrimental to this species.

Sage-grouse populations have declined primarily due to habitat loss, degradation, and fragmentation (Connelly and Braun 1997, Braun 1998, Wirth and Pyke 2003). However, several other factors have contributed to the decline in sage-grouse populations and altered sagebrush ecosystems including: changes in fire regimes (Connelly et al. 2004), conversion of sagebrush for grass and crop production (Braun et al. 1977), disease (Naugle et al. 2005), drought (Connelly and Braun 1997), energy development (Remington and Braun 1991, Braun 1998), excessive grazing (Dobkin 1995), predation (Braun 1998, Willis et al. 1993), pesticides (Blus et al. 1989), and roads, power-lines, and urbanization (Braun 1998). Consequently, greater sage-grouse and Gunnison sage-grouse (*Centrocercus minimus*) have had least nine petitions to list them as a threatened or endangered by the U.S. Fish and Wildlife Service under the Endangered Species Act; however, findings have concluded that they have not been warranted for listing (U.S. Department of the Interior 2005).

Greater sage-grouse are distributed across extreme southwest North Dakota and northwest South Dakota where the eastern most extension of sagebrush steppe communities occur (Figure 1-1; Schroeder et al. 1999). Sage-grouse populations in the Dakotas have been genetically linked to neighboring populations (e.g. Alberta, Montana, Wyoming; Oyler-McCance et al. [2005]) and are thought to be continuous with larger populations in eastern Montana and Wyoming (Smith et al. 2004). Populations of sage-grouse in North Dakota and South Dakota have declined from historic estimates. From 1985 to 1994, populations in North Dakota and South Dakota declined by an estimated 27 and 45%, respectively (Connelly and Braun 1997). The number of active leks has remained unchanged due to the discovery of new leks in the region; however, most abandoned leks occur in the eastern portion of their distribution in the Dakotas (Smith et al. 2004). Yet, steady declines in the numbers of males attending leks have occurred in North Dakota and South Dakota since population monitoring began (Smith et al. 2004). Consequently, sage-grouse are listed as a priority level 1 species of concern in both North Dakota and South Dakota. Because of population declines and limited knowledge of their population dynamics, research on all aspects of their annual life-cycle is critical to understanding their ecology and improving management in this region.

Sage-grouse populations are characterized by their low productivity, as adults often have high survival and recruitment of juveniles is generally low (Crawford et al.

2004). Sage-grouse are considered habitat obligates, but their use of sagebrush depends on their life-history stage (Patterson 1952, Connelly et al. 2003*a*). Habitat management is critical to sage-grouse populations because it is one of the few areas where research has shown that productivity can be altered (Crawford et al. 2004). Previous research in the Dakotas has shown that sage-grouse have high nest initiation rates (95% in ND, 96% in SD), low renesting rates (9.5% in ND, 28.6% in SD), low to moderate nest success (31% in ND, 47.9% in SD), and poor recruitment (15% in ND, 6% in SD) (Herman-Brunson 2007, Kaczor 2008). They also determined that nesting and brood-rearing habitat was characterized by short, low density sagebrush cover with higher grass cover than in core sage-grouse range. However, information regarding annual ecology (i.e., survival, seasonal movements, brood breakup) and winter habitat use of sage-grouse is not available in this region.

Understanding factors that influence survival of sage-grouse is important because of the long-term decline of this species and because future population growth is sensitive to the abundance and survival of breeding-age (≥1 year) females (Moynahan et al. 2006). Identifying critical periods of survival during their annual life-cycle is important to support biologically based management actions (Moynahan et al. 2006). However, biologists are usually forced to make educated guesses pertaining to factors that influence survival and the annual maintenance of sage-grouse populations. Mortality in sage-grouse has been shown to vary by age, gender, year, and season (Zablan 2003, Moynahan 2006) and is primarily caused by predation or hunter harvest (Connelly et al. 2000, Connelly et al. 2003*b*) and more recently West Nile virus (Walker et al. 2004, Naugle et al. 2005). Models that examine the variation in survival rates of avian species across groups and time are important for understanding the life history of a species (Cezilly et al. 1996). However, no information exists regarding factors influencing survival of sage-grouse at the eastern edge of their range.

During the winter, sage-grouse are dependent on sagebrush for food and cover (Wallestad et al. 1975); however, deep snow can limit the amount of available sagebrush (Hupp and Braun 1989). Winter habitat tends to be limited compared to other seasonal habitats (Beck 1977, Remington and Braun 1985) and its availability influences sage-grouse distributions (Hanf et al. 1994). Therefore, identifying region-specific winter habitat requirements may be critical because the persistence of sage-grouse populations could be disproportionately affected by degradation of winter habitat (Doherty et al. 2008). Furthermore, characterization of sage-grouse winter habitat is important because it allows land-use management agencies to assess current habitat conditions and develop management strategies aimed at the conservation of critical habitats. Currently, no information is available that describes sage-grouse winter habitat use in this region. This information may be important because species at the edge of their range may use habitats differently than in core areas (Channell and Lomolino 2000).

Movement between seasonal ranges (i.e., winter, breeding, summer) is common in many populations of sage-grouse (Connelly et al. 2004). Proximity to seasonal habitats has been suggested to be a factor contributing to whether populations are migratory or resident (Berry and Eng 1985). Many species migrate in response to environmental conditions or because of temporal and spatial variation in resource abundance (French et al. 1989). Nevertheless, the underlying factors that influence seasonal movements of sage-grouse are poorly understood. Migration in sage-grouse has been suggested to occur in response to severe winter weather, seasonal habitat differences, and because of site fidelity (Berry and Eng 1985, Connelly et al. 1988, Schroeder and Robb 2004). Although sage-grouse may migrate long distances between seasonal ranges (Connelly et al. 1988), it is unknown whether migration strategies can differ among individual sage-grouse in the same population. Furthermore, knowledge of dispersal movements is limited (Dunn and Braun 1985), but it could be important because it may affect the genetic maintenance of populations (Pitman et al. 2006).

Identifying movement patterns of juvenile grouse is challenging because they tend to be secretive, difficult to capture, and have the ability to move large distances when they separate from their parent (Hannon and Martin 2006). Brood breakup in sage-grouse has been suggested to occur when juveniles are 10-12 weeks of age (Patterson 1952) and independent of dispersal movements (Browers and Flake 1985). Juvenile sage-grouse become independent when they separate from the brood (i.e., brood breakup) during late summer and early fall. Prior knowledge of brood breakup was based on probable broods or field observations (Patterson 1952, Browers and Flake 1985) and no studies have been conducted over large regional scales to evaluate the timing and movement patterns associated with brood breakup in sage-grouse. This information could provide new insight into the life-history requirements for this species.

# OBJECTIVES

My primary research objectives for this study were to: 1) estimate annual and seasonal survival rates and evaluate factors that influence survival during their annual life-cycle for breeding-age (≥1 year of age) and juvenile (≥10 weeks of age) sage-grouse, 2) evaluate factors that influence winter habitat use by sage-grouse, 3) evaluate regional patterns of sage-grouse seasonal movements (e.g., migration, dispersal), 4) evaluate patterns of their seasonal distribution and core seasonal ranges, 5) estimate the timing and distance of natal dispersal by juvenile sage-grouse, and 6) identify patterns of movement, timing, and juvenile survival associated with brood breakup of sage-grouse.

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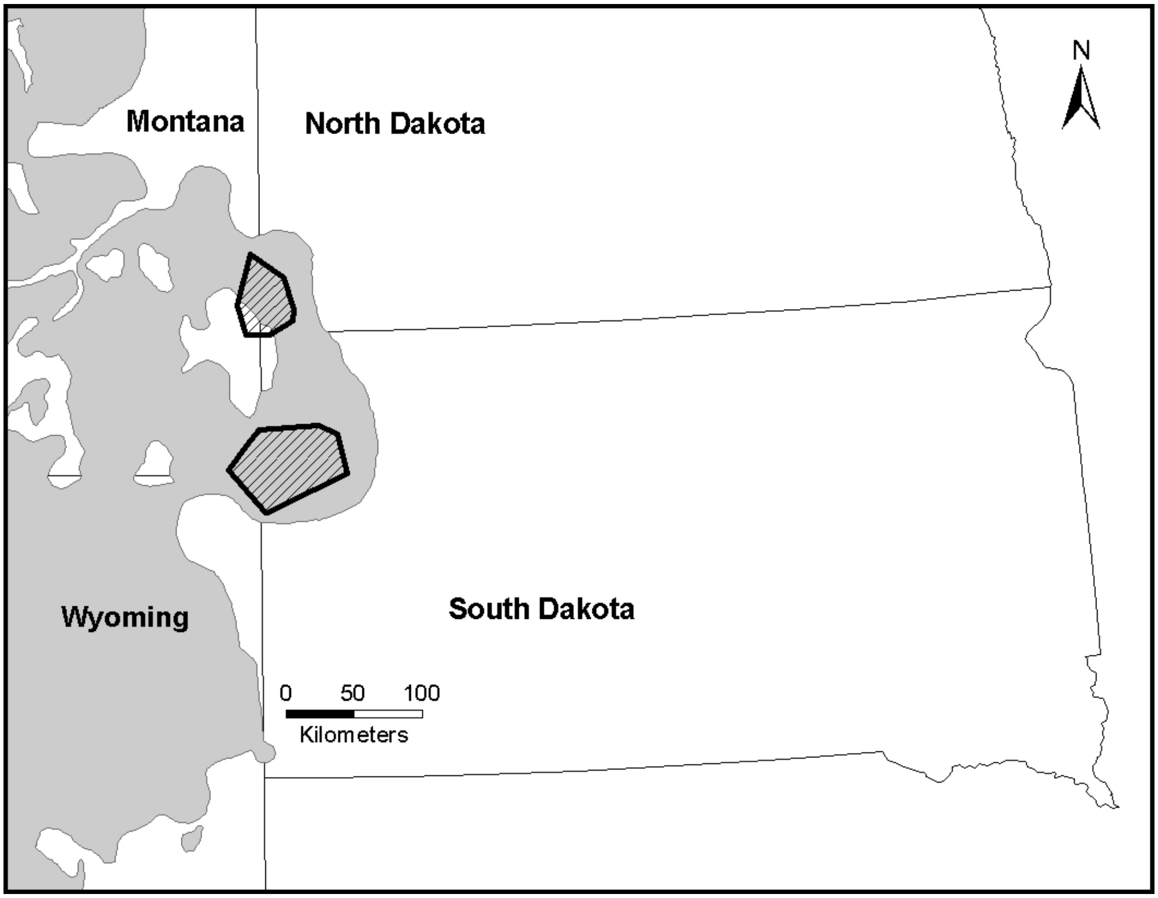

Figure 1-1. Study areas for sage-grouse research during 2005–2007 in North Dakota and 2006–2008 in South Dakota. The light grey shaded area encompasses known sage-grouse range (Schroeder et al. 2004) and the dashed area represents 100% minimum convex polygon of sage-grouse locations during this study.

# CHAPTER 2

# FACTORS INFLUENCING SURVIVAL OF GREATER SAGE-GROUSE IN THE DAKOTAS

**Abstract:** Identifying critical periods of survival in greater sage-grouse (*Centrocercus urophasianus*) during their annual life-cycle is important to support biologically based management actions. However, there is limited knowledge of survival of sage-grouse populations. I evaluated factors influencing survival of 219 breeding-age (≥1 year of age) and juvenile (≥10 weeks of age) radio-marked sage-grouse during 2005-2007 in North Dakota and during 2006-2008 in South Dakota. I used known-fate models in program MARK to evaluate factors influencing annual (1 Mar – 28 Feb) and seasonal survival during five periods that reflected the chronology of their life-cycle in this region including: breeding (1 Mar – 15 Apr), nesting (16 Apr – 15 Jun), early brood-rearing (16 Jun – 15 Jul), late brood-rearing (16 July – 31 Oct), and winter (1 Nov – 28 Feb). Survival was generally high except during the late-brood rearing period when there was high mortality (>50%) related to West Nile outbreaks and predation. Low recruitment compounded by the negative effects of West Nile virus may limit the sustainability of the low density sage-grouse population in this region.

*Key words*: *Centrocercus urophasianus*, greater sage-grouse, known-fate models, predation, program MARK, survival, West Nile virus.

# INTRODUCTION

Understanding demographic processes are fundamental to determine whether populations are likely to persist (Holsinger 2000). Estimation of survival in animal populations is necessary because it allows biologists to identify factors influencing vital rates and changes in population size (Murray and Patterson 2006). Populations of greater sage-grouse (*Centrocercus urophasianus*) are characterized by low recruitment and high adult survival (Schroeder et al. 1999, Connelly et al. 2004, Crawford et al. 2004). However, despite their high reproductive capability (Crawford et al. 2004), breeding populations have declined from their historic levels (Connelly and Braun 1997). Conversion of sagebrush (*Artemisia* spp.) to crops and grasslands, fragmentation, and deterioration of ecological condition in sagebrush communities have acted as a catalyst for the range-wide decline of sage-grouse populations (Connelly and Braun 1997, Braun 1998).

Several factors may directly or indirectly affect sage-grouse populations including: disease (Naugle et al. 2005), drought (Connelly and Braun 1997), energy development (Braun 1998, Lyon and Anderson 2003), fire (Fischer et al. 1996, Pedersen et al. 2003), herbicides and insecticides (Ward et al. 1942, Blus et al. 1989), hunting (Connelly et al. 2003), livestock grazing (Beck and Mitchell 2000), predation (Braun 1998, Willis et al. 1993, Schroeder and Baydack 2001), and roads, power-lines, and urbanization (Braun 1998). Because population declines have occurred range-wide and are not limited to specific regions, knowledge of factors influencing survival is necessary for improved adaptive management of sage-grouse. Identifying critical periods of survival during their annual life-cycle also is important to support biologically based management actions (Connelly et al. 2004, Moynahan et al. 2006). Additionally, predictive models that examine the variation in survival rates among groups and over time are important for understanding the life history of a species (Cezilly et al. 1996).

Previous research on sage-grouse survival has emphasized survival of translocated birds (Musil et al. 1993, Baxter et al. 2008), annual survival estimation from band-recovery data (Zablan et al. 2003), temporal variation in annual survival (Moynahan et al. 2006), and estimation of juvenile survival from 10 weeks of age to recruitment (Beck et al. 2006). However, information regarding factors influencing annual and seasonal survival of sage-grouse at the eastern edge of their range does not exist. The purpose of this study was to estimate annual and seasonal survival rates and evaluate factors that influence annual and seasonal survival during all biological periods (breeding, nesting, early brood-rearing, late brood-rearing, and winter) for breeding-age (≥1 year of age) and juvenile (≥10 weeks of age) sage-grouse in North Dakota and South Dakota. I hypothesized that predation would be the main source of mortality and annual survival would be affected by high periods of mortality during late summer because of West Nile outbreaks.

## STUDY AREA

This study was conducted in Bowman County, North Dakota (46º 7' 22.368″ N, 104º 0' 24.318″ W) and Butte County, South Dakota (45º 1' 52.329″ N, 103º 44' 41.196″ W) and adjacent parts of Montana and Wyoming. This region was semiarid sagebrush rangeland characterized by gentle slopes to steep buttes and ridges with elevations that ranged from 640 to 1225 m above sea level (Opdahl et al. 1975, Johnson 1976). Vegetation in this region was described by Opdahl et al. (1975), Johnson (1976), and Johnson and Larson (1999) and was considered low shrubland with short- to mid-grass prairie being dominant. Shrubs in the area were dominated by Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*), but also included silver sagebrush (*Artemisia cana* spp. *cana*), broom snakeweed (*Gutierrezia sarothrae*), rubber rabbitbrush (*Ericameria nauseosus*), and greasewood (*Sarcobatus vermiculatus*). Common perennial grasses were green needle-grass (*Nassella viridula*), Junegrass (*Koeleria macrantha*), western wheatgrass (*Pascopyrum smithii*), Kentucky bluegrass (*Poa pratensis*), Japenese brome (*Bromus japonicus*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), buffalograss (*Buchloe dactyloides*), needleandthread (*Hesperostipa comata)*, and little bluestem (*Schizachrium scoparium)*. Common forbs were common dandelion (*Taraxacum officinale*), textile onion (*Allium textile*), field pennycress (*Thlaspi arvense*), and western yarrow (*Achillea millefolium*). Land use was dominated by livestock grazing; 45% of Bowman County and 5% of Butte County was farmed for cultivated crops.

The climate was continental with cold dry winters and warm summers with most of the precipitation occurring in late spring and early summer. Average monthly temperatures in North Dakota were -9.7 ºC in January and 20.8 ºC in July with average annual precipitation and snowfall of 39.4 and 122.7 cm, respectively. Average monthly temperatures in South Dakota were -4.8 ºC in January and 22.7 ºC in July with average annual precipitation and snowfall of 45.54 and 89.9 cm, respectively (National Climatic Data Center 1971-2000).

## METHODS

### *CAPTURING AND MARKING*

I captured breeding-age sage-grouse near leks during the breeding season and juveniles from early July to mid September at night using spotlights (Giesen et al. 1982, Wakkinen et al. 1992) and a thermal infrared imaging camera. Hens were fitted with a necklace-type radio transmitter (model A4060, Advanced Telemetry Systems, Isanti, Minnesota) with an 8-hour mortality switch that weighed 21.6 g, and had an expected battery life of 434 days. Males were fitted with a backpack-type radio transmitter (model A1135, Advanced Telemetry Systems, Isanti, Minnesota) with an 8-hour mortality switch that weighed 17.9 g, and had an expected battery life of 297 days. I classified birds as adults (≥2 years old, second or later breeding season), yearlings (≥1 years old, first breeding season), or juvenile (≥10 week of age) based on the length and shape of the 9th and 10th primaries (Beck et al. 1975) and assigned gender based on plumage characteristics (Bihrle 1993). All radio-transmitters were less than 3% of the body weight of birds at the time of attachment. All capture and handling protocols were approved by the South Dakota State University Institutional Animal Care and Use Committee (approval number: 07-A032).

### *TELEMETRY*

I located radio-marked sage-grouse from 1 April 2005 to 28 February 2007 in North Dakota and from 1 April 2006 to 28 February 2008 in South Dakota. Radio-marked sage-grouse were located ≥1 times per week with a receiver and hand-held antenna or by fixed wing aircraft with 2-element Yagi antennas mounted on wing struts. All locations were recorded with a Global Positioning System (GPS) receiver in Universal Transverse Mercator (UTM) coordinates (NAD27; UTM Zone 13).

### *PROBABLE CAUSES OF MORTALITY*

Mortality was assessed via evidence collected at the death site, field necropsy, or laboratory examination. Because of the lag-time in recovery of carcasses and the potential for scavengers to move carcasses or mask true mortality cause (Bumann and Stauffer 2002), I refer to "probable causes of mortality." I classified the probable cause of mortality as predation if evidence at the kill site contained dorsal guard hairs, feces, tracks, and pulled tendons, bite or puncture marks on carcass or radio-transmitter. I further classified predation deaths as mammal or raptor if there was sufficient evidence at the death site. Potential predators that were observed during this study included: golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*), rough-legged hawk (*Buteo regalis*), prairie falcon (*Falco mexicanus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), and American badger (*Taxidea taxus*). I considered deaths to be accidental if the bird was killed by collision with a power-line or fence-line or if it died from being dismembered by farm machinery. I classified deaths as unknown when only a transmitter was found or when several feathers were the only evidence at the kill site. I recovered all transmitters emitting a mortality pulse upon detection to limit potential sources of error caused by scavengers (Hagen et al. 2007) and to collect remaining tissues to test for West Nile virus.

I sent remaining sage-grouse parts (i.e., carcass, head, bones, tissue) to test for West Nile virus if deaths occurred from June through October. Samples were evaluated for West Nile virus at veterinary laboratories by complete necropsy and microscopic examination of tissues (Naugle et al. 2005). Real Time Polymerase Chain Reaction (Shi 2001) and immunohistochemistry (IHC; Kiupel et al. 2003) analysis was used to test for West Nile virus. West Nile virus was confirmed when these tests were positive by isolation of the virus from 1 or more tissues (brain, heart, kidney, or bone marrow) in Vero cell cultures (Steele et al. 2000).

### *DATA ANALYSIS*

I estimated survival using the Kaplan-Meier method modified for staggered entry (Kaplan and Meier 1958, Pollack et al. 1989) in Program MARK 4.1 (White and Burnham 1999). I right-censored grouse if they disappeared from the study area and were never relocated, when they could not be accessed on private lands, or because of radio-transmitter failure.

I developed multiple sets of competing models to explain the annual and seasonal variation in survival of sage-grouse. I used program MARK to evaluate support for all candidate known fate models using an information-theoretic approach (Burnham and Anderson 2002). I constructed models using the design matrix tool and a logit link function in Program MARK. Models were selected models based on Akaike Information Criterion ($AIC_c$) corrected for small sample size and Akaike weights ($w_i$) (Burnham and Anderson 2002). Akaike weight represented the probability of a model being the best approximating model of those evaluated (Burnham and Anderson 2002). I removed models from the analysis when pretender variables were evident in models with $\Delta$AIC $\leq 2$ of the highest ranked model (Burnham and Anderson 2002). Models with $\Delta$AIC $>10$ were considered non-significant and were not presented (Burnham and Anderson 2002). I computed model-averages when the difference in $AIC_c$ values between the most supported and alternative models were $\leq 2$ (Burnham and Anderson 2002). Model averaging allowed me to compute seasonal survival and asymmetric logit-transformed 95% confidence intervals surrounding survival estimates.

I evaluated factors influencing annual (1 Mar – 28 Feb) survival using monthly intervals and five individual covariates: age (adult, yearling, or juvenile), study area (North Dakota or South Dakota), year (2005, 2006, or 2007), gender, and West Nile virus (months [Jul-Oct] where mosquitoes [*Culex tarsalis*], the primary vector of West Nile virus in sage-grouse [Naugle et al. 2005] occurred). I used 1 March (start of breeding period) as the start of the annual period because classification of age (adult or yearling) of sage-grouse changed based on age during first or second breeding seasons. Because breeding-aged sage-grouse tend to have higher survival than juveniles (Crawford et al. 2004), I hypothesized that age could significantly contribute to variation in survival. Gender was examined to evaluate if survival was influenced by the inherent risks that males (e.g., displaying on leks) and females (e.g., nesting and brood-rearing activities) have during their annual life-cycle. I examined the effect of study area to account for spatial. Temporal effects (i.e., month, year, West Nile virus) were included in the models because they potentially explain variation not specifically addressed in any other sources of variation.

After interpretation of the annual model set, I conducted a second analysis to evaluate seasonal variation of survival using weekly intervals during five time periods indicative of the chronology of sage-grouse life-history in the Dakotas including: breeding (1 Mar – 15 Apr), nesting (16 Apr – 15 June), early brood-rearing (16 June – 15 July), late brood-rearing (16 July – 31 Oct), and winter (1 Nov – 28 Feb). This allowed me to evaluate trends in mortality that were evident from output of the annual survival models. I included the following covariates: age, gender, study area, and year using weekly intervals in all candidate sets of seasonal survival. I did not construct all reduced parameter models, as this would have resulted in superfluous model building.

For the nesting season analysis, I hypothesized that nesting status (nest initiation and nest fate) would influence hen survival. Specifically, nest initiation was examined to determine if nesting hens would have a lower probability of survival than non-nesting females. Nest fate was examined to determine if success of the nesting hen caused survival to differ from hens with nests that failed because of their increased incubation time.

I divided the brood-rearing period into two seasons: early and late because of the differences in brood behavior and food requirements during these periods (Berry and Eng 1985, Drut et al. 1994). During the early brood-rearing period, chicks 8-10 days old brood with the hen to thermoregulate (Boggs et al. 1977), they mainly consume insects for the first 1-2 weeks of life (Drut et al. 1994), and they remain close to the nest for the first 2-3 weeks of life (Berry and Eng 1985). I used the variable brood to examine whether hens that had a brood during the early and late brood-rearing seasons had a lower probability of survival than broodless hens.

Because known-fate data modified for staggered entry produces survival estimates for each group within the saturated model, the deviance of the saturated model from itself cannot be estimated. Thus, there is no reliable goodness-of-fit test for known-fate data because the saturated model fits the data perfectly (Cooch and White 2008).

## RESULTS

I fitted 219 (97 breeding-age females, 54 breeding-age males, 68 Juvenile) sage-grouse with radio-transmitters. Of these, I captured 86 birds (34 in 2005, 52 in 2006) in North Dakota and 133 birds (80 in 2006, 53 in 2007) in South Dakota, respectively. I maintained adequate sample sizes throughout the study: average weekly sample size during this study (*n* = 45) was larger than the minimum of 40 required for precise survival estimates (Pollack et al. 1989). I right-censored the encounter histories of 20 birds because of collar failure (45%), lost signal (45%), or failed access to private land (10%). I included 199 birds in the analysis.

### *ANNUAL SURVIVAL*

Of the 15 candidate models of annual survival, the most supported model ($AIC_c$ weight = 0.83) of sage-grouse survival included the effects of month and year (Table 2-1). The effect of month was significant during August ($\beta = -2.71$, 95% CI -4.14—-1.27), September ($\beta = -2.51$, 95% CI -3.96—-1.06), and October ($\beta = -2.51$, 95% CI -3.96—-1.06). The confidence interval for the coefficient overlapped zero during the remaining months. Monthly survival rate, during the period that *C. tarsalis* mosquitos carrying

West Nile virus occurred (Jul-Oct), was 0.87 (SE = 0.01) and was lower than monthly survival rate during other months (Nov-June; $S = 0.97$, SE < 0.01).

Annual survival estimates ranged from 0.351 (SE = 0.06) to 0.73 (SE = 0.09) (Table 2-2). Survival of females ranged from 0.41 (SE = 0.07) to 0.78 (SE = 0.06) and male survival ranged from 0.00 to 0.35 (SE = 0.12).

### *SEASONAL SURVIVAL*

#### *Nesting season*

Of the 18 candidate models, the most supported model ($AIC_c$ weight = 0.57) of sage-grouse survival included the additive effects of age and nest fate (Table 2-3). The effect of nest fate ($\beta = 2.00$, 95% CI 0.51–3.51) was positive indicating that nesting females ($S = 0.94$, SE = 0.03) had a higher probability of survival when their nest was successful compared to females that had failed nests or did not nest ($S = 0.71$, SE = 0.12). Survival during the nesting period was 0.84 (SE = 0.04, 95% CI 0.75–0.91) for adults and 0.95 (SE = 0.03, 95% CI 0.85–0.98) for yearlings. Sage-grouse survival during the nesting season was 0.90 (SE = 0.02) and ranged from 0.89 (SE = 0.09) to 0.94 (SE = 0.05; Table 2-4, Appendix 2-A).

#### *Early brood-rearing season*

Study area specific survival was the highest ranked model of the 18 candidate models ($AIC_c$ weight = 0.15); however, constant survival ($\beta = 4.03$, 95% CI 3.41–4.66) in the third ranked model ($AIC_c$ weight = 0.13; Table 2-5) also was competitive indicating that the effect of covariates was minimal during this period. Model-averaged survival estimates during this period was 0.94 (SE = 0.02, 95% CI 0.88–0.98) for adults and 0.95

(SE = 0.02, 95% CI 0.87–0.98) for yearlings. Sage-grouse survival during the early brood-rearing season was 0.94 (SE = 0.03) and ranged from 0.88 (SE = 0.04) to 0.97 (SE = 0.02) (Table 2-4, Appendix 2-B).

### *Late brood-rearing season*

Of the 18 candidate models, gender influenced survival during this period (Table 2-6). Sage-grouse females ($\beta = 2.38$, 95% CI 1.75–3.00) had a higher probability of survival than males ($\beta = 1.74$, 95% CI 1.09–2.38), respectively. The addition of year also was significant in the most supported model. Model-averaged estimates of survival during this period were 0.50 (SE = 0.04, 95% CI 0.42–0.57) and 0.50 (SE = 0.04, 95% CI 0.42–0.58) for adults and yearlings and 0.51 (SE = 0.05, 95% CI 0.40–0.61) for juveniles, respectively. Survival during the late brood-rearing season was 0.59 (SE = 0.03) and ranged from 0.44 (SE = 0.07) to 0.76 (SE = 0.07) (Table 2-4, Appendix 2-C).

### *Winter season*

The highest ranked of the 11 candidate models ($AIC_c$ weight = 0.98) included the additive effects of age and time (Table 2-7). Age dependent survival in the model resulted from higher juvenile ($n = 4$) mortality than adults ($n = 1$) or yearlings ($n = 2$). Time dependent survival was significant in the model because all juveniles died during different weeks. Survival during the winter season for all sage-grouse were 0.94 (SE = 0.02) and ranged from 0.91 (SE = 0.05) to 0.98 (SE = 0.02) (Table 2-4, Appendix 2-D).

### *Breeding season*

Of the 11 candidate models, gender influenced survival during this period as males ($S = 0.79$, SE = 0.07) had lower survival than females ($S = 0.99$, SE < 0.01; Table

2-8). The time-dependent variation in survival occurred during weeks 5 and 6 of the breeding season when all male (*n* = 5) and female (*n* = 1) mortalities occurred. Model-averaged estimates of survival during the period was 0.94 (SE = 0.05, 95% CI 0.76–0.99) for adults and 0.95 (SE = 0.04, 95% CI 0.76–0.99) for yearlings, respectively. Survival during the breeding season was 0.95 (SE = 0.01) and ranged from 0.93 (SE = 0.05) to 0.98 (SE = 0.02), respectively (Table 2-4, Appendix 2-E).

### *PROBABLE CAUSES OF MORTALITY*

I recorded 135 deaths (45 in ND, 90 in SD) during this study. The majority of these deaths occurred from late July to early October (Figure 2-1). Evidence of predation was found at 71% (*n* = 96) of all death sites (Figure 2-2). Of these, I was unable to classify 11 deaths by type of predator, the remaining 58 and 42% of deaths by predation were caused by mammals and raptors (Figure 2-3). I tested 6 birds in 2005, 17 in 2006, and 18 in 2007 for West Nile virus. I confirmed West Nile virus in 7% (*n* = 10) of sage-grouse deaths including: 2 adult females, 1 yearling female, 3 adult males, and 4 juveniles, respectively. The average date of confirmed West Nile virus death was 21 August (range = 20 July to 20 Sept). All intact carcasses found in 2005 (*n* = 1) and in 2007 (*n* = 4) tested positive for West Nile virus. Two deaths (1%) were caused by a late spring snow storm that had freezing rain and approximately 56 cm of snow over a two day period. Both of these birds were hens and were found intact and near a sagebrush shrub. No evidence of a nest (e.g., eggs, nest bowl) was found at the death site of either bird. Two deaths (1%) were considered accidental because one sage-grouse was found dead under a power-line with evidence from collision and another was hit by farm machinery in an alfalfa (*Medicago sativa*) field. I was unable to attribute 19% ($n$ = 25) deaths to any specific cause (Figure 2-2). Seventeen of these unknowns resulted from inconclusive tests for West Nile virus in 2006. The eight remaining were unknown because only a few feathers or only the radio-transmitter was found. Although sage-grouse were hunted during this study, I did not record any deaths from hunting.

## DISCUSSION

### *ANNUAL VARIATION IN SURVIVAL*

Grouse select life-history strategies that maximize their survival and reproduction (i.e., fitness) (Bergerud and Gratson 1988). My results indicated that survival of sage-grouse was year dependent and tended to be higher during the months of November through June and lower during the months of July through October. Previous research suggests that adult sage-grouse have high survival rates (Crawford et al. 2004) resulting in low annual turnover (Zablan 1993, Connelly et al. 1994). Although methods used to estimate survival differed among other studies, I found that annual breeding-age female survival of 64% was similar, while male breeding-age annual survival of 36% was considerably lower than other studies (Crawford et al. 2004). Results from this study indicate that annual sage-grouse survival was influenced by brief periods of high mortality when 54% of all mortalities occurred during the late summer. Timing of mortality during these months coincided with West Nile virus outbreaks in conjuction with predation. Thus, I estimated survival of sage-grouse during different periods to gain information on factors influencing survival during their annual life-cycle.

## *SEASONAL VARIATION IN SURVIVAL*

### *Nesting season*

Sage-grouse survival during the nesting season was influenced by nesting status and age of the individual. Compared to birds that lost their nest or did not nest at all, females with successful nests had a higher probability of survival if their nest was successful. This was contrary to our original expectation that hen survival would be lower for nesting hens and proportional to the amount of time they spent incubating due to the increased risk for nest depredation. Moynahan et al. (2006) documented similar patterns of survival for nesting versus non-nesting hens in north-central Montana. They suggested that the physical condition of the female prior to nesting and the visibility of non-nesting birds influence their probability of survival. I considered females to be in excellent body condition prior to nesting because females exhibited high nest initiation rates (Herman-Brunson 2007, Kaczor 2008) and were approximately 125 g heavier (Kaczor 2008) than in other studies (Schroeder et al. 1999), and because mild winters preceded the nesting seasons during this study. Nonetheless, females with unsuccessful nests had a lower probability of survival than successful females. Mean body mass of male sage-grouse during this study was 2940 g and was high relative to other studies (Schroeder et al. 1999). The conspicuous behavior of males that displayed on leks into mid May and the loss of concealment provided by the nest for non-nesting females may also have resulted in lower survival and increased vulnerability to predators.

My model also indicated that age influenced survival of adult and yearling sage-grouse. Because the peak of male lek attendance occurs approximately 3 weeks after peak hen attendance (Connelly et al. 2004), most males are still attending leks through the majority of the nesting season. Although yearling males are physiologically capable of breeding (Eng 1963, Bergerud 1988), they often remain inconspicuous and do not breed because of the competition from adult males (Bergerud 1988). Findings from this study and Zablan (2003) confirm that yearling males have a higher probability of survival than adult males, which likely resulted from less time attending leks than adult males did following peak hen attendance. Similarly, Hagen et al. (2005) hypothesized that male lesser prairie-chickens (*Tympanuchus pallidicinctus*) ≥2 years of age have lower survival because of the increased cost of reproductive activity at leks. Nonetheless, more information is needed regarding male survival during this period because my sample size for yearlings was low. Yearling female survival was also higher than adult females. Nesting female grouse are less mobile and have reduced ranges compared to non-nesting females, which indirectly reduces their risk of predation (Bergerud and Gratson 1988). The concealment of the nest may allow a nesting female to avoid visually oriented predators due to the structural heterogeneity around the nest, which has been suggested to decrease the foraging efficiency of predators that rely on olfaction (Bowman and Harris 1980, Jimenez and Conover 2001). However, cover alone around the nest may not protect birds against detection by predators. Behavioral responses by female sage-grouse in response to predators can affect survival (Schroeder 1997). Nesting females will defend their nests against potential predators using distraction displays; however, this behavior is more typical of adults than yearlings (Peterson 1980). These age-specific behavioral responses may contribute to the pattern of age-specific survival in females I observed in this study.

*Early brood-rearing season*

Survival of female tetraonids during the brood-rearing season may be affected by their need to maximize reproductive output at the cost of survival (Hagen et al. 2005). Although females with broods may have an increased cost (i.e., brooding during inclement weather) to manage the brood, my results do not indicate any differential survival between brood hens and broodless hens. Moreover, I did not detect any significant effects of age or gender during this period, which suggested that all birds had a constant probability of survival. Less conspicuous behavior by males and reduced movements by females with broods near her nest may have contributed to high survival during this period.

*Late brood-rearing season*

Previous studies have documented that survival of sage-grouse during the late summer is high (Schroeder et al. 1999, Connelly et al. 2000*a*, Aldridge and Brigham 2003). During this study, mortality was high in sage-grouse from mid July through the first hard frost in autumn, which occurred by 12 October. Hens had higher survival than male sage-grouse. Reasons why male survival was lower than hens may potentially be related to the increased demands that heavier males have to meet their energetic requirements (Swenson 1986). Both male and female sage-grouse tend to be lighter in the autumn than during reproductive periods (Schroeder et al. 1999); however, I do not have any evidence suggesting that the constraint of body size on survival would be different than during other seasons. Nonetheless, it was surprising that male survival was 57.5% lower than female survival during 2006 in North Dakota and 26.1% lower overall.

Male survival may have also been influenced by natural and sexual selection. In most vertebrate species, males tend to exhibit higher rates of disease than females, which are influenced by either ecological or physiological mechanisms (Rizzoli et al. 2002). Natural selection may have favored larger male body sizes for reproduction in sage-grouse, while incidences of disease may been more common in males because they have high amounts of testosterone which tends to be immunosuppressive (Grossman 1985). Potentially, male sage-grouse may have been more susceptible to mortality from West Nile virus because of these selection mechanisms. Yet, evidence from other research on avian species suggests that there is no sex-biased mortality that is caused by viral diseases (Brand et al. 1987, Yaremych et al. 2004). Additional research is required to understand why mortality rates in male sage-grouse are higher during the late summer.

I observed considerable yearly variation in survival during the late brood-rearing period. Previous research indicates that 39% of annual mortality occurs mainly from hunting during September and October, but harvest mortality can vary annually (Connelly et al. 2000*a*). Although sage-grouse mortality was high in August and September during this study, my data were more indicative of the findings of Braun and Beck (1985) and Wallestad (1975) that showed that hunting had minimal influence on annual mortality. Rather, the year effect I observed was related to annual fluctuations in predation and West Nile virus outbreaks. It was not surprising that predation appeared to be the source for most mortality, as this is typical for most prairie grouse (Schroeder and Baydack 2001).

I observed the highest survival during 2005, a year of higher nest success and recruitment than in 2006 in North Dakota (Herman-Brunson 2007). I confirmed one West Nile virus death during 2005 and believe that there was a limited outbreak in 2005 because only one of four total deaths that occurred before a hard frost on 26 September tested positive for the virus. The remaining mortalities were attributed to predation and occurred after the hard frost when I did not observe mosquitoes. Walker et al. (2004) suggested that surface water persisting late into the summer in xeric landscapes could act as a catalyst for abundance of exotic virus-vector complexes (e.g., West Nile virus) in native wildlife. During this study, May-September precipitation was actually highest in North Dakota during 2005 (32.6 cm) compared to 2006 (14.0 cm) and in South Dakota during 2006 (22.7 cm) and 2007 (20.2 cm; High Plains Regional Climate Center 2009). Yet, survival was higher in 2005 even though the amount of precipitation received was greater than in 2006 or 2007. While my results are not conclusive regarding precipitation, I suggest that there may be other environmental variables such as temperature, which is a key regulator of *C. tarsalis* that carries West Nile virus (Brust 1991), that are better indicators of yearly variation of sage-grouse survival.

My results support the findings of Naugle et al. (2005) and Walker et al. (2007) in relationship to temperature and the occurrence of West Nile virus mortality in sage-grouse. I found that the higher rate of West Nile virus mortalities in 2007 coincided with mean daily temperatures that were 2.7ºC higher than the long-term average (1915-2007) for July and August (High Plains Regional Climate Center 2009). Conversely, the lower incidence of West Nile virus in 2005 corresponded with temperatures that were 0.52ºC lower than the long-term average. Coincidentally, 2005 was the only year when the average temperature in July and August was below 21ºC; the threshold for development of *C. tarsalis* (Brust 1991). Although I cannot be certain that the high mortality rate of 2006 was linked to West Nile virus, temperatures were 1.93 and 2.53ºC higher in North Dakota and South Dakota than the long-term average and well above 21ºC.

I also suggest that the high incidence of mortalities during the late summer attributed to predation may have been amplified by outbreaks of West Nile virus. Even though I attempted to monitor the signals of most birds on a daily basis from late July through the first frost believed to kill adult *C. tarsalis*, predators may have killed sick birds or consumed birds that had died from other causes (e.g., West Nile virus) before I could retrieve them. For example, I retrieved portions (wings, skeleton, soft tissues) of a sage-grouse (1803B) in 2007 that had been killed by a Red-tailed Hawk that tested positive for West Nile virus. When I approached the kill site, the red-tailed hawk flushed off of the carcass of 1803B. Interestingly, another sage-grouse that was not marked had also been freshly killed within 3 meters of the kill site of 1803B. Potentially, the number of deaths caused by West Nile virus could have been substantially higher for 2 reasons: 1) temperatures during 2006 and 2007 were optimal for development of *C. tarsalis*, and 2) sage-grouse may have been highly susceptible to predation during this period because of the overt signs of illness that sage-grouse demonstrate after being infected with West Nile virus (Clark et al. 2006). Experimental research conducted by Clark et al. (2006)

indicate that non-vaccinated captive sage-grouse die within 3.7 days of West Nile virus infection and have several signs of illness prior to death that may cause them to be more susceptible to predation. These symptoms include: watery oral and nasal discharge, isolation, complete loss of coordinated locomotion, and unwillingness to escape danger. Ostensibly, infected sage-grouse that were isolated, immobile, and lacked all innate escape tendencies would certainly be more susceptible to predation. Although I cannot confirm these hypotheses, circumstantial evidence from the field supports my hypothesis that predation rate increases on sage-grouse during years with adequate growing conditions for *C. tarsalis* as a result of deleterious symptoms caused by West Nile virus. Similar relationships also have been documented regarding the predation rate of wolves (*Canis lupus*) on moose (*Alces alces*) from a gastrointestinal parasite (Joly and Messier 2004) and in European Sparrowhawks (*Accipiter nisus*) and Eurasian Goshawks (*Accipiter gentiles*) increased predation rate after their prey contracted vector-borne malaria (Moller and Nielsen 2007).

### *Winter season*

Mortality during the winter is considered to be low for adult and juvenile sage-grouse (Connelly et al. 2000*b*, Beck et al. 2006) unless acute periods of high snowfall and extreme cold temperatures limit available forage and thermal cover (Moynahan et al. 2006). Body condition typically improves during moderate winters (Beck and Braun 1978) because of their reliance on Wyoming big sagebrush, which contains twice the protein found in winter diets of other grouse species (Moss and Hanssen 1980, Remington and Braun 1985). The winters during this study were mild because snow accumulation was minimal and temperatures were moderate. During the winter, overall survival of 94.4% was among the highest reported for sage-grouse. Survival may be higher for sage-grouse during the winter because larger flock sizes may allow them to detect and avoid predation (Wallestad 1975). I suggest that sage-grouse physiological condition improves during mild winters in the Dakotas, as evidence from Kaczor (2008) indicated that sage-grouse were heavier entering their reproductive period than in other studies (Schroeder et al. 1999).

Juvenile survival was 11.2% lower than survival of breeding-aged birds during winter and was similar to juvenile sage-grouse in southeastern Idaho (Beck et al. 2006). Survival of juvenile grouse species tends to be lower than adults from autumn through spring (Hannon and Martin 2006) and may be influenced by their vulnerability to migrating raptors (Smith and Willebrand 1999, Pitman et al. 2006). Juvenile grouse also move farther and use a wider range of habitats than adults during winter (Hannon and Martin 2006, Chapter 5), which may have reduced their survival by settling in unfamiliar environments or potentially unproductive habitats. Potentially, dispersal movements by juveniles during winter (Chapter 4) may have increased their vulnerability to predators during winter.

### *Breeding season*

My findings indicate that male sage-grouse have a lower probability of survival than females during the breeding season. The timing of mortality was an important predictor of survival as all mortalities coincided with the timing of peak hen attendance; from 5-11 April (Herman-Brunson 2007). Adult males had higher mortality than yearling males, which potentially was a function of the amount of time that adults spend attending leks during peak hen attendance (Emmons and Braun 1984) and because male courtship display attracts predators (Boyko et al. 2004). Adult males may have been more susceptible to predation during peak hen attendance because they were more abundant and distracted by courting females. Although lekking behavior in grouse evolved as a way to increase predator detection (Lack 1968, Wittenberger 1978, Bergerud 1988), male sage-grouse may only benefit from increased predator detection when few females are attending leks (i.e., peak male attendance during early May) and they are less distracted. Conversely, females potentially had a higher probability of survival because they remain inconspicuous prior to visiting leks during the breeding season.

## MANAGEMENT IMPLICATIONS

Results from this study indicate that annual survival of sage-grouse varied by year and was influenced by intense periods of high mortality that occurred in late summer. I documented >50% mortality in sage-grouse in South Dakota during 2006 and 2007, which I believe was related to outbreaks of West Nile virus. Thus, managers should be vigilant of years when temperatures exceed 21ºC during July and August because development of *C. tarsalis* is greatly enhanced above this threshold (Brust 1991) and sage-grouse mortality could be high during these years. Mortality during this period likely affects future production potential; therefore, managers may need to limit harvest of infected populations during these years or temporarily close seasons. Unfortunately, predicting future outbreaks of West Nile virus is difficult because there is a limited understanding of how host-vector relationships affect the spread of West Nile virus in sagebrush habitats (Naugle et al. 2005). I suggest that researchers visually locate sage-grouse on a daily basis using telemetry to limit scavenging or decay of carcasses and determine true West Nile virus infection rates. Detection of West Nile virus requires adequate planning and intensive monitoring by field crews large enough to locate radio-marked birds from mid July until approximately one week after the first hard frost that kills adult mosquitoes (Walker et al. 2004). Although sage-grouse currently exhibit minimal resistance to West Nile virus (Walker et al. 2007), additional research that assesses whether the symptoms of West Nile virus negatively influence the behavior of wild sage-grouse by increasing their susceptibility to predation may be important to understand how West Nile virus progresses in avian populations.

My results indicate that survival of sage-grouse was high (86.6-97.7%) during the nesting, early-brood rearing, winter, and breeding periods and does not appear to limit the persistence of these populations. Conversely, the high mortality during the late summer along with low renesting rates (9.5% in North Dakota, 28.6% in South Dakota), low to moderate nest success (31% in North Dakota, 47.9% in South Dakota), and poor recruitment (15% in North Dakota, 6% in South Dakota; Herman-Brunson 2007, Kaczor 2008) may severely decrease the low density sage-grouse populations in this region. Thus, managers may need to try to improve demographic processes (e.g., productivity, recruitment) and maintain high adult survival because of the implications for future population growth (Johnson and Braun 1999, Moynahan et al. 2006). Unfortunately, there are limited strategies (e.g., eliminating man-made water sources) to mitigate the negative effects of West Nile virus in sage-grouse (Walker et al. 2007). Therefore, management could focus on implementing actions that they can regulate to positively effect sage-grouse populations such as conservative hunting seasons to limit mortality, improved range condition to increase nest success and chick survival, prevention of overgrazing, regulating mesopredator densities, limiting anthropogenic disturbances (i.e., roads, power-lines, energy development) to critical seasonal habitats or leks, and developing cooperative agreements with landowners to maintain or improve sagebrush habitat.

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Table 2-1. Known-fate models of annual greater sage-grouse survival in North Dakota, 2005–2006 and South Dakota, 2006–2007.

| Model[a] | $AIC_c$[b] | $\Delta AIC_c$[b] | $w_i$[b] | K[b] | Deviance |
|---|---|---|---|---|---|
| S(Month + Year) | 939.573 | 0.000 | 0.832 | 12 | 915.433 |
| S(Global) | 943.038 | 3.465 | 0.147 | 15 | 912.823 |
| S(Month + Age) | 948.312 | 8.739 | 0.011 | 12 | 924.172 |
| S(Month) | 948.329 | 8.756 | 0.010 | 12 | 924.189 |

[a] Candidate models including covariates for Age = adult, yearling, or juvenile; constant = constant monthly survival with no effect of covariates; Gender = male or female; Global = includes effect of all covariates; Month = time interval; State = North Dakota or South Dakota; West Nile virus = July through October; Year = 2005, 2006, or 2007;

[b] $AIC_c$ = Akaike's Information Criterion adjusted for small sample size; $\Delta AIC_c$ = $AIC_c$ relative to the most parsimonious model; $w_i$ = Akaike weight; K = number of parameters

Table 2-2. Annual survival estimates by age and gender for greater sage-grouse in North Dakota, 2005 and 2006 and in South Dakota, 2006 and 2007.

| Season | State | # Birds | # Dead | # Censor | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|
| Adult female 2005 | ND | 9 | 2 | 0 | 0.778 | 0.139 | 0.506 | 1.000 |
| Adult female 2006 | ND | 22 | 9 | 4 | 0.547 | 0.123 | 0.307 | 0.788 |
| Adult female 2006 | SD | 24 | 7 | 0 | 0.695 | 0.093 | 0.513 | 0.878 |
| Adult female 2007 | SD | 35 | 21 | 1 | 0.389 | 0.084 | 0.224 | 0.555 |
| Yearling female 2005 | ND | 15 | 4 | 1 | 0.692 | 0.121 | 0.454 | 0.930 |
| Yearling female 2006 | ND | 16 | 4 | 2 | 0.695 | 0.121 | 0.457 | 0.933 |
| Yearling female 2006 | SD | 17 | 2 | 1 | 0.875 | 0.083 | 0.713 | 1.037 |
| Yearling female 2007 | SD | 10 | 5 | 0 | 0.500 | 0.158 | 0.190 | 0.810 |
| Adult male 2005 | ND | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Adult male 2006 | ND | 11 | 9 | 2 | 0.000 | 0.000 | 0.000 | 0.000 |
| Adult male 2006 | SD | 17 | 9 | 2 | 0.349 | 0.115 | 0.124 | 0.574 |
| Adult male 2007 | SD | 16 | 12 | 1 | 0.188 | 0.098 | 0.000 | 0.379 |
| Yearling male 2005 | ND | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male 2006 | ND | 7 | 4 | 3 | 0.000 | 0.000 | 0.000 | 0.000 |
| Yearling male 2006 | SD | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male 2007 | SD | 11 | 6 | 0 | 0.397 | 0.138 | 0.127 | 0.667 |
| All hens 2005 | ND | 24 | 6 | 1 | 0.732 | 0.092 | 0.552 | 0.912 |
| All hens 2006 | ND | 38 | 13 | 6 | 0.664 | 0.082 | 0.503 | 0.824 |
| All hens 2006 | SD | 41 | 9 | 1 | 0.784 | 0.063 | 0.659 | 0.908 |
| All hens 2007 | SD | 45 | 26 | 1 | 0.409 | 0.074 | 0.264 | 0.555 |
| All males 2005 | ND | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| All males 2006 | ND | 18 | 13 | 5 | 0.000 | 0.000 | 0.000 | 0.000 |
| All males 2006 | SD | 17 | 9 | 2 | 0.349 | 0.115 | 0.124 | 0.574 |
| All males 2007 | SD | 27 | 18 | 1 | 0.300 | 0.089 | 0.126 | 0.474 |
| All Juvenile 2005 | ND | 9 | 3 | 0 | 0.667 | 0.152 | 0.362 | 0.970 |
| All Juvenile 2006 | ND | 16 | 9 | 0 | 0.440 | 0.120 | 0.189 | 0.673 |
| All Juvenile 2006 | SD | 23 | 16 | 0 | 0.300 | 0.098 | 0.121 | 0.487 |
| All Juvenile 2007 | SD | 19 | 14 | 1 | 0.250 | 0.110 | 0.033 | 0.470 |
| All breeding-age 2005 | ND | 24 | 6 | 1 | 0.732 | 0.092 | 0.552 | 0.912 |
| All breeding-age 2006 | ND | 56 | 26 | 11 | 0.511 | 0.076 | 0.361 | 0.660 |
| All breeding-age 2006 | SD | 58 | 18 | 3 | 0.692 | 0.062 | 0.570 | 0.814 |
| All breeding-age 2007 | SD | 72 | 44 | 2 | 0.351 | 0.057 | 0.240 | 0.461 |
| All birds | ND | 33 | 9 | 1 | 0.792 | 0.075 | 0.644 | 0.939 |
| All birds | ND | 72 | 35 | 11 | 0.498 | 0.065 | 0.369 | 0.626 |
| All birds | SD | 81 | 34 | 3 | 0.589 | 0.056 | 0.479 | 0.697 |
| All birds | SD | 91 | 58 | 3 | 0.351 | 0.057 | 0.239 | 0.461 |

Table 2-3. Known-fate models of greater sage-grouse survival during the nesting season in North Dakota, 2005–2006 and in South Dakota, 2006–2007.

| Model[a] | $AIC_c$[b] | $\Delta AIC_c$[b] | $w_i$[b] | K[b] | Deviance |
|---|---|---|---|---|---|
| S(Age + Nest fate) | 192.148 | 0.000 | 0.565 | 4 | 184.111 |
| S(Nest fate + Nest initiation) | 194.525 | 2.376 | 0.172 | 4 | 186.488 |
| S(Nest fate) | 194.617 | 2.468 | 0.164 | 3 | 188.595 |
| S(Global) | 198.292 | 6.144 | 0.026 | 8 | 182.158 |
| S(Age + Gender) | 198.682 | 6.534 | 0.022 | 3 | 192.660 |
| S(Age) | 198.754 | 6.606 | 0.021 | 2 | 194.743 |
| S(Age + State) | 200.758 | 8.610 | 0.008 | 3 | 194.736 |
| S(Gender) | 201.047 | 8.899 | 0.007 | 2 | 197.036 |
| S(.) | 201.265 | 9.117 | 0.006 | 1 | 199.261 |

[a] Candidate models including covariates for Age = adult or yearling; constant = constant weekly survival with no effect of covariates; Gender = male or female; Global = includes effect of all covariates; Nest fate = successful nest or failed/no nest; Nest initiation = initiated nest or did not initiate nest; State = North Dakota or South Dakota; Year = 2005, 2006, or 2007; Week = time interval for nesting season.

[b] $AIC_c$ = Akaike's Information Criterion adjusted for small sample size; $\Delta AIC_c$ = $AIC_c$ relative to the most parsimonious model; $w_i$ = Akaike weight; K = number of parameters

Table 2-4. Seasonal survival estimates for greater sage-grouse during the nesting, early brood-rearing, late brood-rearing, winter, and breeding seasons in North Dakota, 2005 and 2006 and in South Dakota, 2006 and 2007.

| Season | State | # Birds | # Dead | # Censor | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|
| Nesting 2005[a] | ND | 19 | 1 | 0 | 0.947 | 0.051 | 0.847 | 1.000 |
| Nesting 2006 | ND | 38 | 5 | 2 | 0.866 | 0.057 | 0.755 | 0.978 |
| Nesting 2006 | SD | 52 | 5 | 1 | 0.904 | 0.041 | 0.823 | 0.985 |
| Nesting 2007 | SD | 66 | 7 | 0 | 0.894 | 0.038 | 0.819 | 0.968 |
| Early brood-rearing 2005 [a] | ND | 23 | 1 | 0 | 0.957 | 0.043 | 0.873 | 1.000 |
| Early brood-rearing 2006 | ND | 42 | 5 | 0 | 0.881 | 0.050 | 0.783 | 0.979 |
| Early brood-rearing 2006 | SD | 48 | 2 | 1 | 0.958 | 0.029 | 0.901 | 1.000 |
| Early brood-rearing 2007 | SD | 57 | 2 | 1 | 0.965 | 0.025 | 0.916 | 1.000 |
| Late brood-rearing 2005 [a] | ND | 31 | 7 | 1 | 0.767 | 0.077 | 0.615 | 0.918 |
| Late brood-rearing 2006 | ND | 58 | 21 | 8 | 0.603 | 0.071 | 0.465 | 0.741 |
| Late brood-rearing 2006 | SD | 69 | 25 | 1 | 0.444 | 0.074 | 0.299 | 0.590 |
| Late brood-rearing 2007 | SD | 78 | 43 | 1 | 0.462 | 0.057 | 0.349 | 0.574 |
| Winter 2005-06 [a] | ND | 21 | 1 | 0 | 0.952 | 0.046 | 0.861 | 1.000 |
| Winter 2006-07 | ND | 29 | 2 | 1 | 0.931 | 0.047 | 0.839 | 1.000 |
| Winter 2006-07 | SD | 43 | 1 | 0 | 0.977 | 0.023 | 0.932 | 1.000 |
| Winter 2007-08 | SD | 33 | 3 | 0 | 0.907 | 0.051 | 0.807 | 1.000 |
| Breeding 2006[b] | ND | 27 | 2 | 0 | 0.926 | 0.050 | 0.827 | 1.000 |
| Breeding 2006 | SD | 44 | 1 | 0 | 0.977 | 0.022 | 0.933 | 1.000 |
| Breeding 2007 | SD | 60 | 4 | 1 | 0.932 | 0.032 | 0.869 | 0.996 |

[a] Survival estimates did not include breeding-age males during 2005.

[b] Because of the timing of when the study was initiated, no estimates of survival were obtained during the breeding season in 2005.

Table 2-5. Known-fate models of greater sage-grouse survival during the early brood-rearing season in North Dakota, 2005–2006 and in South Dakota, 2006–2007.

| Model[a] | $AIC_c$[b] | $\Delta AIC_c$[b] | $w_i$[b] | K[b] | Deviance |
|---|---|---|---|---|---|
| S(State) | 102.568 | 0.000 | 0.153 | 2 | 98.547 |
| S(Brood + State) | 102.759 | 0.191 | 0.139 | 3 | 96.717 |
| S(.) | 102.797 | 0.229 | 0.136 | 1 | 100.790 |
| S(Brood) | 103.511 | 0.943 | 0.095 | 2 | 99.491 |
| S(Gender + State) | 103.639 | 1.071 | 0.089 | 3 | 97.597 |
| S(Age + State) | 104.589 | 2.020 | 0.055 | 3 | 98.547 |
| S(Age + State + Brood) | 104.773 | 2.205 | 0.050 | 4 | 96.703 |
| S(Age) | 104.797 | 2.229 | 0.050 | 2 | 100.777 |
| S(Gender + Brood) | 105.102 | 2.530 | 0.043 | 3 | 99.060 |
| S(Week) | 105.141 | 2.573 | 0.042 | 4 | 97.071 |
| S(Age + Brood) | 105.532 | 2.963 | 0.034 | 3 | 99.490 |
| S(State + Year) | 105.883 | 3.315 | 0.029 | 4 | 97.813 |
| S(Age + Gender) | 106.042 | 3.474 | 0.026 | 3 | 100.001 |
| S(Age + Week) | 107.162 | 4.593 | 0.015 | 5 | 97.056 |
| S(Age + State + Year + Brood) | 107.825 | 5.257 | 0.011 | 6 | 95.677 |
| S(Age + Year) | 107.859 | 5.290 | 0.010 | 4 | 99.789 |
| S(Age + State + Year) | 107.917 | 5.349 | 0.010 | 5 | 97.812 |
| S(Global) | 109.494 | 6.926 | 0.004 | 7 | 95.297 |

[a] Candidate models including covariates for Age = adult or yearling; brood = hen with brood at start of season; Constant = constant weekly survival with no effect of covariates; Gender = male or female; Global = includes effect of all covariates; State = North Dakota or South Dakota; Year = 2005, 2006, or 2007; Week = time interval for early brood-rearing season.

[b] $AIC_c$ = Akaike's Information Criterion adjusted for small sample size; $\Delta AIC_c$ = $AIC_c$ relative to the most parsimonious model; $w_i$ = Akaike weight; K = number of parameters

Table 2-6. Known-fate models of greater sage-grouse survival during the late brood-rearing season in North Dakota, 2005–2006 and in South Dakota, 2006–2007.

| Model[a] | $AIC_c$[b] | $\Delta AIC_c$[b] | $w_i$[b] | K[b] | Deviance |
|---|---|---|---|---|---|
| S(Gender + Year) | 749.530 | 0.000 | 0.507 | 5 | 739.500 |
| S(Gender) | 750.537 | 1.007 | 0.306 | 3 | 744.525 |
| S(Gender + Brood) | 752.565 | 3.035 | 0.111 | 5 | 742.535 |
| S(Global) | 753.604 | 4.074 | 0.066 | 11 | 731.470 |
| S(Gender + Week + Year) | 758.115 | 8.585 | 0.007 | 18 | 721.766 |

[a] Candidate models including covariates for Age = adult, yearling, or juvenile; Brood = had brood at start of season; Constant = constant weekly survival with no effect of covariates; Gender = male or female; Global = includes effect of all covariates; Gtate = North Dakota or South Dakota; Year = 2005, 2006, or 2007; Week = time interval for late brood-rearing season.

[b] $AIC_c$ = Akaike's Information Criterion adjusted for small sample size; $\Delta AIC_c$ = $AIC_c$ relative to the most parsimonious model; $w_i$ = Akaike weight; K = number of parameters

Table 2-7. Known-fate models of greater sage-grouse survival during the winter season in North Dakota, 2005–2007 and in South Dakota, 2006–2008.

| Model[a] | $AIC_c$[b] | $\Delta AIC_c$[b] | $w_i$[b] | K[b] | Deviance |
|---|---|---|---|---|---|
| S(Age + Week) | 75.128 | 0.000 | 0.983 | 7 | 61.058 |
| S(Age) | 84.583 | 9.456 | 0.009 | 2 | 80.576 |

[a] Candidate models including covariates for Age = adult or yearling; Constant = constant weekly survival with no effect of covariates; gender = male or female; Global = includes effect of all covariates; shrub cover = % sagebrush canopy cover at use site, shrub height = sagebrush height (cm) at use site, State = North Dakota or South Dakota; Year = 2006 or 2007; Week = time interval for winter season.

[b] AICc = Akaike's Information Criterion adjusted for small sample size; $\Delta AIC_c$ = $AIC_c$ relative to the most parsimonious model; $w_i$ = Akaike weight; K = number of parameters.

Table 2-8. Known-fate models of greater sage-grouse survival during the breeding season in North Dakota, 2006 and in South Dakota, 2006 and 2007.

| Model[a] | $AIC_c$[b] | $\Delta AIC_c$[b] | $w_i$[b] | K[b] | Deviance |
|---|---|---|---|---|---|
| S(Gender + Week) | 45.519 | 0.000 | 0.496 | 4 | 37.331 |
| S(Gender) | 46.295 | 0.776 | 0.336 | 2 | 42.240 |
| S(Age + Gender + Year) | 48.712 | 3.193 | 0.100 | 4 | 40.525 |
| S(Global) | 49.618 | 4.099 | 0.064 | 5 | 39.336 |

[a] Candidate models including covariates for Age = adult or yearling; constant = constant weekly survival with no effect of covariates; Gender = male or female; Global = includes effect of all covariates; State = North Dakota or South Dakota; Year = 2006 or 2007; Week = time interval for breeding season.

[b] AICc = Akaike's Information Criterion adjusted for small sample size; $\Delta AIC_c$ = $AIC_c$ relative to the most parsimonious model; $w_i$ = Akaike weight; K = number of parameters.

Figure 2-1. Monthly mortalities of greater sage-grouse during 2005 and 2006 in North Dakota and during 2006 and 2007 in South Dakota.

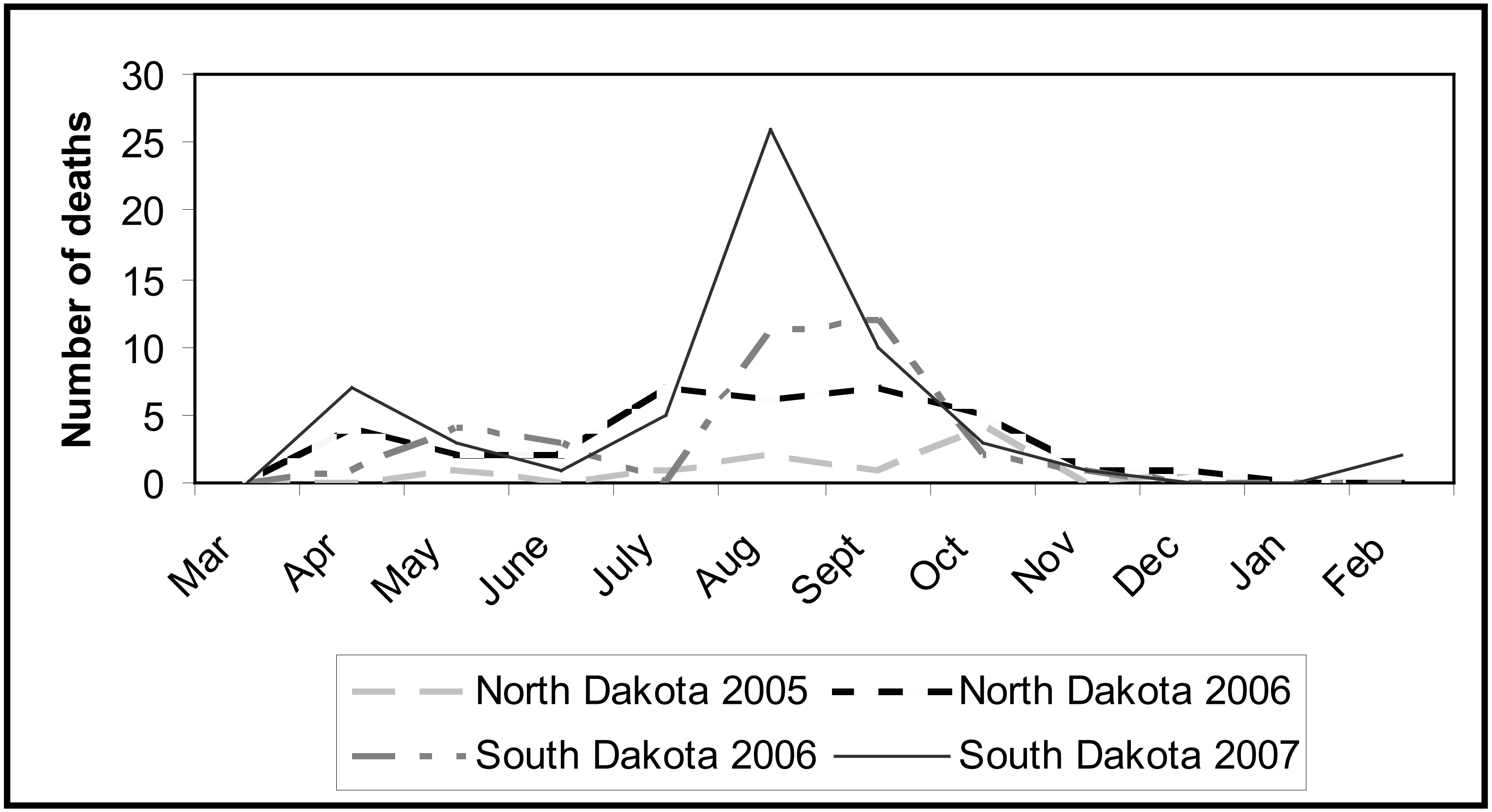


Figure 2-2. Probable causes of mortality for greater sage-grouse pooled by age and gender in North Dakota, 2005-2007 and in South Dakota, 2006-2008.

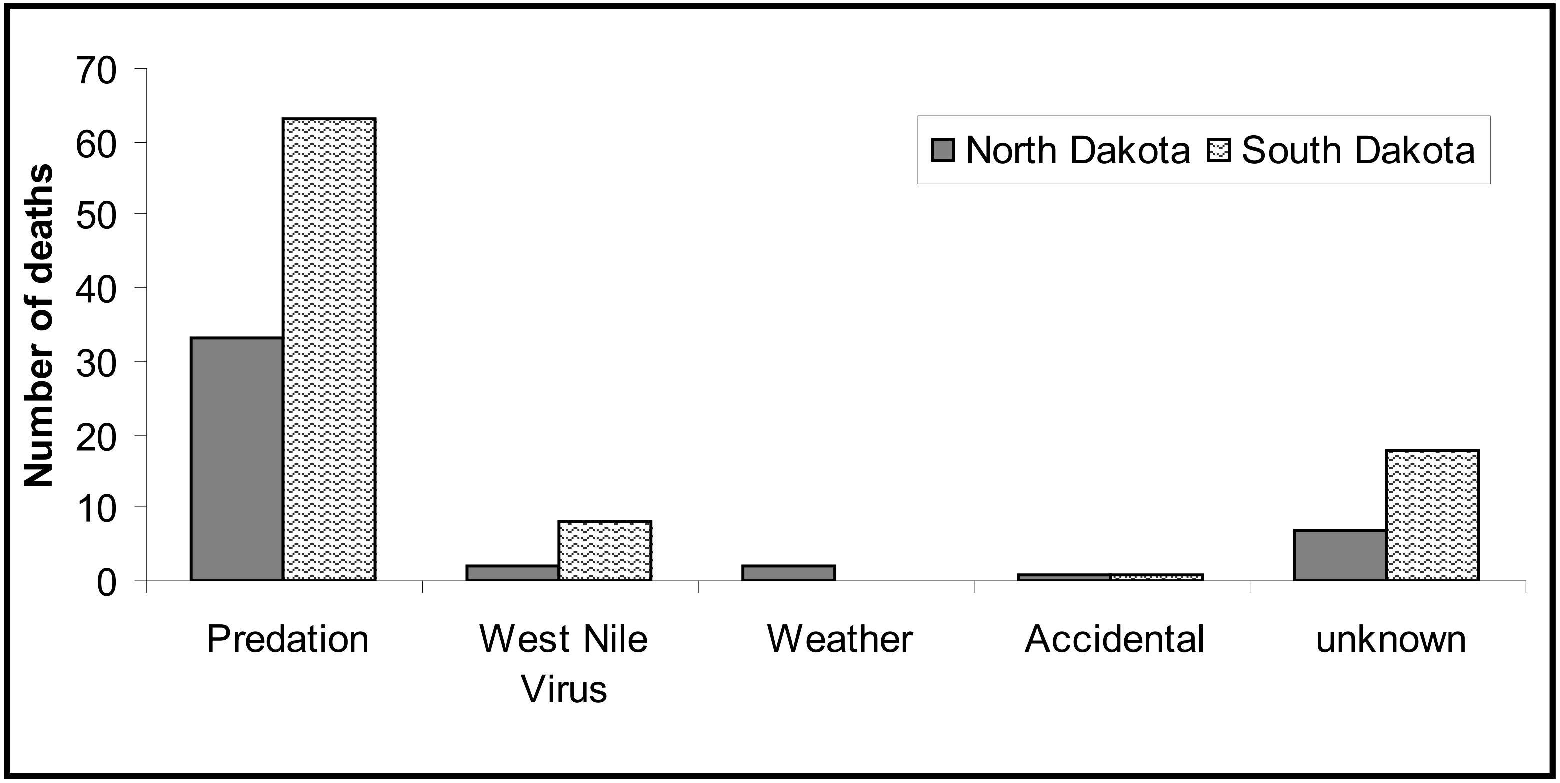
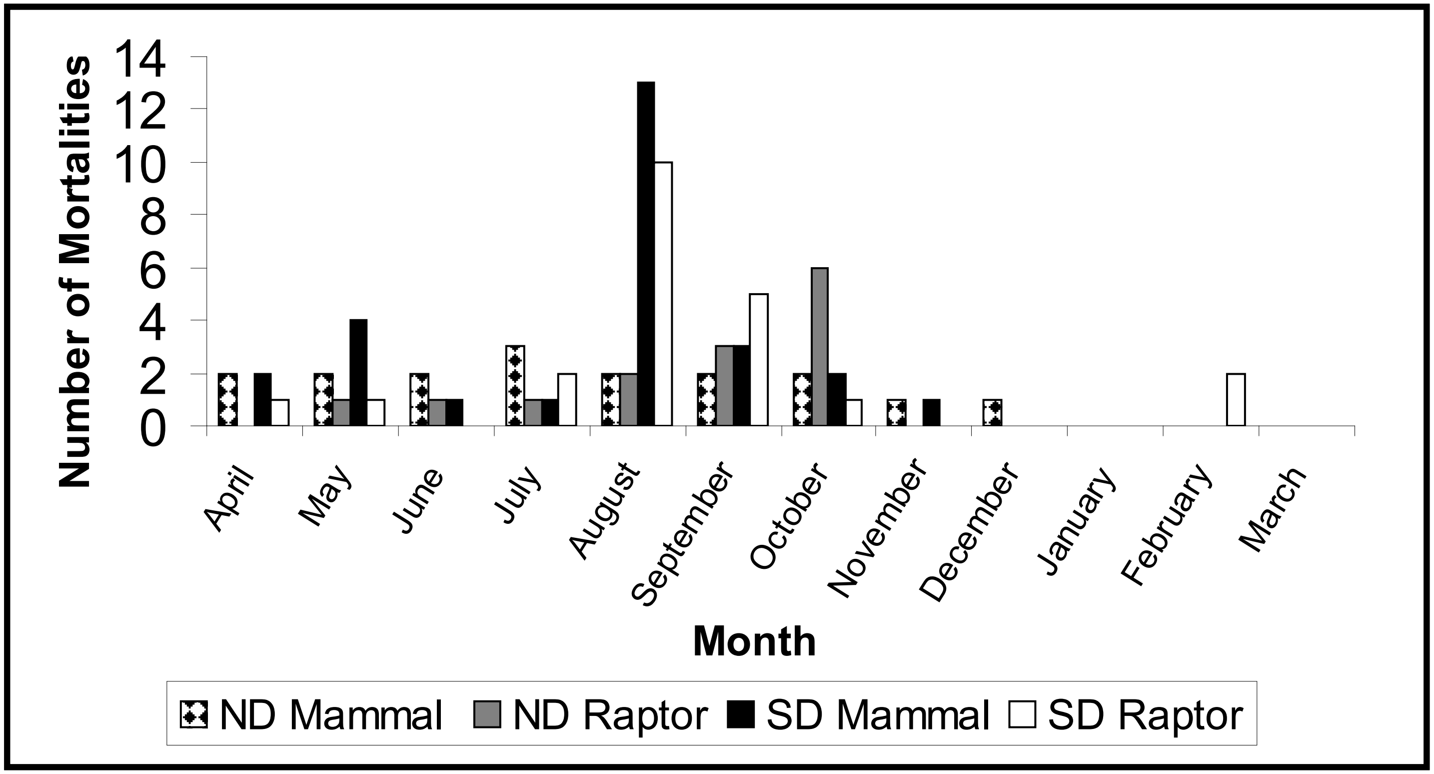


Figure 2-3. Timing of mortality of Greater sage-grouse caused by mammals or raptors in North Dakota, 2005-2007 and in South Dakota, 2006-2008.



# CHAPTER 3

## GREATER SAGE-GROUSE WINTER HABITAT USE ON THE EASTERN EDGE OF THEIR RANGE

**Abstract:** Numerous studies have described greater sage-grouse (*Centrocercus urophasianus*) winter habitat use at the core of their range, yet no information exists at the eastern edge of their distribution. I evaluated factors influencing greater sage-grouse winter habitat use in North Dakota 2005-06 and 2006-07 and in South Dakota 2006-07 and 2007-08. I used conditional logistic regression to test competing models of winter habitat use at used (*n* = 340) and dependent random sites (*n* = 340 at 250 m & 340 at 500 m) from 124 radio-marked sage-grouse. Percent sagebrush (*Artemisia* spp.) canopy cover was the primary factor influencing winter habitat use in this region. Habitat used by sage-grouse was characterized by 7.6% higher sagebrush canopy cover than at random sites. My results indicated that sagebrush canopy cover (15%) and sagebrush height (20 cm) meet their winter habitat requirements during mild winters. Management could focus on avoiding additional loss of sagebrush habitat, identifying areas of critical winter habitat, and implementing management actions based on causal mechanisms (e.g., soil moisture, precipitation) that affect sagebrush community structure in this region.

*Key words: Centrocercus urophasianus,* conditional logistic regression, greater sage-grouse, North Dakota, sagebrush, South Dakota, winter habitat

# INTRODUCTION

Understanding resource selection provides insight into population sustainability and the impact that selected resources have in meeting species life-history requirements (Manly et al. 1993). Resource selection is based on a spatially hierarchical set of choices (Johnson 1980). Identifying the scale at which resource selection is defined within this hierarchy is important for proper representation of habitat use (Alldredge and Griswold 2006). Individuals select habitats to secure access to food or mates, reduce their vulnerability to predators, and limit their exposure to climatic stressors as a result of natural selection or prior learning (Wiens 1985). Resource management agencies rely on information gained from habitat selection studies to guide their future decisions and assess the long-term needs of populations under their jurisdiction (Manly et al. 2002).

Greater sage-grouse (*Centrocercus urophasianus*) are considered a landscape-scale species (Wakkinen 1990) whose distribution coincides with the occurrence of sagebrush habitat (*Artemisia* spp.; Schroeder et al. 2004). Sagebrush habitats have been degraded from >100 million ha to ~43 million ha (Rowland et al. 2005) and much of the loss of sagebrush habitats has been associated with agriculture, changes in fire regimes, energy development, fragmentation, grazing, pesticides, and urbanization (Braun 1998, Schroeder et al. 1999, West and Young 2000, Crawford et al. 2004). Sage-grouse populations have dramatically declined in conjunction with the sagebrush biome and are limited to 55% of their historical distribution (Schroeder et al. 2004). Consequently, natural resource agencies managing sagebrush lands have focused their efforts on reducing further degradation to the sagebrush ecosystem (Bureau of Land Management 2002, Knick et al. 2003).

Winter habitat selection by sage-grouse has been documented across most of their range (Dalke et al. 1963, Eng and Schladweiler 1972, Ihli et al. 1973, Beck 1977, Connelly 1982, Schoenberg 1982, Robertson 1991, Doherty et al. 2008). During winter, sage-grouse depend on sagebrush for food and cover (Dalke et al. 1963, Wallestad et al. 1975, Remington and Braun 1985); however, snow depth can severely limit the amount of available sagebrush (Hupp and Braun 1989). Winter habitat typically is located in areas that provide topographical relief and accessibility to sagebrush above the snow (Beck 1977, Connelly 1982, Robertson 1991) and may be located in close proximity to leks (Connelly et al. 1988). Winter habitat tends be limited compared to other seasonal habitats (Beck 1977, Remington and Braun 1985) and its availability influences sage-grouse distributions (Hanf et al. 1994). Therefore, identifying region-specific winter habitat requirements may be critical because the persistence of sage-grouse populations could be disproportionately affected by degradation of winter habitat (Doherty et al. 2008). However, sage-grouse winter habitat use has not been described at the eastward extension of sagebrush steppe communities.

Sage-grouse in the Dakotas occur within an ecotone between the eastern edge of the sagebrush distribution and the western edge of the prairie (Smith et al. 2006). Although species at the edge of their range can have high turnover rates (where deaths often exceed births) resulting in sink populations (Doherty et al. 2003), these populations may have unique local adaptations or evolutionary traits that allow them to persist when core populations undergo habitat destruction (Channell and Lomolino 2000). Also, populations at the edge of their range may use habitats differently than those in core areas because edge habitats tend to be more fragmented (Channell and Lomolino 2000).

The purpose of this study was to evaluate factors that influence winter habitat use by sage-grouse in North Dakota and South Dakota. I hypothesized that sage-grouse would use areas with the highest available percent sagebrush canopy cover available to meet their needs for food and cover during winter.

## STUDY AREA

This study was conducted in Bowman County, North Dakota (46º 7' 22.368″ N, 104º 0' 24.318″ W) and Butte County, South Dakota (45º 1' 52.329″ N, 103º 44' 41.196″ W) and adjacent parts of Montana and Wyoming. This region was semiarid sagebrush (*Artemisia* spp.) rangeland characterized by gentle slopes to steep buttes and ridges with elevations that ranged from 640 to 1225 m above sea level (Opdahl et al. 1975, Johnson 1976). Vegetation in this region was described by Opdahl et al. (1975), Johnson (1976), and Johnson and Larson (1999) and was considered low shrubland with short- to mid-grass prairie being dominant. Shrubs in the area were dominated by Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*), but also included silver sagebrush (*Artemisia cana* spp. *cana*), broom snakeweed (*Gutierrezia sarothrae*), rubber rabbitbrush (*Ericameria nauseosus*), and greasewood (*Sarcobatus vermiculatus*). Common perennial grasses were green needle-grass (*Nassella viridula*), Junegrass (*Koeleria macrantha*), western wheatgrass (*Pascopyrum smithii*), Kentucky bluegrass (*Poa pratensis*), Japenese brome (*Bromus japonicus*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), buffalograss (*Buchloe dactyloides*), needleandthread (*Hesperostipa comata)*, and little bluestem (*Schizachrium scoparium)*. Common forbs were common dandelion (*Taraxacum officinale*), textile onion (*Allium textile*), field pennycress (*Thlaspi arvense*), and western yarrow (*Achillea millefolium*). Land use was dominated by livestock grazing, 45% of Bowman County and 5% of Butte County was farmed for cultivated crops.

The climate was continental with cold dry winters and warm summers with most of the precipitation occurring in late spring and early summer. Average monthly temperatures in North Dakota were -9.7 ºC in January and 20.8 ºC in July with average annual precipitation and snowfall of 39.4 and 122.7 cm. Average monthly temperatures in South Dakota were -4.8 ºC in January and 22.7 ºC in July with average annual precipitation and snowfall of 45.54 and 89.9 cm, respectively (National Climatic Data Center 1971-2000).

## METHODS

### *CAPTURING AND MARKING*

I captured and radio-marked sage-grouse from late March to early May near active leks and from early July to mid September for broods using spotlights (Giesen et al. 1982, Wakkinen et al. 1992) and a thermal infrared imaging camera at night. Hens were fitted with a necklace-type radio transmitter (model A4060, Advanced Telemetry Systems, Isanti, Minnesota) with an 8-hour mortality switch that weighed 21.6 g, and had an expected battery life of 434 days. Males were fitted with a backpack-type radio transmitter (model A1135, Advanced Telemetry Systems, Isanti, Minnesota) with an 8-

hour mortality switch that weighed 17.9 g, and had an expected battery life of 297 days. I classified birds as adults (≥2 yr, second or later breeding season) and yearlings (≥1 yr, first breeding season) based on the length and shape of the 9th and 10th primaries (Beck et al. 1975) and assigned gender based on plumage characteristics (Bihrle 1993). All radio-transmitters were less than 3% of the body weight of birds at the time of attachment. All capture and handling protocols were approved by the South Dakota State University Institutional Animal Care and Use Committee (approval number: 07-A032).

### *TELEMETRY*

During this study, I located sage-grouse to evaluate winter habitat use from 1 November through 28 February during: 2005–2006 and 2006–2007 in North Dakota, and 2006–2007 and 2007–2008 in South Dakota. I located radio-marked sage-grouse ≥1 times per week with a hand-held antenna or by fixed wing aircraft when signals were not detected from the ground. All locations were recorded with a Global Positioning System (GPS) receiver in Universal Transverse Mercator (UTM) coordinates (NAD27; UTM Zone 13).

### *VEGETATION CHARACTERIZATION*

I measured vegetation along a 100 m transect at the location of a radio-marked sage-grouse and at two dependent random locations. Dependent random sites were measured at 250 and 500 m in a random cardinal direction from the location of the bird. I retained only one bird's location to be included in the habitat analysis to reduce the likelihood of pseudoreplication when more than one radio-marked sage-grouse was located in a flock. I measured live sagebrush density (*A. tridentata spp.* and *A. cana spp.*)

and height at 10 m intervals (*n* = 11) using the point-centered-quarter method (Cottam and Curtis 1956). I estimated maximum vegetation height using a modified Robel pole (Robel et al. 1970, Benkobi et al. 2000) at 10 m intervals (*n* = 11). I estimated percent canopy cover of vegetation cover, grass cover, forb cover (including plains pricklypear [*Opuntia polyacantha*], prairie sagewort [*Artemisia frigida*], and winterfat [*Krascheninnikovia lanata*]), sagebrush cover, snow cover, and litter cover using a 0.1 $m^2$ quadrat at 10 m intervals (*n* = 11; Daubenmire 1959). I placed four quadrats at each 10 m interval, 1 m away from the center of the interval and 1 m away from the transect collectively forming an H-pattern to measure percent canopy cover, totaling 44 quadrats per transect. I categorized percent canopy cover for all variables based upon 6 cover percentages (0 = no cover, 1 = 1–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–95%, 6 = 96–100%; Daubenmire 1959). Only the above snow portions of sagebrush were measured for height and percent canopy cover.

### *DATA ANALYSIS*

I summarized all measurements to an overall site value by averaging the matching intervals (i.e., 50's, 40's, 30's, 20's, 10's m) and the 0 m interval. Average site values were calculated for the following variables: percent total vegetation cover, percent grass cover, percent forb cover, percent sagebrush cover, percent big sagebrush cover, percent silver sagebrush cover, percent snow cover, percent litter cover, and vegetation height. Average site values included estimates of zero when percent canopy cover was calculated. Sagebrush density and height were estimated using a maximum likelihood estimate (Pollard 1971) summarized for the site. I pooled data across gender and age because sage-grouse flocks tended to be large and intermixed during the winter. I conducted a univariate analysis of variance (ANOVA) to test for differences in canopy cover for all habitat variables between used and random sites. I used a conservative estimate of $P \leq 0.15$ from the ANOVA to retain habitat variables in conditional logistic regression models to ensure all important variables were considered (Hosmer and Lemeshow 2000). I tested the remaining subset for collinearity ($[r \geq |0.6|]$; Pearson correlation coefficient), if variables were correlated, I selected one variable to include in the model based upon biological importance and evidence from other researchers. Burnham and Anderson (2002) recommend exclusion of models without biological support from the candidate sets, preliminary significance and correlation tests were used to remove variables to prevent superfluous model building.

I used multivariate conditional logistic regression to compare winter habitat characteristics on continuous scales to determine habitat associations (Ramsey et al. 1994) based on the habitat conditions available to the animal (Boyce 2006). I used the same candidate set of models at the state and regional levels to evaluate if competing models would predict habitat use at each level with similar outcomes. I used PROC LOGISTIC (SAS 2000) to make model comparisons and to set all variables at dependent random sites equal to each other (250 m dependent random = 500 m dependent random) allowing them to be compared simultaneously against habitat used by sage-grouse.

The conditional logistic regression models predicting winter habitat use included the variables: percent sagebrush canopy cover, sagebrush height, percent snow cover, vegetation height, and percent grass cover. Because biological significance should be considered more important than statistical significance (Yoccoz 1991, Kirk 1996), I included percent snow canopy cover in the models because it has been shown to influence winter habitat use (Beck 1977).

Output from the conditional logistic regression analysis was evaluated using the information-theoretic approach (Burnham and Anderson 2002) to quantify third-order selection (Johnson 1980) of winter habitat used by sage-grouse at the state and regional levels. Akaike's Information Criterion (AIC) was used to rank competing models. I considered models with the lowest AIC value, $\Delta$AIC $\leq$2 of highest ranked model, and Akaike weights ($w_i$) to determine model support (Burnham and Anderson 2002). Additionally, odds ratios were evaluated to assess the influence of variables within the top model; values > 1 indicate a positive relationship, values < 1 indicate a negative relationship. If variables included 1 within the 95% CI, the variable was considered not to contribute to the overall model (Hosmer and Lemeshow 2000). I removed models from the analysis when pretender variables were evident in models with $\Delta$AIC $\leq$2 of the highest ranked model (Burnham and Anderson 2002). Models with $\Delta$AIC >10 were considered non-significant and were not presented (Burnham and Anderson 2002).

I evaluated model fit using a confusion matrix to develop resubstitution misclassification estimates based on the number of correct or incorrect classifications for the best model (Boyce et al. 2002).

## RESULTS

### *TELEMETRY*

During this study, I located 124 radio-marked sage-grouse that were previously captured during the spring or summers of 2005–2007. In North Dakota, 22 and 30 birds were monitored during the winters of 2005–2006 and 2006–2007 and 42 and 30 birds were monitored during the winters of 2006–2007 and 2007–2008 in South Dakota, respectively.

### *WINTER HABITAT*

I collected habitat measurements at 340 paired (177 ND, 163 SD) sage-grouse used and random sites during this study (Table 3-1). Used sites were characterized by 3.8% higher vegetation cover, 4.3% less grass cover, 7.6% higher sagebrush cover, approximately 1.2 more shrubs per $m^2$, 1.4 cm higher vegetation height, and 1.3 cm shorter sagebrush height compared to random sites (Table 3-2).

### *MODELS PREDICTING WINTER HABITAT USE*

#### *North Dakota*

The most supported of the 21 candidate models of sage-grouse winter habitat use included terms for percent sagebrush cover ($\beta = 0.33$, SE = 0.04), sagebrush height ($\beta = -0.04$, SE = 0.02), and percent snow cover ($\beta = 0.03$, SE = 0.01), respectively (Table 3-3). Model weight ($w_i = 0.51$) indicated that this model had considerable support. Point estimates from the best model indicated that percent sagebrush cover (1.39, 95% CI 1.29–1.49) and percent snow cover (1.03, 95% CI 1.01–1.06) were positively related to winter habitat use, while sagebrush height (0.96, 95% CI 0.92–0.99) had a negative relationship. The most supported model was 84.4% accurate in classifying model fit to the data.

*South Dakota*

The highest ranked model (21 candidate models) included terms for percent sagebrush cover (β = 0.41, SE = 0.05) and sagebrush height (β = -0.18, SE = 0.05) and had a model weight ($w_i$) of 0.69 (Table 3-4). Point estimates were positive for percent sagebrush cover (1.50, 95% CI 1.36–1.66) and negative for sagebrush height (0.84, 95% CI 0.75–0.93). The highest ranked model was 90% accurate in classifying model fit to the data.

*Regional scale*

Percent sagebrush cover and sagebrush density (r = 0.70) and percent grass cover and percent total cover (r = 0.80) were correlated variables. I retained percent sagebrush cover and percent grass cover for all models. The highest ranked model ($w_i$ = 0.78; 21 candidate models) included percent sagebrush cover (β = 0.35, SE = 0.03) and sagebrush height (β = -0.07, SE = 0.02), respectively (Table 3-5). Odd ratios from the highest ranked model indicated that percent sagebrush (1.41, 95% CI 1.34–1.50) was positive, while sagebrush height (0.94, 95% CI 0.90–0.97) was negatively related to sage-grouse winter habitat use. The highest ranked model was 86.2% accurate in classifying model fit to the data.

## DISCUSSION

During this study, sage-grouse used habitat that provided the highest available sagebrush canopy cover. Sagebrush canopy cover occurred in all top models and was the highest ranked variable regardless of the level of habitat use was evaluated. Previous studies have documented similar findings suggesting that sagebrush vegetation cover was the primary factor influencing habitat use of sage-grouse during winter (Eng and Schaldweiler 1972, Connelly et al. 2000, Doherty et al. 2008). However, winter habitat in the Dakotas was characterized by less sagebrush cover and shorter sagebrush compared to core areas (Eng and Schaldweiler 1972, Schoenberg 1982, Hupp 1987, Robertson 1991). Specifically, sagebrush canopy cover in North Dakota (11.4%) and in South Dakota (18.8%) was lower than previously reported (Eng and Schladweiler 1972, Wallestad 1975, Autenrieth 1981, Connelly 1982, Schoenberg 1982, Hupp 1987, Robertson 1991). These studies also had >20% sagebrush canopy cover with the exception of Robertson (1991) that documented 15% sagebrush canopy cover in Idaho. Secondly, sagebrush heights at used sites were lower than at random sites and did not meet Connelly et al.'s (2000) recommendation for sagebrush height (25-35 cm) during winter. In core areas of sage-grouse range, sagebrush heights are generally taller at used sites compared to random sites (Robertson 1981, Connelly 1982). Although sagebrush height was statistically meaningful in relation to habitat use, I believe that it was not biologically important and that sage-grouse were not selecting for shorter sagebrush height. Rather, sage-grouse selected the highest canopy cover and these areas were characterized by shorter sagebrush. Thus, in this region, the areas with the highest sagebrush canopy cover generally have lower sagebrush heights.

As expected, sage-grouse used dense sagebrush to meet their requirements for food and cover. I suggest that factors influencing sage-grouse winter habitat use are not different compared to in core areas; however, the mechanisms affecting sagebrush vegetation in this region could be the main reason why sagebrush is less dense and shorter than in other regions. Differences in sagebrush vegetation in the Dakotas may be a reflection of sagebrush growth potential, effects of grazing, and timing of precipitation in this region.

Characteristics of habitat used by sage-grouse in the Dakotas appear to be different than core areas because of the synecology of sagebrush subspecies in these systems. The sagebrush I measured at used sites was characterized by a monotypic stand of Wyoming big sagebrush collected during mild winters when snow depths rarely exceeded 10 cm. In general, Wyoming big sagebrush shrubs tend to be smaller, favor xeric conditions, and have slower growing seedlings, even when nutrients are not limiting than the other two widely distributed big sagebrush subspecies (basin big sagebrush [*Artemisia tridentata tridentata*] and mountain big sagebrush [*Artemisia tridentata vaseyana*]; Howard 1999, Welch 2005) found in core sage-grouse range.

Wyoming big sagebrush also is considered to be the most palatable subspecies of big sagebrush and it is heavily grazed by ungulates during winter (Schlatterer 1973, Tweit and Houston 1980). In fact, pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) selection for and consumption of big sagebrush peaks during winter (Olsen and Hansen 1977, Wambolt 1996). These ungulates consume big sagebrush for its high lipid content to help maintain their fat reserves (Martinka 1967), which directly influences their future reproductive success (Peterson 1984). After several mild winters, ungulate density was considered high and domestic livestock (e.g., cattle [*Bos taurus*], sheep [*Ovis aries*]) were common throughout the region, which may have prevented big sagebrush seedlings or mature plants from achieving their growth potential (Houston 1961, Frischknecht and Harris 1973, McArthur et al. 1988) if they were overgrazed or trampled.

Another factor potentially influencing big sagebrush in this region was the timing of precipitation received prior to the peak of annual sagebrush growth. Because of the extensive and deep root system of big sagebrush spp., precipitation received mainly as snow during the winter (e.g., core areas) favor the growth and development of big sagebrush spp. because the moisture from the snow percolates deeper into the soil profile (Comstock and Ehleringer 1992, Schwinning et al. 2003). Conversely, precipitation is more likely to be evaporated before infiltrating the soil in the Dakotas because most of the precipitation occurs as rain from April through July (Schwinning et al. 2003). Therefore, the soil moisture conditions in the Dakotas may result in reduced shrub size and less shrub cover compared to similar stands of Wyoming big sagebrush (e.g., core areas). Wyoming big sagebrush is uniquely adapted to take advantage of good soil moisture conditions by retaining about one-third of its leaves in winter and by developing ephemeral leaves early in the spring. This allows Wyoming big sagebrush to begin photosynthesis and growth when soil moisture conditions are optimal (DePuit and

Caldwell 1973, Miller and Schultz 1987). Wyoming big sagebrush in the Dakotas may not develop its ephemeral leaves to the same extent that the plant does in core sage-grouse range, which could reduce shrub size and canopy cover. Furthermore, if Wyoming big sagebrush begins each year under poor growing conditions, the effects of any additional grazing pressure may only compound the deficiencies in size structure of the sagebrush community in the Dakotas. Findings from this study, Herman-Brunson (2007), and Kaczor (2008) regarding sagebrush height (20-38 cm) and sagebrush canopy cover (4.7-18.8%) indicate that sagebrush community structure is limited by these causal mechanisms (e.g., soil moisture, precipitation) compared to more favorable conditions in core areas. By understanding the causal mechanisms influencing sagebrush in a given region, management could focus on developing strategies that limit further degradation of sagebrush.

Findings from this study were indicative of the winter habitat characteristics used by sage-grouse on the eastern edge of their range. Sagebrush density and height in this region was lower than in core areas and may lack the potential to exist at levels recommended by Connelly et al. (2000). Nonetheless, sage-grouse had high survival (>90 %; Chapter 2) during winter and Kaczor (2008) noted that females in this region were heavier prior to nesting than in other studies (Schroeder et al. 1999). These factors indicate that current winter habitat conditions allow sage-grouse to meet their physiological needs during mild winters and enter the reproductive period in good physiological condition. Unfortunately, I could not determine the effect of severe winter weather on habitat use or survival during this study. During prolonged periods of severe winter weather, mortality could be higher (Moynahan et al. 2006) and sage-grouse would likely move long distances into Montana and Wyoming to escape deep snow that could limit availability of the low sagebrush in this region.

## MANAGEMENT IMPLICATIONS

My findings indicate that sagebrush canopy cover was the primary factor influencing winter habitat use. I suggest that sagebrush in the Dakotas have different conditions for growth than in core sage-grouse range and will likely remain on the low end or below the Connelly et al. (2000) recommendations for winter sagebrush canopy cover (i.e., 10-30%). I suggest that management agencies may need to develop regional based management strategies that reflect the synecology of a particular sagebrush system rather than focusing on range-wide guidelines for sagebrush habitat. Management could limit activities that cause disturbance (e.g., trampling by domestic livestock) to sagebrush plants during their growth period because of the negative effects to the size structure of sagebrush in this region. Instead of trying to manage sagebrush habitat to meet range-wide recommendations, it may be more beneficial for managers to understand the causal mechanisms that affect the growth and density of Wyoming big sagebrush and develop regional management strategies that address the annual requirements of both sagebrush and sage-grouse. Additional research in this region is needed to evaluate the effects that timing and density of livestock and wild ungulate grazing have on Wyoming big sagebrush. At a minimum, critical wintering areas could be identified and maintained without further habitat loss.

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Table 3-1. Average vegetation characteristics of winter habitat for sage-grouse at 340 (177 ND, 163 SD) used and 250 and 500 m dependent random sites in North Dakota 2005–2007 and South Dakota 2006–2008.

| | North Dakota | | | | | | South Dakota | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | Use | SE | 250 | SE | 500 | SE | Use | SE | 250 | SE | 500 | SE |
| Sagebrush cover (%) [a] | 11.43 | 0.57 | 4.76 | 0.34 | 4.40 | 0.32 | 18.79 | 0.44 | 10.94 | 0.47 | 9.93 | 0.53 |
| Grass cover (%) | 11.83 | 0.91 | 14.57 | 1.09 | 15.49 | 1.10 | 11.69 | 0.61 | 17.04 | 0.88 | 17.12 | 0.78 |
| Forb cover (%) | 7.74 | 0.81 | 7.78 | 0.79 | 7.91 | 0.83 | 4.04 | 0.34 | 3.55 | 0.40 | 3.86 | 0.40 |
| Total vegetation cover | 33.50 | 1.45 | 29.56 | 1.81 | 29.87 | 1.90 | 40.30 | 1.15 | 36.99 | 1.27 | 36.08 | 1.22 |
| Snow cover (%) | 32.03 | 2.47 | 31.17 | 2.66 | 31.05 | 2.67 | 31.26 | 2.69 | 33.15 | 2.84 | 32.85 | 2.86 |
| Litter cover (%) | 3.16 | 0.24 | 4.51 | 0.35 | 4.47 | 0.40 | 5.63 | 0.43 | 6.27 | 0.47 | 7.11 | 0.57 |
| Big sagebrush cover | 10.68 | 0.57 | 4.31 | 0.32 | 4.03 | 0.30 | n/a | -- | n/a | -- | n/a | -- |
| Silver sagebrush cover | 0.61 | 0.18 | 0.42 | 0.10 | 0.41 | 0.12 | n/a | -- | n/a | -- | n/a | -- |
| Vegetation height (cm) | 14.68 | 0.24 | 12.40 | 0.21 | 12.88 | 0.21 | 13.08 | 0.15 | 12.67 | 0.15 | 11.99 | 0.19 |
| Sagebrush height (cm) | 22.93 | 0.64 | 24.19 | 0.76 | 24.46 | 0.73 | 16.85 | 0.28 | 18.11 | 0.36 | 18.13 | 0.35 |
| Sagebrush density | 1.27 | 1.08 | 0.49 | 0.06 | 0.48 | 0.06 | 3.02 | 0.10 | 1.48 | 0.09 | 1.29 | 0.10 |

[a] Big sagebrush cover was the only *Artemisia* spp. estimated in South Dakota.

[b] Refer to sagebrush cover for South Dakota.

[c] No silver sagebrush was measured in South Dakota.

Table 3-2. Comparison (ANOVA) of greater sage-grouse winter habitat use site and dependent random site variables at the landscape level in North Dakota 2005–2007 and South Dakota 2006–2008.

| Variable | Use | SE | 250[a] | SE | 500[b] | SE | Test | *P*- |
|---|---|---|---|---|---|---|---|---|
| Sagebrush cover (%) | 14.97 | 0.41 | 7.72 | 0.33 | 7.05 | 0.34 | 190.80 | <0.01 |
| Grass cover (%) | 11.76 | 0.56 | 15.76 | 0.71 | 16.27 | 0.68 | 14.55 | <0.01 |
| Forb cover (%) | 5.97 | 0.46 | 5.75 | 0.47 | 5.97 | 0.48 | 0.08 | 0.92 |
| Total vegetation | 36.76 | 0.95 | 33.12 | 1.14 | 32.84 | 32.85 | 4.13 | 0.02 |
| Vegetation height | 13.91 | 0.14 | 12.53 | 0.13 | 12.44 | 0.14 | 5.25 | <0.01 |
| Sagebrush height | 20.01 | 0.40 | 21.28 | 0.46 | 21.43 | 0.45 | 3.63 | 0.03 |
| Sagebrush density | 2.11 | 0.09 | 0.97 | 0.06 | 0.87 | 0.06 | 120.65 | <0.01 |
| Snow cover (%) | 31.66 | 1.82 | 32.12 | 1.94 | 31.92 | 1.95 | -- | -- |
| Litter cover (%) | 4.34 | 0.25 | 5.36 | 0.29 | 5.74 | 0.35 | -- | -- |

[b] Dependent random site.

Table 3-3. Conditional logistic regression models predicting greater sage-grouse winter habitat use (*n* = 177) versus dependent random sites (*n* = 354) using data collected in North Dakota, 2005–2007.

| Candidate Models | | | | | |
|---|---|---|---|---|---|
| Model[a] | -2LL[b] | K[c] | AIC[d] | ΔAIC[e] | $w_i$[f] |
| SAGE + SGHT + SNOW | 218.345 | 4 | 226.345 | 0.000 | 0.511 |
| SAGE + SNOW | 223.264 | 3 | 229.264 | 2.919 | 0.119 |
| GLOBAL | 218.054 | 6 | 230.054 | 3.709 | 0.080 |
| SAGE + SGHT | 224.164 | 3 | 230.164 | 3.819 | 0.076 |
| SAGE + SNOW + VGHT | 222.449 | 4 | 230.449 | 4.104 | 0.066 |
| SAGE + GRASS + SGHT | 223.724 | 4 | 231.724 | 5.379 | 0.035 |
| SAGE + VGHT + SGHT | 223.915 | 4 | 231.915 | 5.570 | 0.032 |
| SAGE + SNOW + GRASS + VGHT | 222.032 | 5 | 232.032 | 5.687 | 0.030 |
| SAGE + GRASS | 226.913 | 3 | 232.913 | 6.568 | 0.019 |
| SAGE | 229.068 | 2 | 233.068 | 6.723 | 0.018 |
| SAGE + VGHT | 228.323 | 3 | 234.323 | 7.978 | 0.009 |
| VGHT + SAGE + GRASS | 226.906 | 4 | 234.906 | 8.561 | 0.007 |

[a] We included the following variables in the models: % sagebrush canopy cover (SAGE), % residual grass canopy cover (GRASS), % snow canopy cover (SNOW), sagebrush height (SGHT), and vegetation height (VGHT).

[b] -2LL = -2loglikelihood

[c] K = number of parameters

[d] AIC = Akaike's Information Criterion

[e] ΔAIC = change in AIC from the top model (ΔAIC)

[f] $w_i$ = Akaike weight; computed as ratio: exp(-½ΔAIC)/Σ exp(-½ΔAIC)

Table 3-4. Conditional logistic regression models predicting greater sage-grouse winter habitat use ($n$ = 163) versus dependent random sites ($n$ = 326) using data collected in South Dakota, 2006–2008.

| Candidate Models | | | | | |
|---|---|---|---|---|---|
| Model[a] | -2LL[b] | K[c] | AIC[d] | ΔAIC[e] | $w_i$[f] |
| SAGE + SGHT | 126.648 | 3 | 132.648 | 0.000 | 0.694 |
| SAGE + SGHT + GRASS + SNOW | 125.033 | 5 | 135.033 | 2.385 | 0.210 |
| GLOBAL | 124.784 | 6 | 136.784 | 4.136 | 0.087 |

[a] We included the following variables in the models: % sagebrush canopy cover (SAGE), % residual grass canopy cover (GRASS), % snow canopy cover (SNOW), sagebrush height (SGHT), and vegetation height (VGHT).

[b] -2LL = -2loglikelihood

[c] K = number of parameters

[d] AIC = Akaike's Information Criterion

[e] ΔAIC = change in AIC from the top model (ΔAIC)

[f] $w_i$ = Akaike weight; computed as ratio: exp(-½ΔAIC)/Σ exp(-½ΔAIC)

Table 3-5. Conditional logistic regression models predicting greater sage-grouse winter habitat use ($n$ = 340) versus dependent random sites ($n$ = 680) using data collected in North Dakota during 2005-2007 and in South Dakota during 2006–2008.

| Candidate Models | | | | | |
|---|---|---|---|---|---|
| Model[a] | -2LL[b] | K[c] | AIC[d] | ΔAIC[e] | $w_i$[f] |
| SAGE + SGHT | 365.476 | 3 | 371.476 | 0.000 | 0.781 |
| GLOBAL | 362.320 | 6 | 374.320 | 2.844 | 0.188 |
| SAGE + GRASS | 374.101 | 3 | 380.101 | 8.625 | 0.010 |

[a] We included the following variables in the models: % sagebrush canopy cover (SAGE), % residual grass canopy cover (GRASS), % snow canopy cover (SNOW), sagebrush height (SGHT), and vegetation height (VGHT).

[b] -2LL = -2loglikelihood

[c] K = number of parameters

[d] AIC = Akaike's Information Criterion

[e] ΔAIC = change in AIC from the top model (ΔAIC)

[f] $w_i$ = Akaike weight; computed as ratio: exp(-½ΔAIC)/Σ exp(-½ΔAIC)

# CHAPTER 4

# SEASONAL MOVEMENTS OF SAGE-GROUSE: MIGRATION, SURVIVAL, AND NATAL DISPERSAL

**Abstract:** Movement behavior of greater sage-grouse (*Centrocercus urophasianus*) varies by region and may be affected by the configuration of seasonal habitats; however, knowledge of seasonal movements of sage-grouse within the eastern-most extension of sagebrush steppe communities is lacking. I evaluated movements of sage-grouse in the Dakotas during all aspects of their life-cycle to: 1) evaluate the timing and frequency of sage-grouse migration, 2) estimate survival of migratory and non-migratory sage-grouse, 3) estimate seasonal distribution and core seasonal ranges, and 4) evaluate the timing and distance of natal dispersal by juvenile sage-grouse. I captured and radio-marked 219 (97 females, 54 males, 68 juvenile) sage-grouse during 2005 and 2006 in North Dakota and during 2006 and 2007 in South Dakota. I collected 6,072 locations, documented 89 seasonal migrations (21 in ND, 68 in SD) and 158 instances of non-migratory behavior (73 in ND, 85 in SD) during eight migration periods. Sage-grouse were partially migratory with most (58%) birds considered resident. Average distance moved by migratory sage-grouse between breeding/nesting and summer range was 11.1 and 9.6 km, summer and winter range was 11.8 and 16.8 km, and winter and breeding range was 6.5 and 15.8 km in North Dakota and South Dakota, respectively. Timing of spring migration coincided with abandonment of leks by males and age of chicks (i.e., 3-4 weeks) for females. Timing of migration from summer to winter and winter to breeding ranges was variable as movements were gradual and occurred over several months.

Overall, survival of migratory sage-grouse differed from non-migratory sage-grouse in North Dakota ($\chi^2_1 = 4.65$, $P = 0.03$) and was similar in South Dakota ($\chi^2_1 = 0.95$, $P = 0.33$). However, survival did not differ among males ($\chi^2_1 = 0.22$, $P = 0.88$) and females ($\chi^2_1 = 0.39$, $P = 0.84$). Median date of natal dispersal of juveniles ($n = 11$) was 7 January (range = 15 October to 15 April) with a median dispersal distance of 11.7 km that was similar ($P = 0.13$) between females and males and between study areas ($P = 0.24$). Evidence of migration in this region indicates that highly interspersed seasonal habitats may not completely regulate migration in sage-grouse populations.

*Key words: Centrocercus urophasianus,* greater sage-grouse, migration, natal dispersal, North Dakota, seasonal movement, South Dakota, survival

## INTRODUCTION

Seasonal movements (i.e., migration, dispersal) of greater sage-grouse (*Centrocercus urophasianus*) vary by region and are dependent upon the proximity of seasonal habitats (Berry and Eng 1985). At high elevations, sage-grouse are often migratory (Dalke et al. 1960, Connelly 1982), while populations occupying low elevations are often non-migratory (Wallestad 1975). On an annual basis, sage-grouse may migrate between two-stage (winter/breeding and summer range) or three-stage (breeding, summer, and winter) seasonal ranges (Connelly et al. 2004). However, factors influencing sage-grouse seasonal movements during their life-cycle are poorly understood. Patterns of migration in animals have evolved to exploit spatial and temporal variation in the environment (French et al. 1989). Factors that have been suggested to influence sage-grouse migration include: differences in topography and precipitation, tradition, configuration of seasonal habitats, distribution of succulent vegetation during summer, site fidelity, and severe winter weather (Autenrieth 1981, Berry and Eng 1985, Connelly et al. 1988, Connelly et al. 2003, Schroeder and Robb 2004). Because sage-grouse are considered a landscape-scale species (Patterson 1952, Wakkinen 1990), it is important to understand factors that influence seasonal movements at both local and landscape levels.

Migration is thought to maximize fitness because animals can choose habitats that improve their reproductive success (Fretwell 1972). However, several migration strategies can occur within the same population due to environmental heterogeneity, behavioral plasticity, and differential survival between migrators and residents (Fretwell 1972, Nicholson et al. 1997, Scheiner 1993). Migratory individuals have inherent risks of traversing unfamiliar habitats that can increase their vulnerability to predators, whereas, residents may avoid migration because of suitable resources or decreased competition within their territory (Kokko and Lundberg 2001, White et al. 2007). Because migratory individuals may leave temporarily unfavorable conditions, their survival may be higher compared to those that stayed (Kokko and Lundberg 2001). Yet, it is unknown whether migration in sage-grouse populations improves survival.

Sage-grouse may use an area of up to several thousand kilometers on an annual basis (Patterson 1952). The distribution of sage-grouse in the Dakotas lies within the eastward extension of sagebrush (*Artemisia* spp.) steppe communities and coincides with the occurrence of Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) and silver sagebrush (*Artemisia cana* spp. *cana*; Schroeder et al. 1999). However, sage-grouse critical seasonal ranges have not been identified and information regarding the proximity and interspersion of these ranges is lacking in the Dakotas.

Dispersal is one of the least understood aspects of animal population dynamics (Macdonald and Johnson 2001). Dispersal in many species is influenced by genetic factors, social pressures, habitat quality, and experience (Kenward et al. 2001). Dispersal enables species to avoid extinction by linking metapopulations (Levins 1969), reduces inbreeding (Pusey and Wolf 1996), maintains genetic flow (Caizergues and Ellison 2002, Bouzat and Johnson 2004), and decreases intraspecific competition (Greenwood 1980). However, dispersal movements can result in decreased individual fitness and an uncertainty in finding suitable habitat (Gaines and McClenaghan 1980, Van Vuren and Armitage 1994). Dispersal is difficult to quantify in grouse because they generally have short life spans (Beaudette and Keppie 1992) and dispersal is not completely understood in sage-grouse (Dunn and Braun 1985, Connelly et al. 2004).

Natal dispersal is considered the permanent movement of an individual from its birth site to an area where reproduction occurs (Howard 1960). Female sage-grouse typically disperse farther distances than males (Dunn and Braun 1985). However, sage-grouse may also be philopatric because yearlings have been documented to attend their natal-area lek. Female sage-grouse tend to make inter-lek movements during the breeding period to select the best mate, which could be the reason for the gender based dispersal bias (Dunn and Braun 1985). Nonetheless, reasons as to why dispersal distances can differ by gender of lekking species are not clearly understood (Caizergues and Ellison 2002) and information does not exist on sage-grouse dispersal in the Dakotas.

Knowledge of seasonal movements of sage-grouse within the eastern-most extension of sagebrush steppe communities is lacking. This information could be important for sage-grouse management in the Dakotas due to recent population declines (Smith et al. 2004, Chapter 2) and the limited understanding of sage-grouse ecology in this region (Smith et al. 2006). Therefore, I documented movements of radio-marked sage-grouse in the Dakotas during all aspects of their life-cycle to: 1) evaluate the timing and frequency of sage-grouse migration, 2) estimate survival of migratory and non-migratory sage-grouse, 3) estimate seasonal distribution and core seasonal ranges, and 4) evaluate the timing and distance of natal dispersal by juvenile sage-grouse.

## STUDY AREA

This study was conducted in Bowman County, North Dakota (46º 7' 22.368″ N, 104º 0' 24.318″ W) and Butte County, South Dakota (45º 1' 52.329″ N, 103º 44' 41.196″ W) and adjacent parts of Montana and Wyoming. This region was semiarid sagebrush (*Artemisia* spp.) rangeland characterized by gentle slopes to steep buttes and ridges with elevations that ranged from 640 to 1225 m above sea level (Opdahl et al. 1975, Johnson 1976). Vegetation in this region was described by Opdahl et al. (1975), Johnson (1976), and Johnson and Larson (1999) and was considered low shrubland with short to mid grass prairie being dominant. Shrubs in the area were dominated by Wyoming big sagebrush, but also included silver sagebrush, broom snakeweed (*Gutierrezia sarothrae*), rubber rabbitbrush (*Ericameria nauseosus*), and greasewood (*Sarcobatus vermiculatus*). Common perennial grasses were green needle-grass (*Nassella viridula*), Junegrass (*Koeleria macrantha*), western wheatgrass (*Pascopyrum smithii*), Kentucky bluegrass

(*Poa pratensis*), Japenese brome (*Bromus japonicus*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), buffalograss (*Buchloe dactyloides*), needleandthread (*Hesperostipa comata)*, and little bluestem (*Schizachrium scoparium)*. Common forbs were common dandelion (*Taraxacum officinale*), textile onion (*Allium textile*), field pennycress (*Thlaspi arvense*), and western yarrow (*Achillea millefolium*). Land use was dominated by livestock grazing, 45% of Bowman County and 5% of Butte County was farmed for cultivated crops.

The climate was continental with cold dry winters and warm summers with most of the precipitation occurring in late spring and early summer. Average monthly temperatures in North Dakota were -9.7 ºC in January and 20.8 ºC in July with average annual precipitation and snowfall of 39.4 and 122.7 cm. Average monthly temperatures in South Dakota were -4.8 ºC in January and 22.7 ºC in July with average annual precipitation and snowfall of 45.54 and 89.9 cm, respectively (National Climatic Data Center 1971-2000).

## METHODS

### *CAPTURING AND MARKING*

I captured breeding-age (≥1yr) sage-grouse near leks during the breeding season and juveniles (≥10 weeks) from early July to mid September at night using spotlights (Giesen et al. 1982, Wakkinen et al. 1992) and a thermal infrared imaging camera. Hens were fitted with a necklace-type radio transmitter (model A4060, Advanced Telemetry Systems, Isanti, Minnesota) with an 8-hour mortality switch that weighed 21.6 g, and had an expected battery life of 434 days. Males were fitted with a backpack-type radio transmitter (model A1135, Advanced Telemetry Systems, Isanti, Minnesota) with an 8-hour mortality switch that weighed 17.9 g, and had an expected battery life of 297 days. Captured birds were classified as adults (≥2 yr, second or later breeding season), yearlings (≥1 yr, first breeding season), or juvenile based on the length and shape of the 9th and 10th primaries (Beck et al. 1975) and assigned a gender based on plumage characteristics (Bihrle 1993). All radio-transmitters were less than 3% of the body weight of birds at the time of attachment. All capture and handling protocols were approved by the South Dakota State University Institutional Animal Care and Use Committee (approval number: 07-A032).

### *TELEMETRY*

I located radio-marked sage-grouse from 1 April 2005 to 28 February 2007 in North Dakota and from 1 April 2006 to 28 February 2008 in South Dakota. I visually located sage-grouse ≥1 times per week with a hand-held antenna or by fixed wing aircraft when signals were not detected from the ground. All locations were recorded with a Global Positioning System (GPS) receiver in Universal Transverse Mercator (UTM) coordinates (NAD27; UTM Zone 13). Mortality was assessed via evidence collected at the death site, field necropsy, or laboratory examination.

### *SEASONAL MOVEMENTS*

I plotted sage-grouse locations in ArcGIS 9.2 Geographic Information System (ESRI, Redlands, California) to assess seasonal movements (i.e, migration, dispersal). I defined migration as the temporary movement between non-overlapping seasonal ranges, measured as the straight-line distance between centers of seasonal ranges. I used the home range tools (HRT) analysis extension in ArcGIS to generate 95% minimum convex polygons (MCP) of individual sage-grouse locations on seasonal ranges. If overlap existed between seasonal ranges, migration did not occur. The median date between the last known observation and first date of observation at a new seasonal range was considered the migration date. I defined late spring migration as the movement from nesting/breeding area to summer range, late summer migration as the movement from summer to winter range, and late winter migration as the movement from winter to breeding range. Dispersal was defined as the permanent movement of individual sage-grouse from an established seasonal range to a new, non-overlapping home area.

### *SURVIVAL*

I used the Kaplan-Meier method (Kaplan and Meier 1958) modified for the staggered entry design (Pollack et al. 1989) to estimate pooled annual survival from 1 March to 28 February of migratory and resident breeding-age sage-grouse. I estimated survival across years within and between study areas. I also estimated survival across years within and between study areas for males and females. I classified migratory sage-grouse as those that made ≥1 migration between seasonal ranges (i.e., late spring, late summer, or late winter) on an annual basis. Sage-grouse that did not migrate during >3 consecutive migration periods were classified as residents. Because a limited number of migrations occurred during each migration period in a given year, I combined data by study area and across years to increase robustness of survival estimates. I right-censored grouse if they disappeared from the study area and were never relocated, when the bird could not be accessed on private lands, or because of radio-transmitter failure.

### *DISTRIBUTION OF SAGE-GROUSE*

I estimated the core 50% distribution of sage-grouse locations within each biological period including: nesting (16 Apr – 15 Jun), early brood-rearing (16 Jun – 15 Jul), late brood-rearing (16 Jul – 31 Oct), winter (1 Nov – 28 Feb), and breeding (1 Mar – 15 April). I created 50% MCP's using the HRT tool in ArcGIS for North Dakota and for South Dakota as an indicator of core distribution. I used a MCP as a conservative estimate of core seasonal ranges. A 95% MCP also was created to determine the cumulative distribution of sage-grouse locations in each study area. Area of each MCP was calculated using Hawth's analysis tools (Beyer 2004) in ArcGIS.

I also evaluated sage-grouse distribution relative to active leks. I calculated the percent of locations near active leks within 3.2 and 5 km buffers during four of five seasonal periods that were representative of their annual life-history in this region including: nesting, early brood-rearing, late brood-rearing, and winter. I did not estimate the percent of locations near active leks during the breeding season because I had <5 locations per individual sage-grouse, which I believed was insufficient to determine percent use. I evaluated movements relative to a 3.2 km buffer because the Bureau of Land Management (BLM) delineates their protection (i.e., surface use) of active leks within this buffer from 1 March to 15 June. I also evaluated a 5 km buffer based on Herman-Brunson (2007) recommendation of an expanded buffer to protect additional nesting habitat. I created 3.2 and 5 km buffers using the vector editing tool around active leks using Hawth's analysis tools (Beyer 2004) in ArcGIS. Percent use was calculated within each buffer as the number of sage-grouse locations during each seasonal period within the lek buffer divided by the sum of locations for each individual grouse. Then, I calculated overall percent use during each season for female, male, and juveniles and by study area as the total number of locations for all grouse within the buffer divided by the sum of the total locations for all grouse.

### *NATAL DISPERSAL*

Natal dispersal was considered the movement of an individual from its birth site to the breeding/reproductive area (Howard 1960). I plotted juvenile sage-grouse locations in ArcGIS and measured natal dispersal distance between birth site and breeding/reproductive area. Female natal dispersal distance was measured as the straight-line distance from birth site to nest site the following spring. For males, it was the straight-line distance from the birth site to the center of their locations during the breeding season. I obtained locations from 1 March to 17 August 2007 from a separate study (unpublished data, South Dakota State University) to determine natal dispersal for juvenile sage-grouse captured during 2006 in North Dakota. Natal dispersal for juveniles captured during 2007 in South Dakota could not be estimated because this study ended before dispersal movements were complete.

### *DATA ANALYSIS*

I tested for differences among sage-grouse migration distance and date using fixed effects two-way analysis of variance (ANOVA); alpha set at $P \leq 0.05$. Migration distance and date was compared between gender and study area and among years within study area. I used one-way ANOVA’s when data were only available for one gender or one study area; alpha set at $P \leq 0.05$. Natal dispersal distance and date were compared between gender and study areas using Kruskal-Wallis tests; alpha set at $P \leq 0.05$. I did not examine year effects for natal dispersal because of small sample size.

I compared survival estimates by gender, migration type, and study area using Program CONTRAST (Hines and Sauer 1989); alpha was set at $P \leq 0.05$.

## RESULTS

I captured and radio-marked 219 (97 females, 54 males, 68 juvenile) sage-grouse during 2005 and 2006 in North Dakota and during 2006 and 2007 in South Dakota. Of these, I captured 86 birds (34 in 2005, 52 in 2006) in North Dakota and 133 birds (80 in 2006, 53 in 2007) in South Dakota, respectively. A total of 6,072 locations were collected in North Dakota ($n$ = 2,407) and in South Dakota ($n$ = 3,665). I identified three periods when migration occurred between seasonal ranges: late spring (15 May – 15 July), late summer (15 August – 15 December), late winter (1 Feb – 15 April). I documented 89 seasonal movements (21 in ND, 68 in SD) and 158 instances of non-migratory behavior (73 in ND, 85 in SD) during eight total migratory periods; late spring 2005 ($n$ = 13), late summer 2005 ($n$ = 14), late winter 2006 ($n$ = 9), late spring 2006 ($n$ = 36 in ND, $n$ = 44 in SD), late summer 2006 ($n$ = 22 in ND, $n$ = 30 in SD), late winter 2007 ($n$ = 28), late spring 2007 ($n$ = 39), and late summer 2007 ($n$ = 12), respectively.

### *SEASONAL MOVEMENT*

### *Late spring*

During 2005, 1 of 13 (7.7%) female sage-grouse in North Dakota migrated 8.1 km from its nesting area to summer range. The remainder of sage-grouse did not migrate to different range. During 2006, 8 of 36 (22.2%; 21 F, 15 M) sage-grouse in North Dakota migrated an average of 11.5 km (SE = 1.6) and 22 of 44 (50%; 33 F, 11 M) sage-grouse in South Dakota migrated 10.5 km (SE = 1.2), respectively. Average date of migration was 19 June ± 3.8 days and was similar between study areas ($F_{1,\,29} = 0.61$, $P = 0.44$) but was earlier ($F_{1,\,29} = 9.80$, $P < 0.01$) for males (1 June ± 4.8 days) than females (22 June ± 4.7 days). During 2007, 15 of 39 (38.5%; 30 F, 19 M) sage-grouse migrated 8.2 km (SE = 1.0) in South Dakota. Average date of migration was 15 June ± 6.0 days and was earlier ($F_{1,\,37} = 17.31$, $P < 0.01$) for males (3 June ± 3.7 days) than females (28 June ± 10.4 days) and did not differ ($F_{1,\,37} = 0.31$, $P = 0.58$) between years in South Dakota. Overall, movement distance did not vary by gender or between study areas (Table 4-1).

More hens migrated that had failed nests ($n = 18$) versus hens that migrated and had successful nests ($n = 10$). Furthermore, hens with failed nests moved approximately 9 days earlier (25 June ± 5.3 days) and 2.4 km (11.5 km, SE = 1.4) farther on average than those that migrated and had successful nests (4 July ± 4.2 days; 9.1 km, SE = 1.9).

### *Late summer*

During 2005, 1 of 14 (7.1%; 14 F) sage-grouse in North Dakota migrated 6.96 km on 17 October. During 2006, 8 of 22 (36.4%; 21 F, 1 M) sage-grouse in North Dakota migrated 12.4 km (SE = 2.1) and 13 of 30 (43.3%; 28 F, 2 M) sage-grouse in South Dakota migrated 15.8 km (SE = 2.2), respectively. All migratory individuals were female. Average date of migration was 12 October ± 5.6 days and was similar between study areas ($F_{1,\,20} = 0.93$, $P = 0.35$). During 2007, 5 of 12 (41.7%; 10 F, 2 M) sage-grouse migrated 19.2 km (SE = 1.8). Similar to 2006, I only observed migratory behavior in females. Average date of migration was 28 October ± 4.0 days and was similar ($F_{1, 17}$ = 1.49, $P$ = 0.24) between years in South Dakota. Overall, females migrated farther in South Dakota than in North Dakota.

### *Late winter*

During 2006, 3 of 9 (33.3%; 9 F) sage-grouse in North Dakota migrated 6.5 km (SE = 0.2) on 25 February ± 12.7 days. During 2007, 13 of 28 (46.4%; 27 F, 1M) sage-grouse in South Dakota migrated 15.8 km (SE = 2.2). Average date of migration was 12 March ± 4.4 days and was similar between study areas ($F_{1, 15}$ = 1.36, $P$ = 0.26). All migratory sage-grouse were female.

## *SURVIVAL*

Sage-grouse in North Dakota that migrated ($n$ = 13) between seasonal ranges had a higher rate of survival ($\chi^2_1$ = 4.65, $P$ = 0.03) than those that did not migrate ($n$ = 31; Table 4-2). In South Dakota, survival of migratory sage-grouse ($n$ = 31) was similar ($\chi^2_1$ = 0.95, $P$ = 0.33) to those that did not migrate ($n$ = 29). Overall, survival of migratory sage-grouse was similar to non-migratory sage-grouse among males ($\chi^2_1$ = 0.23, $P$ = 0.88) and females ($\chi^2_1$ = 0.39, $P$ = 0.84).

## *DISTRIBUTION OF SAGE-GROUSE*

The area of 95% MCP of sage-grouse locations was 377.9 and 2,419.7 km$^2$ in North Dakota (Figure 4-1) and South Dakota (Figure 4-2), respectively. Area of 50% MCP for sage-grouse locations during the breeding, nesting, early brood-rearing, late brood-rearing, and winter seasons in North Dakota was 112.4, 88.4, 128.1, 123.9, and 85.1 km$^2$ and in South Dakota was 541.1, 632.8, 332.7, 299.9, and 355.8 km$^2$, respectively.

The distribution of sage-grouse locations relative to active leks within 3.2 and 5 km buffers showed that sage-grouse in North Dakota were located more often within these buffers during the nesting, early brood-rearing, late brood-rearing, and winter seasons than in South Dakota (Table 4-3).

### *NATAL DISPERSAL*

I determined natal dispersal for 11 juveniles (5 in ND, 6 in SD) that survived from hatch through the following spring reproductive period (breeding and nesting seasons). Median distance of natal dispersal was 11.7 km and was similar ($P = 0.13$) between females (8.4 km) and males (18.9 km) and between study areas ($P = 0.24$). Median date that dispersal movements were initiated from natal area was 7 January (range = 15 Oct – 15 Apr) and was similar ($P = 1.00$) between females (7 Jan, range = 15 Oct – 15 Apr) and males (24 Dec, range = 15 Nov – 10 Apr) and between study areas ($P = 0.80$). I did not document any dispersal of breeding-aged birds during this study.

## DISCUSSION

### *SEASONAL MOVEMENTS*

Previous studies have documented migratory (Berry and Eng 1985, Connelly et al. 1988, Bradbury et al. 1989) and non-migratory (Eng and Schladweiler 1972, Wallestad 1975) behavior of sage-grouse populations. However, mixed migration strategies by sage-grouse in the same population have not been documented. Sage-grouse populations during this study exhibited mixed migration strategies; most (58%) birds were resident. Populations are exhibit mixed migrations strategies when some, but not all, individuals migrate (White et al. 2007). Berry and Eng (1985) and Connelly et al.

(1988) suggested that the configuration of seasonal habitats can influence migration behavior in sage-grouse and most migrations are less than 17 km (Dusek et al. 2002). Although seasonal habitats in the Dakotas were closely interspersed and all core seasonal ranges overlapped, average migration distance of 10.9 and 12.7 km were similar and maximum migration distance of 21.7 and 33.3 km in North Dakota and South Dakota were shorter to those of Dalke et al. (1963) and Connelly et al. (1988). Seasonal habitats during these studies were not closely interspersed; therefore, my results indicate that sage-grouse have the potential to migrate long distances (>10 km) even when habitats are interspersed.

Reasons why some sage-grouse migrated may have been related to conditional factors such as an individual's genotype (Pulido et al. 1996, Sutherland 1998, Hazel et al. 2004, van Noordwijk et al. 2006), previously learned behavior, predation risk, or resource availability. Some species may have unique local adaptations or evolutionary traits that allow them to persist at the edge of their range (Channell and Lomolino 2000). Because there was variation in habitat characteristics among closely interspersed seasonal ranges in this region (Herman-Brunson 2007, Kaczor 2008, Chapter 3), sage-grouse migration behavior, may have been a function of differences in habitat conditions for each individual grouse. Potentially, resident sage-grouse may have had access to all seasonal habitats within their annual range and did not need to migrate. Conversely, sage-grouse that were migratory may have exhibited this behavior because of tradition (Connelly et al. 1998), because of fidelity to natal or breeding areas (Schroeder and Robb 2004), or because of seasonal variation in resource abundance (Alerstam et al. 2003).

*Late spring*

My results indicate that migratory male and female sage-grouse exhibited similar patterns of movement following nest/lek attendance as in areas considered core sage-grouse range (i.e., Idaho, Connelly et al. 1988). Male sage-grouse began departing leks in mid May and all males migrated to summer range by mid June. Movements to summer range were abrupt with most males arriving on summer range within a few days of lek departure. However, 60% of males were non-migratory and had summer ranges that overlapped their breeding range. Moreover, approximately half of all male locations during the brood-rearing seasons were within 3.2 km of active leks. Females with broods did not make rapid departures from nesting areas to summer ranges. Instead, females often remained near the area where they nested until late June when chicks were approximately three to four weeks of age (Herman-Brunson 2007, Kaczor 2008). Migratory females with broods likely made movements away from nesting habitats to find succulent forbs in mesic areas (Autenrieth 1981, Fischer et al. 1997), whereas, females with broods that did not migrate may have had adequate food and cover near their nests to rear the brood. Most females (71%) did not migrate between nesting and summer ranges, which may indicate of the interspersion of seasonal habitats and their proximity to leks in this region.

Movements of females without broods to summer range were earlier than females with broods. However, movements of females were highly variable after their nests failed. In some instances, females made rapid movements (>10 km) to summer range in less than a week. Other females remained near their initial nest or second nest if they renested for up to four weeks before moving to summer range. Some of these females made more gradual movements to summer range that occurred over 1-3 weeks. Potentially, migratory males and females without broods move earlier to summer range than females with broods because they are not restricted by the developing chicks and they may be influenced by the availability of forbs (Gregg et al. 1993).

### *Late summer*

During this study, most sage-grouse (65%) did not migrate between summer and winter ranges. However, when migration did occur, it was gradual and generally occurred over a 2-4 week period which was similar to sage-grouse in Idaho (Connelly et al. 1988). Migration began in late August and all sage-grouse had completed movements to winter range by early December. Similar to Berry and Eng (1985) movements to winter range occurred without the presence of severe winter weather (e.g., deep snow and cold temperatures). Therefore, sage-grouse may not have needed to migrate to a different winter range to find suitable habitat not covered by snow. This could have potentially increased the number of sage-grouse that were non-migratory during this study. Unfortunately, I was unable to determine if severe winter weather could influence migration during winter because sage-grouse were not exposed to severe conditions. Migration may have been related to the increased survival benefits on winter range such as reduced predation and denser sagebrush than other seasonal habitats provided (Herman-Brunson 2007, Kaczor 2008, Chapters 2, 3). Sage-grouse that did not migrate tended to shift within their summer range to areas where sage-grouse concentrated during the winter (e.g., dense sagebrush). Compared to other seasons, sage-grouse were located the least within 3.2 km of active leks during the late brood-rearing period when most migrations to winter range occurred. My results indicate that sage-grouse tend to be located near leks during most of their annual cycle, which indicates that minor shifts within seasonal ranges (i.e., late brood-rearing season) in this region may allow non-migratory sage-grouse to occupy critical habitats. Thus, sage-grouse in this region may occupy a similar range on an annual basis, but make minor shifts within seasonal ranges or migrate between seasonal ranges to meet their needs.

### *Late winter*

Most sage-grouse (57%) did not migrate between winter and breeding ranges in the Dakotas. Similar to other migration periods, winter and breeding habitats were highly interspersed, which may have influenced the rate of movement during this period. For migratory individuals, I observed movements beginning in late January with completion prior to peak hen attendance (~April 9). Unfortunately, most males died during previous seasons (Chapter 3) resulting in a low male sample size. Therefore, I was unable to observe migration behavior for male sage-grouse in this region outside of the late spring period.

Movement from winter to breeding range in sage-grouse has been suggested to be related to decreasing snow levels and sagebrush availability (Dalke et al. 1960, Schoenberg 1982). However, there was limited snow that covered the ground during this study and access to sagebrush was considered equal among all areas. Therefore, migration of sage-grouse between winter and breeding areas was likely caused by other factors. Sage-grouse may have exhibited migratory behavior during this period because of lek fidelity (Berry and Eng 1985, Schroeder and Robb 2004). Sage-grouse that migrated may have had fidelity to leks outside of their winter range, while those that did not migrate likely had fidelity to leks within their winter range. However, additional research is needed to determine if breeding site fidelity influences the migration of sage-grouse in this region.

### *SURVIVAL*

Animals that migrate between seasonal ranges often face inherent risks such as predation and unfamiliarity of habitats compared to residents (White et al. 2007), which has been shown to affect survival when mixed migration strategies occur in the same population (Nicholson et al. 1997). Therefore, a tradeoff may exist for animals to migrate or stay on their seasonal range. Animals that migrate may have access to high quality habitats that should maximize their fitness (Fretwell 1972). In North Dakota, seasonal ranges are closely interspersed and migration rates were lower than in South Dakota. However, sage-grouse that migrated in North Dakota had higher survival than residents. Conversely, survival of migratory sage-grouse in South Dakota was similar to residents. Reasons why migratory sage-grouse in North Dakota had higher survival than residents may be related to occupancy of habitats that decreased their risk for predation while improving their overall fitness. Because sage-grouse have been shown to avoid areas with high density energy development (Doherty et al. 2008) and energy development contributes to population declines (Holloran 2005, Walker et al. 2007), migratory sage-grouse may have occupied larger areas of sagebrush in North Dakota with less infrastructure or disturbance related energy development. Potentially, resident sage-grouse in North Dakota could have had a lower probability of survival if their fitness was decreased when they occupied areas surrounded by energy development. In this region, migration may be a function of tradition for some individuals and habitat differences within seasonal ranges for others.

### *DISTRIBUTION OF SAGE-GROUSE*

The interspersion of seasonal habitats has been suggested to influence migration of sage-grouse populations (Eng and Schladweiler 1972, Connelly et al. 1998). During this study, core seasonal ranges of sage-grouse were closely interspersed and in some cases one seasonal range completely overlapped another. I suggest that size and interspersion of seasonal habitats may influence migration. When entire populations were limited to small areas where critical habitats were concentrated (i.e., North Dakota), migration rate decreased. Conversely, interspersion of larger core seasonal ranges (i.e., South Dakota) tended to increase the proportion of migratory sage-grouse. In South Dakota, the average size of seasonal range (432.4 $km^2$) was four times larger than in North Dakota (107.6 $km^2$) and the cumulative distribution of sage-grouse in South Dakota was approximately 6.5 times the area of North Dakota's population. Therefore, it was not surprising that the migration rate was higher during all three migration periods in South Dakota. Thus, migration behavior in sage-grouse in areas where seasonal ranges are closely configured may be a reflection of the size and distribution of critical habitats.

### *NATAL DISPERSAL*

Timing of natal dispersal was highly variable during this study and was not influenced by any single factor (i.e., photoperiod, environmental conditions).

Movements were variable and ranged from slow to sporadic as juveniles were often located in different flocks in different areas on successive locations prior to establishment of breeding/nesting area. Only two juveniles did not disperse outside their natal area to a different breeding/nesting area. However, yearlings (formally juveniles) exhibited high philopatry to their natal area during this study. Of the nine that survived to the next summer, 67% (4 F, 2 M) were located within 1 km of their natal area for the remainder of the following summer. Only one yearling (male) made a long-distance dispersal (~35 km) from its natal area in South Dakota to Montana the following summer. Unfortunately, this individual died in mid August and I could not determine if this was a true dispersal. The remaining juveniles (1 F, 1 M) occupied areas that were 7.6 and 5.9 km away from their natal area. Unlike other grouse species, I did not observe female-biased dispersal (Caizergues and Ellison 2002) and natal dispersal distances were similar for females and approximately 12 km farther for males than in Colorado (Dunn and Braun 1985). Because juveniles did not emigrate outside of the study areas and most established their future seasonal ranges near their natal ranges, sage-grouse may be poor pioneers of habitat. Nonetheless, sage-grouse populations were considered to be low during this study and there may not have been a need to disperse long distances because of vacancies among seasonal habitats.

Dispersal in avian species has evolved as a way to maintain genetic diversity within populations (Ims and Yoccoz 1997, Wilson and Arcese 2008). Because most bird species have high fidelity to their first breeding area (Greenwood 1980), gene flow in this region may be maintained by sage-grouse occupying leks outside of their natal areas during their first breeding season. Because males tended to move farther away from their natal area to breeding areas, they may be contributing more to genetic exchange than females do in this region. Nonetheless, both emigration and migration rates appeared to be low during this study, which also could influence gene flow among these populations. I could not estimate immigration of sage-grouse into this region, but I assumed it was low because sage-grouse rarely emigrated outside of the study area. Potentially low emigration/immigration coupled with poor recruitment, low to moderate nest success (Herman-Brunson 2007, Kaczor 2008), and high annual mortality (Chapter 2) may indicate that sage-grouse cannot meet their life-history needs (i.e., sink population) in the Dakotas and populations could progress towards local extirpation without immigration of new individuals from source populations (Pulliam 1988).

## MANAGEMENT IMPLICATIONS

Prior to this study, managers lacked information on seasonal movements that are necessary for sage-grouse management in this region. My findings indicate that both size and interspersion of seasonal habitats influence migration rate in this region. Minor shifts within annual ranges in this region may allow non-migratory sage-grouse to occupy critical habitats. Identifying habitat in areas that sage-grouse occupied after attending leks for males and after chicks reached 3-4 weeks of age for females could allow managers to prioritize areas to manipulate or preserve based on habitat suitability. Management of sage-grouse in this region could focus on maintaining or increasing population sizes because sage-grouse rarely migrated outside the study areas and emigration/immigration rates appear to be low. If population sizes continue to decline, genetic diversity could be lost and populations could undergo a severe bottleneck or become locally extirpated. Managers may need to translocate sage-grouse from neighboring populations in Wyoming or Montana (Oyler-McCance et al. 2005) to prevent loss of genetic diversity and maintain populations. Managers could place specific emphasis on the sage-grouse population in North Dakota because core seasonal habitats were much smaller than in South Dakota and because these habitats may have an increased risk of fragmentation due to recent energy development. Additional research is necessary in North Dakota to develop landscape scale models of survival and habitat use to evaluate differences in survival between migratory and resident sage-grouse. In the Dakotas, sage-grouse spend about 62% of their time within 3.2 km of active leks outside of the breeding season and the 5 km buffer only marginally increased percent use near active leks. Because core seasonal ranges coincided with many active leks, farther degradation of habitats within 3.2 km of leks could affect sage-grouse during all stages of their life-cycle in this region. Any region-specific strategy that conserves or improves habitat near active leks on an annual basis would likely be beneficial because sage-grouse centered their annual activity near active leks. Furthermore, additional spatial restrictions related to energy development may be necessary because sage-grouse center their annual activity within 3.2 km of leks and remaining critical seasonal habitats are limited in size and distribution in this region. Managers could be less restrictive during the late-brood rearing season because sage-grouse spent the least amount of time near active leks (~44%) compared to other seasons. At a minimum, managers could extend restrictions on surface use near active leks to 15 July because most sage-grouse broods remained near their nests into July and the average distance from sage-grouse nests to nearest lek was 2.7 and 2.1 km in North Dakota and South Dakota (Herman-Brunson 2007, Kaczor 2008), respectively. Additional research on sage-grouse populations in this region is necessary to determine if source-sink dynamics influence maintenance of populations in the Dakotas.

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Table 4-1. Average movement distance between seasonal ranges for radio-marked breeding-aged (>1yr) females and males combined by years in North Dakota 2005 and 2006 and in South Dakota 2006 and 2007 and pooled across study areas and years.

| | Female[a] | | Male[a] | | Pooled[a] | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Seasonal movement[*] | ND | SD | ND[b] | SD | Female | Male[c] | F[d] | *P*-value | ND | SD | *F*[d] | *P*-value |
| Late spring | 12.6<br>(6, 1.9) | 10.3<br>(22, 1.4) | 9.7<br>(3, 3.0) | 8.5<br>(15, 0.6) | 10.6<br>(28, 1.1) | 8.7<br>(18, 0.7) | 0.47<br>(1, 46) | 0.50 | 11.1<br>(9, 1.5) | 9.6<br>(37, 0.8) | 0.46<br>(1, 46) | 0.50 |
| Late summer | 11.8<br>(9, 1.9) | 16.8<br>(18, 1.7) | n/a | n/a | 15.1<br>(27, 1.4) | n/a | -- | -- | 11.8<br>(9, 1.9) | 16.8<br>(18, 1.7) | 3.18<br>(1, 27) | 0.09 |
| Late winter | 6.5<br>(3, 0.2) | 15.8<br>(13, 2.2) | -- | n/a | 14.1<br>(16, 2.0) | n/a | -- | -- | 6.5<br>(3, 0.2) | 15.8<br>(13, 2.2) | 4.00<br>(1, 15) | 0.07 |

[*] Period of movement between seasonal ranges; late spring (15 May – 15 July), late summer (15 August – 15 December), late winter (1 Feb – 15 April).

[a] Average movement distance (km; *n*, SE) between seasonal ranges.

[b] No males were monitored during late winter in North Dakota.

[c] Males did not exhibit seasonal movements during late summer and late winter.

[d] F-value (alpha = 0.05; degrees of freedom ratio).

Table 4-2. Survival of migratory and resident radio-marked breeding-aged (>1yr) female and male sage-grouse combined by years in North Dakota 2005 and 2006 and in South Dakota 2006 and 2007 and pooled across study areas and gender from 1 March to 28 February.

| | Migrator | | Resident | | Pooled | |
|---|---|---|---|---|---|---|
| Survival rate* | ND | SD | ND | SD | Migrator | Resident |
| Female | 0.900 ± 0.108<br>(*n* = 10) | 0.364 ± 0.103<br>(*n* = 22) | 0.671 ± 0.111<br>(*n* = 19) | 0.222 ± 0.097<br>(*n* = 18) | 0.500 ± 0.088<br>(*n* = 32) | 0.476 ± 0.084<br>(*n* = 37) |
| Male | 0.500 ± 0.354<br>(*n* = 3) | 0.222 ± 0.139<br>(*n* = 9) | 0.250 ± 0.125<br>(*n* = 12) | 0.273 ± 0.134<br>(*n* = 11) | 0.286 ± 0.139<br>(*n* = 12) | 0.261 ± 0.092<br>(*n* = 23) |
| Pooled | 0.831 ± 0.121<br>(*n* = 13) | 0.355 ± 0.086<br>(*n* = 31) | 0.504 ± 0.009<br>(*n* = 31) | 0.240 ± 0.079<br>(*n* = 29) | 0.459 ± 0.077<br>(*n* = 44) | 0.392 ± 0.064<br>(*n* = 60) |

*Survival rate including standard error and number sampled.

Table 4-3. Percent of locations within 3.2 and 5 km buffers of active leks for radio-marked females, males and juveniles combined by years in North Dakota 2005 and 2006 and in South Dakota 2006 and 2007 and pooled across study areas, years, and the following seasons: nesting, early brood-rearing, late brood-rearing, and winter.

| | Pooled | | | North Dakota | | | South Dakota | | |
|---|---|---|---|---|---|---|---|---|---|
| 3.2 km buffer | Female | Male | Juvenile | Female | Male | Juvenile | Female | Male | Juvenile |
| Nesting | 76.3 | 88.2 | n/a | 85.5 | 89.5 | n/a | 70.9 | 87 | n/a |
| Early brood-rearing | 66.3 | 53.7 | n/a | 78.8 | 70.8 | n/a | 58.3 | 16.7 | n/a |
| Late brood-rearing | 41 | 46.4 | 23.3 | 50.4 | 62.5 | 34.5 | 36.6 | 22 | 19 |
| Winter | 72.3 | 69.5 | 53.8 | 78.4 | 62.5 | 47.4 | 64.3 | 72.1 | 64.8 |
| Pooled | 63.3 | 61.8 | n/a | 76 | 75.7 | n/a | 53.9 | 39.3 | n/a |
| 5 km buffer | Female | Male | Juvenile | Female | Male | Juvenile | Female | Male | Juvenile |
| Nesting | 89 | 93.3 | n/a | 97.4 | 93.5 | n/a | 84 | 93.1 | n/a |
| Early brood-rearing | 81 | 65.3 | n/a | 86.1 | 75.4 | n/a | 77.9 | 43.3 | n/a |
| Late brood-rearing | 54.3 | 47.1 | 40.5 | 57.1 | 70.8 | 32.3 | 53 | 41.8 | 43.1 |
| Winter | 84.9 | 84.7 | 65.5 | 88.8 | 93.8 | 57 | 79.8 | 79.1 | 80.2 |
| Pooled | 75.5 | 67.4 | n/a | 82.7 | 81.3 | n/a | 69.8 | 44.9 | n/a |

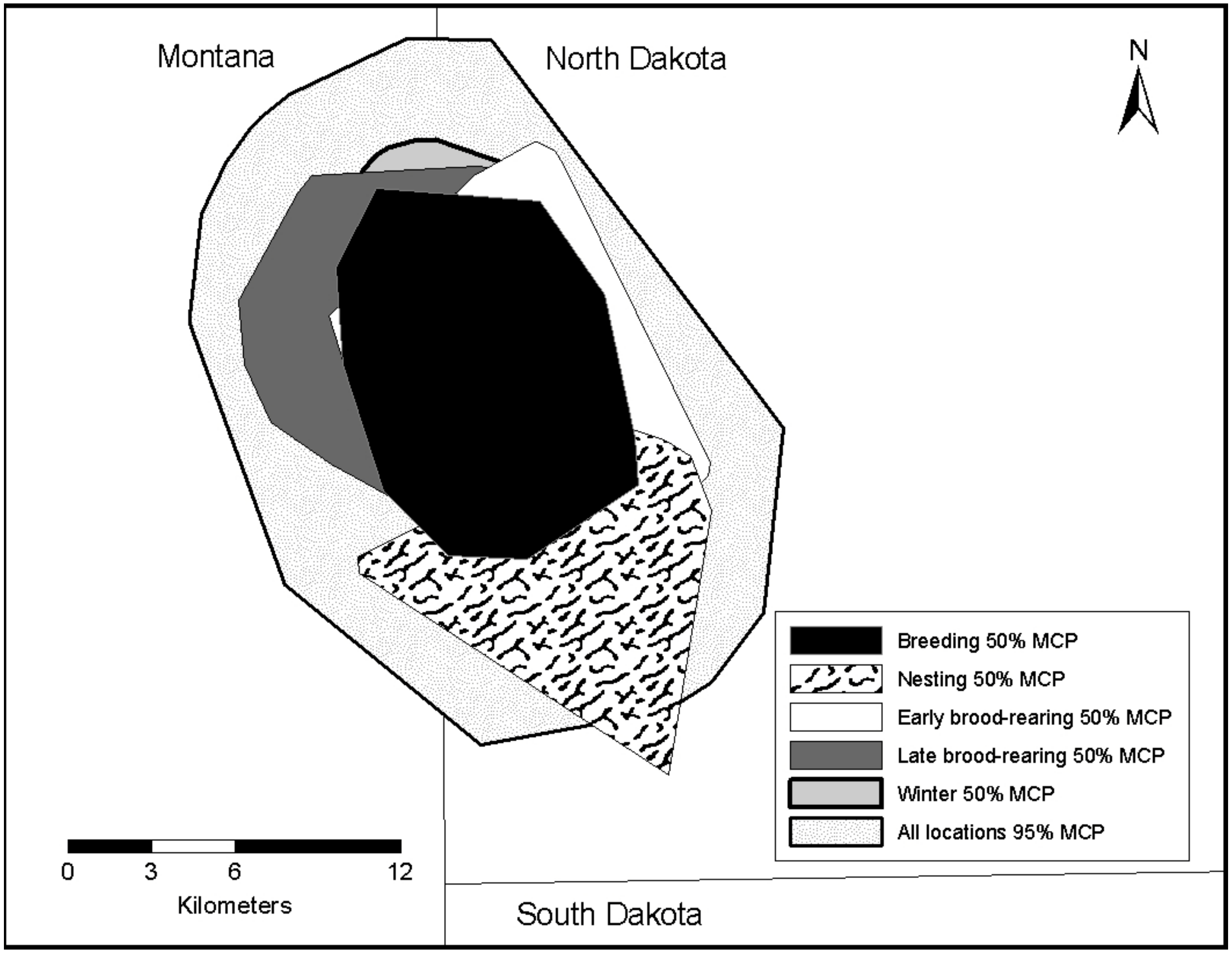

Figure 4-1. Distribution of seasonal ranges using 50% minimum convex polygons (MCP) of sage-grouse locations and cumulative distribution of annual range using 95% MCP of all locations in North Dakota, 2005–2007.

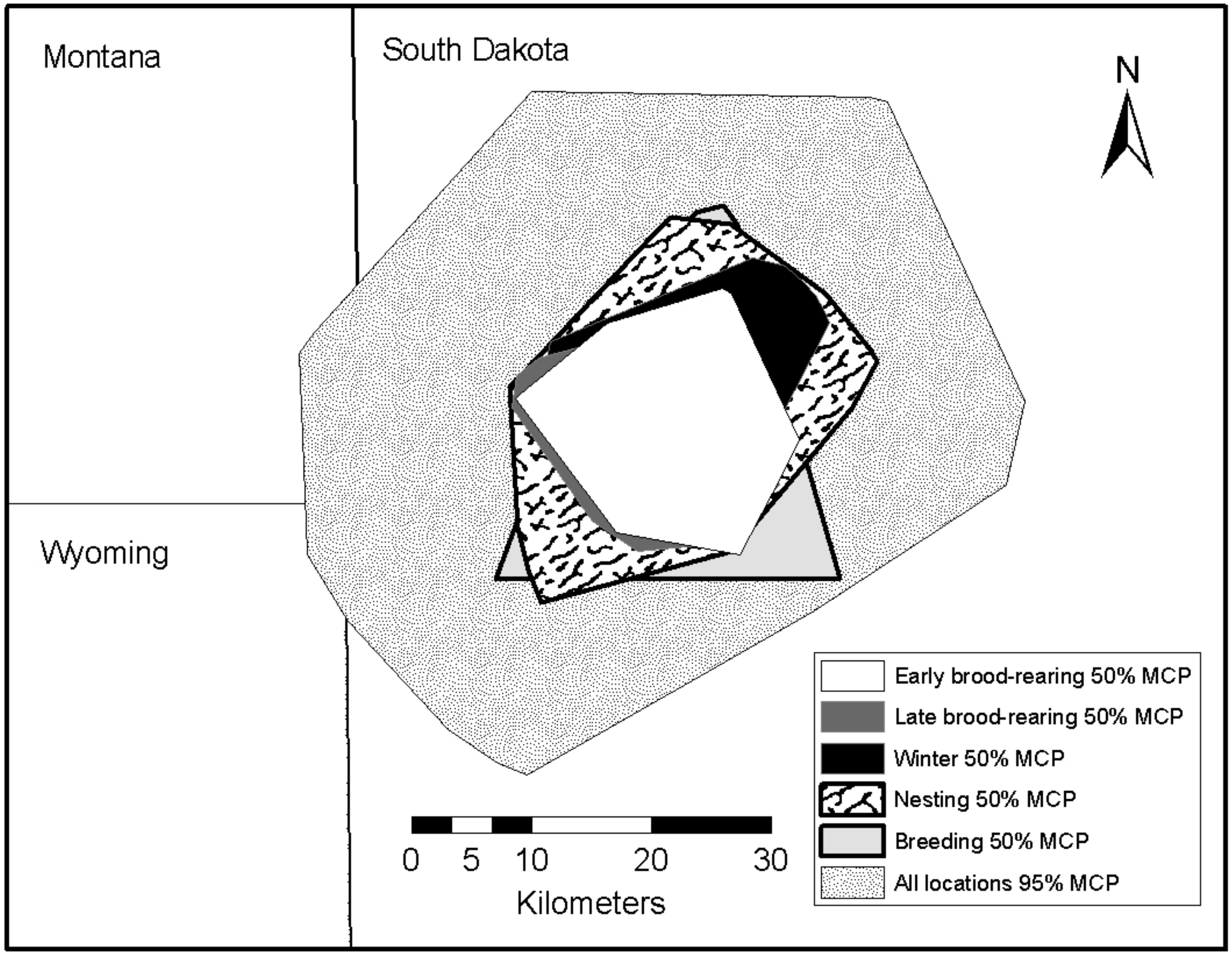

Figure 4-2. Distribution of seasonal ranges using 50% minimum convex polygons (MCP) of sage-grouse locations and cumulative distribution of all sage-grouse locations using a 95% MCP in South Dakota, 2006–2008.

# CHAPTER 5

# BROOD BREAKUP IN GREATER SAGE-GROUSE: MOVEMENT PATTERNS, SURVIVAL, AND TIMING

**Abstract:** Knowledge regarding the life-history strategies of greater sage-grouse (*Centrocercus urophasianus*) is essential to understanding their ecology and developing appropriate management strategies. However, limited information exists on movement patterns of sage-grouse before and after brood breakup, timing of brood breakup, and survival of juveniles (≥10 weeks of age) after brood breakup. I captured and relocated 29 radio-marked broods of sage-grouse to identify movement patterns, timing, and juvenile survival associated with brood breakup during 2005-2006 in North Dakota and 2006-2007 in South Dakota, respectively. Median date of brood breakup was 4 October (range = 17 July – 8 November) when juveniles reached a median age of 134 days (range = 38–173). Timing of brood breakup was independent of gender, juvenile age, brood female age, or study area. Brood breakup was usually initiated by the female and juveniles dispersed within days of the female abandoning the brood. Survival of juveniles from 10 weeks of age to 1 March was lower ($\chi^2_1 = 7.76$, $P < 0.01$) for orphaned juveniles (31.8 ± 0.10%) compared to juveniles (72.2 ± 0.11%) from broods that stayed with the female until brood breakup. Mortality of brood females before brood breakup could be more detrimental in areas with low density sage-grouse populations (i.e., North Dakota and South Dakota) compared to higher density populations because there are fewer breeding-age females available to adopt orphans.

*Key words*: brood breakup, *Centrocercus urophasianus,* greater sage-grouse, initiation, movement, North Dakota, South Dakota, survival

## INTRODUCTION

Survival of grouse (Tetraoninae) depends on the ability to adapt to dynamic predator populations and changing habitat regimes (Bergerud and Gratson 1988). Greater sage-grouse (*Centrocercus urophasianus*) populations occupy landscapes that have undergone substantial change over the past 50 to 100 years (Knick et al. 2003). Some of these habitat changes have fragmented the sagebrush (*Artemisia* spp.) ecosystem (Welch 2005) and, within these fragmented habitats, it is increasingly important to understand sage-grouse behavior (Schroeder and Robb 2004).

Identifying movement patterns of juvenile grouse is challenging because they tend to be secretive, difficult to capture, and have the ability to move large distances when they separate from their parent (Hannon and Martin 2006). Prior to juvenile independence, females invest substantial effort into care of young by providing warmth, access to resources, and protection from predators (Clutton-Brock 1991, Hannon and Martin 2006). However, care of the young is likely to be terminated by the female when the costs of their guidance do not improve the condition or survival prospects of their offspring (Verhulst et al. 1997, Weathers and Sullivan 1989). Unfortunately, no studies have evaluated factors that influence initiation of brood breakup by the female and the cost to juveniles (e.g., survival) as a result of brood breakup.

Limited information exists that accurately describes movement patterns of sage-grouse during brood breakup (Patterson 1952, Browers and Flake 1985). Brood breakup in sage-grouse has been suggested to occur when juveniles are 10-12 weeks of age (Patterson 1952) and independent of dispersal movements (Browers and Flake 1985). Juvenile sage-grouse become independent when they separate from the brood (i.e., brood breakup) during late summer and early fall. Brood breakup is thought to be initiated when the female leaves the brood and the remaining juveniles become independent (Patterson 1952, Dalke et al. 1963, Wallestad 1975). Factors that have been suggested to initiate brood breakup in grouse species include reduced social bonds prior to breakup (Alway and Boag 1979) and changes in photoperiod (Godfrey and Marshall 1969, Bowman and Robel 1977).

Hannon and Martin (2006) suggested that management of juvenile grouse should focus on the autumn when juveniles begin disbanding from their brood bond. However, managers do not have reliable information regarding movement behavior and timing of brood breakup in sage-grouse, which could be incorporated into management strategies. My objectives were to: 1) identify patterns of movement and timing associated with brood breakup of sage-grouse, 2) estimate juvenile survival associated with brood breakup, and 3) examine possible benefits or costs associated with natural brood breakup processes.

## STUDY AREA

This study was conducted in Bowman County, North Dakota (46º 7' 22.368″ N, 104º 0' 24.318″ W) and Butte County, South Dakota (45º 1' 52.329″ N, 103º 44' 41.196″ W) and adjacent parts of Montana and Wyoming. This region is semiarid sagebrush rangeland characterized by gentle slopes to steep buttes and ridges with elevations of 640 to 1,225 m above sea level (Opdahl et al. 1975, Johnson 1976). Vegetation in this region was described by Opdahl et al. (1975), Johnson (1976), and Johnson and Larson (1999) as low shrubland with short to mid grass prairie being dominant. Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) is the dominate shrub vegetation which also includes silver sagebrush (*A. cana* spp. *cana*). Land use was dominated by livestock grazing, 45% of Bowman County and 5% of Butte County was farmed for cultivated crops.

The climate was continental with cold dry winters and warm summers with most precipitation occurring in late spring and early summer. Average monthly temperatures in North Dakota were -9.7 C in January and 20.8 C in July with average annual precipitation and snowfall of 39.4 and 122.7 cm. Average monthly temperatures in South Dakota were -4.8 C in January and 22.7 C in July with average annual precipitation and snowfall of 45.54 and 89.9 cm, respectively (National Climatic Data Center 1971-2000).

## METHODS

### *Capturing and Marking*

I located broods of radio-marked female greater sage-grouse in North Dakota during 2005 and 2006 and in South Dakota during 2006 and 2007. Locations of females and broods were visually verified twice each week to maintain an accurate count of the number of chicks in the brood. I captured all the chicks using spotlights (Giesen et al. 1982, Wakkinen et al. 1992) and a thermal-infrared imaging camera when the brood was approximately 7 weeks of age. I approached radio-marked females using all-terrain vehicles (ATV) stopping every 10–20 m to search for broods with the aid of a 3-element

Yagi antenna to ascertain the directional azimuth of the brood. Two persons carrying long-handled hoop nets made a fast running approach while the person on the ATV maintained spotlight observation of the brood when the brood was located. I fitted each chick captured (average mass = 569.5 ± 15.7 g) with a 10.7 g necklace transmitter (model A3950, Advanced Telemetry Systems, Isanti, Minnesota) and assigned gender (Birhrle 1993). I determined gender at 10 weeks of age if it could not be determined at 7 weeks of age. I recaptured the juveniles to remove the necklace transmitter and fit each bird with a 22 g necklace transmitter (model A4060, Advanced Telemetry Systems, Isanti, Minnesota) at approximately 10 weeks of age, mass was not recorded prior to release. All radio-transmitters were less than 3% of the body weight of birds at time of attachment. All capture and handling protocols were approved by the Institutional Animal Care and Use Committee (approval number: 07-A032) at South Dakota State University.

*Telemetry*

All radio-marked females and their broods were located ≥2 times per week using a hand-held receiver and Yagi antenna or from a fixed-wing aircraft when signals were not detected from the ground. Locations were recorded in Universal Transverse Mercator (UTM) coordinates (NAD27, UTM Zone 13). Mortality was indicated by a change in pulse rate of the transmitter. I considered gender to be unknown when it could not be assigned from plumage characteristics before the chick died or if there was insufficient evidence at the death site.

### *Data Analysis*

Connelly et al. (2003) defined sage-grouse as juveniles at ≥10 weeks of age because they are physiologically capable of being independent based on plumage development (Patterson 1952), body mass (Beck et al. 2006), and diet (Peterson 1970, Wallestad 1975). Brood breakup was considered to have occurred when the female or chick/juvenile permanently separated from the brood. Specifically, I determined date of brood breakup for each individual member of the brood because of variation in initiation among broods. I classified juveniles as orphans when the female died before brood breakup was initiated. Initiation distance was calculated as the straight-line distance from the last location before breakup to the first location following brood breakup. I calculated the average distance moved between locations as the distance between each consecutive location before breakup and the distance between each consecutive location after breakup or after the juvenile was orphaned until recruitment. All broods were located at least twice a week before and after brood breakup.

Sage-grouse brood locations were plotted using ArcView 9.2 (Environmental Systems Research Institute, Redlands, CA USA) to identify timing and movement distances associated with brood breakup. I used fixed-effects analysis of variance (ANOVA) with alpha set at $P \leq 0.05$ to test for differences between initiation dates of brood breakup between adult (≥2 years old, second or later breeding season) and yearling (≥1 years old, first breeding season) females, male and female juveniles, and juveniles and brood females. I used similar tests to compare age of brood breakup between male and female juveniles, between juveniles at each study area and to compare pre- and post-breakup movement distances among brood females, juveniles, and study areas. I compared movement distances of juveniles that were orphaned after brood females died to juveniles that had undergone brood breakup with the female.

I used Kaplan-Meier methodology (Kaplan and Meier 1958) modified for a staggered entry design (Pollack et al. 1989) to estimate survival of juveniles from broods following breakup with the female to those that were orphaned. I pooled juveniles across years and study areas to calculate an overall rate of survival between these two groups. Survival was calculated from 10 weeks of age until juveniles were considered to be recruited into the population on 1 March, the start of their first breeding season. I right-censored grouse if they disappeared from the study area and was never relocated, when the bird could not be accessed on private lands, or because of radio-transmitter failure. I compared survival estimates using Program CONTRAST (Hines and Sauer 1989); alpha was set at $P \leq 0.05$.

## RESULTS

### *Timing and Initiation*

I captured and monitored 29 radio-marked sage-grouse broods including 79 juveniles for brood breakup during this study (Table 5-1). I examined brood breakup for 18 juveniles (9 males, 9 females) that survived from 13 radio-marked broods (3 in North Dakota and 10 in South Dakota). Median date of brood breakup was 4 October (average = 20 Sept; range = 17 Jul to 8 Nov) and did not differ between adult and yearling brood females (Mean difference [MD] = -2.0 ± 24 days; $F_{1, 9} = 2.48$, $P = 0.17$), study area (MD = -2.0 ± 23 days; $F_{1, 16} = 0.10$, $P = 0.93$), juvenile male and female (MD = -4.1 ± 19 days;

$F_{1,\,16} = 0.35$, $P = 0.60$), or when the juvenile compared (MD = 0.2 ± 21 days; $F_{1,\,16} = 0.15$, $P = 0.71$) to the brood female initiated brood breakup. Median juvenile age at brood breakup was 134 days post-hatch (average = 117 days; range = 38–173, $n = 18$) and approached significance between male and female juveniles (MD = -2.0 ± 24 days; $F_{1,\,16} = 3.39$, $P = 0.07$) and between study areas (MD = -2.1 ± 21 days; $F_{1,\,16} = 3.23$, $P = 0.09$). Date of brood breakup for a brood surviving from a renest ($n = 1$) was 5 September when the juvenile ($n = 1$) was 80 days of age. I did not document any instances of brood breakup where multiple siblings separated from the rest of the brood at the same time and then remained together until final separation.

Brood females moved 1.31 ± 0.13 km ($n = 13$) after initiating brood breakup, which was similar between adult and yearling brood females (MD = -2.4 ± 2.0 km; $F_{1,\,11} = 0.42$, $P = 0.53$) and study areas (MD = -1.3 ± 1.4 km; $F_{1,\,11} = 0.64$, $P = 0.44$). Juveniles ($n = 5$) moved 1.60 ± 0.25 km, which was similar between male and females (MD = 1.0 ± 2.1 km; $F_{1,\,4} = 0.43$, $P = 0.63$) to brood female initiation distance (MD = -1.6 ± 1.7 km; $F_{1,\,16} = 0.93$, $P = 0.35$), and between study areas (MD = -0.9 ± 1.7 km; $F_{1,\,4} = 0.08$, $P = 0.82$).

### *Movement Patterns*

Average distance between locations for brood females was less (MD = -0.7 ± 0.2 km; $F_{1,\,246} = 4.74$, $P = 0.03$) before brood breakup than after brood breakup and was greater (MD = -0.7 ± 0.3 km; $F_{1,\,246} = 5.89$, $P = 0.02$) in South Dakota than in North Dakota (Table 5-2). Brood female movement was similar (MD = -0.2 ± 0.2 km; $F_{1,\,334} = 0.68$, $P = 0.41$) to juveniles prior to breakup; however, brood female and juvenile distance between locations was greater (MD = -0.6 ± 0.2; $F_{1,334} = 7.42$, $P < 0.01$) in South Dakota than in North Dakota. Conversely, brood female distance between locations was less (MD = -1.8 ± 0.6; $F_{1,227} = 4.82$, $P = 0.03$) than juveniles during the post-breakup period and differed between study areas (MD = -1.6 ± 0.7 km; $F_{1,227} = 10.38$, $P = 0.01$). Movements were similar (MD = -0.4 ± 0.3 km; $F_{1,149} = 0.52$, $P = 0.47$) between adults and yearlings before breakup, but differed between study areas (MD = -0.7 ± 0.3 km; $F_{1,149} = 3.75$, $P = 0.05$). Movements after brood breakup also were similar (MD = -0.1 ± 0.6 km; $F_{1,97} = 0.001$, $P = 0.97$) for adults and yearlings and between study areas (MD = -1.1 ± 0.5 km; $F_{1,97} = 2.58$, $P = 0.11$). Average pre- and post-breakup movement distances of juveniles (≥10 wks) differed (MD = -0.9 ± 0.3 km; $F_{1,314} = 15.41$, $P <0.01$) and was greater (MD = -1.1 ± 0.4; $F_{1,314} = 15.94$, $P <0.01$) in South Dakota than in North Dakota. Juveniles orphaned (≥10 wks) prior to brood breakup moved similar distances between locations for males and females (MD = -0.2 ± 0.6; $F_{1,144} = 0.34$, $P = 0.99$) and between study areas (MD = -0.1 ± 0.6 km; $F_{1,144} = 0.31$, $P = 0.58$). Juveniles that went though brood breakup with the female moved farther (MD = -1.6 ± 0.4 km; $F_{1,273} = 11.08$, $P < 0.01$) after brood breakup than those that were orphaned.

*Survival*

Survival from 10 weeks to recruitment for juveniles from broods that went through natural brood breakup (72.2 ± 0.11%, $n = 18$) was greater ($\chi^2_1 = 7.76$, $P < 0.01$) than survival during the same period for juveniles (31.8 ± 0.10%, $n = 22$) that were orphaned when the female died. Thirty-five chick sage-grouse died before brood breakup and were not included in the survival analysis. I censored four chick sage-grouse from the analysis because I could not obtain landowner access to retrieve mortality.

## DISCUSSION

Brood breakup in sage-grouse in this study occurred when juveniles were 17 weeks of age. Patterson (1952) suggested the majority of broods in Wyoming separated by 1 September of each year. Timing of brood breakup in North Dakota and South Dakota was similar to brood breakup in other grouse species (Godfrey and Marshall 1969, Bowman and Robel 1977, Hines 1986, Schroeder 1986, Pitman et al. 2006) and independent of gender, juvenile age, brood female age, or study area. Most brood breakup was initiated by females, by moving away from one or more of their young. Juveniles remaining in the brood after female abandonment generally dispersed immediately after the departure of the female. Occasionally, the female abandoned the brood and the brood partially disbanded. One or more of the juveniles were located with the female within a few days of the original breakup. These juveniles tended to follow movements of the brood females for up to a month before final separation. Similar patterns of partial brood breakup have been documented in sharp-tailed grouse (*Tympanuchus phasianellus*; Gratson 1988).

Juvenile sage-grouse are physiologically capable of independence at 10 weeks of age (Patterson 1952, Peterson 1970, Wallestad 1975, Beck et al. 2006). Nonetheless, brood breakup occurred later than previously studies (Patterson 1952, Browers and Flake 1985) and was highly variable relating to initiation date (17 Jul to 8 Nov) and age of chick/juveniles (38 to 173 days post-hatch). Thus, timing of juvenile maturity does not appear to regulate the timing of brood breakup in sage-grouse. Similar findings also have been reported for lesser prairie-chickens (*Tympanuchus pallidicinctus*) and greater prairie-chickens (*Tympanuchus cupido*; Bowman and Robel 1977, Pitman et al. 2006). Furthermore, brood breakup did not seem to be influenced by photoperiod or environmental conditions because of the variability in the timing of brood breakup. Some females ($n$ = 3) may initiate brood breakup during early fall because migration to winter range coincides with the timing of brood breakup in this region (Chapter 4). However, most females likely abandon the brood to focus on their own survivorship (Bergerud and Gratson 1988, Weathers and Sullivan 1989, Verhulst et al. 1997) and prepare for the future reproduction (Bergerud and Gratson 1988).

Behavior of juveniles that initiated separation from the female tended to be different than when the brood female initiated breakup. Typically, when a juvenile initiated breakup, separation occurred independent of the remaining siblings. Movement behavior was more variable in instances where juveniles initiated breakup and was not gender biased. Juveniles initiating breakup exhibited sporadic movements away from the brood, which appeared to be motivated by searching nearby habitat. It may have been possible for the brood to have moved from an individual juvenile. I believe this was not probable because relocations of juveniles that separated from the brood were often in areas not previously used by the brood. Because broods tended to be located in traditional use areas prior to breakup, it was unlikely the remaining brood would have moved into an unfamiliar area it did not frequent.

I observed differences between pre- and post-breakup movement patterns of brood females and juveniles. Chick sage-grouse, like most grouse species, rely on the female for thermoregulation (<4 weeks of age) and the acquisition of learned behavior before independence (Keppie 1977). Sage-grouse broods made synchronized movements and all members of the brood were located together prior to breakup. Their movements still coincided with the brood female and were relatively limited as juveniles approached brood breakup. My results indicate that adult and yearling brood females do not move differently between breakup periods because movement distances between locations were similar before and after breakup. Females likely have equal constraints of defending their brood pre-breakup and post-breakup movements tended to occur near the area the brood were reared. As expected, chick/juvenile movements mirrored that of the brood female before brood breakup. The chicks were concentrated near the brood female during nocturnal and crepuscular periods, but they tended to be farther away from the female during diurnal periods.

Similar to the findings of Dunn and Braun (1986), juvenile movements were sporadic in September and October following brood breakup. Sporadic movements by juveniles post-breakup were the primary reason why juveniles moved farther than brood females. Juvenile movements following brood breakup also appeared to be exploratory, as it was common to locate juveniles with different flocks of grouse and in different areas on successive locations. These movements by independent juveniles may be critical to colonizing new habitats and sustaining grouse populations in areas with rapidly changing landscapes (Hannon and Martin 2006).

Orphaned juveniles had higher mortality than juveniles that remained with the female through normal brood breakup and few orphaned juveniles survived to recruitment, most of their siblings died prior to recruitment. Presence of the female with the brood until brood breakup appeared to be beneficial to survival of juveniles (≥10 wks). Orphaned juveniles may have had a lower probability for survival because they failed to learn important behaviors (i.e., predator avoidance, feeding strategy) demonstrated by the brood female. Orphaned juveniles that survived to recruitment may have learned behavioral traits from other sage-grouse within larger winter flocks or if they were adopted by another female.

I realize that brood adoption occurs in many avian species (Maxson 1978, Eadie et al. 1988, Pitman et al. 2006) and location of juveniles in gang broods (several breeding-aged females with many juveniles) was common after juveniles were orphaned or if they went through breakup with the female. Orphaned juveniles could have been adopted by another female in gang broods after the female died; however, location among gang broods does not necessarily imply that orphaned juveniles were adopted. In fact, most of the broods observed during this study were located in larger gang broods by late August before brood breakup. Also, size of gang broods was not static from mid August until the start of winter (1 Nov) and relocations of radio-marked juveniles were often in gang broods of different sizes on successive locations. Results from this study indicates that probability of survival for juveniles that did not undergo natural brood breakup processes was substantially lower than juveniles that did undergo brood breakup. Loss of the brood females before brood breakup could be more detrimental in areas characterized by low density sage-grouse populations (i.e., North Dakota and South Dakota) compared to higher density populations because there are fewer breeding-age females available to adopt orphans.

## MANAGEMENT IMPLICATIONS

Mortality to sage-grouse brood females before brood breakup appears to be additive to the survival of juveniles when population densities are low. Because grouse population growth is often limited by the survival of juveniles (Sandercock et al. 2005), management strategies aimed at limiting mortality to brood females prior to brood breakup (e.g., conservative hunting seasons) could improve recruitment rates and affect sustainability of low density sage-grouse populations. Additional research that evaluates the effect of adoption rates on survival of juveniles could provide insight into recruitment rates among varying population densities.

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Table 5-1. Capture data for radio-marked greater sage-grouse broods in North Dakota 2005 and 2006 and in South Dakota 2006 and 2007.

| | Broods[a] | Adult females[b] | Yearling females[b] | Juvenile males[a] | Juvenile females[a] | Unknown juveniles[a] |
|---|---|---|---|---|---|---|
| ND 2005 | 5 | 4 | 1 | 4 | 3 | 5 |
| ND 2006 | 3 | 2 | 1 | 6 | 3 | 4 |
| SD 2006 | 11 | 8 | 3 | 8 | 9 | 13 |
| SD 2007 | 10 | 9 | 1 | 5 | 6 | 13 |
| Total | 29 | 23 | 6 | 23 | 21 | 35 |

[a] Number of individual broods and individual juveniles monitored for breakup.
[b] Number of adults or yearlings with broods.

Table 5-2. Average distance moved between locations for sage-grouse during pre- and post-brood breakup periods combined by years in North Dakota 2005 and 2006 and in South Dakota 2006 and 2007 and pooled for brood females and juveniles across study areas and years.

| | **Pre-breakup** | | **Post-breakup** | | **Orphaned** | |
|---|---|---|---|---|---|---|
| Movement[a] | ND | SD | ND | SD | ND | SD |
| Adult female | 0.69 ± 0.82 | 1.38 ± 0.43 | 0.96 ± 0.41 | 2.24 ± 0.61 | n/a | n/a |
| Yearling female | 0.49 ± 0.27 | 1.10 ± 0.50 | 1.30 ± 0.54 | 1.94 ± 0.63 | n/a | n/a |
| Juvenile | 0.60 ± 0.26 | 1.48 ± 0.39 | 1.45 ± 0.53 | 3.70 ± 0.75 | 1.23 ± 0.48 | 1.37 ± 0.72 |

[a] Average movement distance between locations (km; average ± SD).

# CHAPTER 6

# CONCLUSIONS AND FUTURE CONSIDERATIONS

I evaluated survival, winter habitat use, seasonal movements, and brood breakup of radio-marked greater sage-grouse (*Centrocercus urophasianus*) in North Dakota from 2005-2007 and in South Dakota from 2006-2008. No direct information was available prior to this study on survival rates, timing and causes of mortality, characterization of winter sagebrush habitat, causal mechanisms (e.g., soil moisture, precipitation) that affect sagebrush structure, seasonal movements, distribution of seasonal ranges, patterns of natal dispersal, and timing, movement patterns, and survival associated with brood breakup in this region. Information obtained from this study on sage-grouse population dynamics in conjunction with findings on nesting and brood-rearing ecology (Herman-Brunson, Kaczor 2008) provide a greater understanding of factors influencing sage-grouse ecology in this region. Findings from this study provides baseline demographic data in this region, as well as insight into sage-grouse life-history (i.e., brood breakup), that can be used by resource management agencies to improve future management of sage-grouse.

Survival of sage-grouse in the Dakotas was generally high (86.6-97.7%) most of the year (1 Nov – 15 June), but high mortality (>50%) occurred from late July through the first hard frost that killed adult *Culex tarsalis* mosquitos carrying West Nile virus. Mortality varied by year and was high when average July and August temperatures exceeded 21°C; the threshold for *C. tarsalis* development (Brust 1991). Although mortality was primarily caused by predators during this study, years (2006, 2007) with

West Nile virus outbreaks had higher incidences of predation. I suggest that the findings of Clark et al. (2006) regarding symptoms (watery oral and nasal discharge, isolation, complete loss of coordinated locomotion, and unwillingness to escape danger) of captive sage-grouse infected with West Nile virus likely occur in wild sage-grouse. These symptoms may increase the predation rate during late summer in wild populations of sage-grouse during years with outbreaks of West Nile virus. Nonetheless, predation rate has been shown to be related to habitat quality (Schroeder and Baydack 2001) and sage-grouse may have been vulnerable to predation during the late-brood rearing period because they occupied lower density sagebrush cover compared to other periods (Herman-Brunson 2007, Kaczor 2008, Chapter 3). I recommend that additional research is necessary to evaluate true infection rates of West Nile virus. This will involve intensive monitoring of radio-marked sage-grouse visually located on a daily basis by large field crews to observe behavior of potentially infected sage-grouse and reduce the likelihood of predators/scavengers to mask detection of true West Nile virus infection rates. This could allow managers to determine if high mortality during late summer was a function of West Nile virus outbreaks or increased predation because of low habitat quality.

Managers should be vigilant of years with high West Nile virus outbreaks because adult hen survival and recruitment of juveniles is critical to future population productivity (Sandercock et al. 2005, Moynahan et al. 2006). Currently, sage-grouse have limited resistance to infection by West Nile virus (Walker et al. 2007) and no management strategy can directly offset the deleterious effects of this vector-borne disease. Therefore, I recommend that managers make all attempts to reduce additive mortality during years when temperatures are conducive for *C. tarsalis* production. For example, agencies could use conservative hunting seasons (e.g., limited drawing of tags) or temporarily close hunting seasons for one or more years until population size increases.

Sustaining sage-grouse populations in the Dakotas may depend upon focusing on productivity through improved habitat management. I realize that productivity can fluctuate on an annual basis because of changes in environmental conditions; however, habitat is the only consistently manageable factor known to improve productivity and survival in sage-grouse (Connelly et al. 1991, Gregg et al. 1994, DeLong et al. 1995, Sveum et al. 1998, Crawford et al. 2004). Because sage-grouse population growth tends to lag increases in productivity and improvements in habitat (Crawford et al. 2004), I recommend that managers focus their efforts on critical habitats in areas identified during this study, by Herman-Brunson (2007), and by Kaczor (2008). In this region, sage-grouse do not appear to be limited by their body condition, as females were considered to have excellent body mass prior to nesting, which was indicative of the high nest initiation rates, average clutch sizes, and egg hatchability (Herman-Brunson 2007, Kaczor 2008). Yet, nest success and recruitment were low and may be contributing to the low density of sage-grouse in this region. Recruitment was low even in 2005 in North Dakota, a year with low incidence of West Nile virus, which may indicate that factors other than West Nile virus are contributing to survival of chicks to their first breeding season. I suggest that managers emphasize improving nesting and brood-rearing habitats as recommended by Herman-Brunson (2007) and Kaczor (2008) to increase productivity in the Dakotas.

By limiting additive mortality and improving habitat, managers will be making their best effort to sustain sage-grouse populations in this region. Additional research that evaluates the effect of grazing on sagebrush habitats in this region could be important for improving future productivity and developing appropriate habitat management strategies.

Winter habitat used by sage-grouse was characterized by short (~20 cm) and dense (~15 % canopy cover) stands of Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) compared to random sites. Sage-grouse generally occupied large expanses of sagebrush on flat to gentle south facing slopes during winter. Winter sagebrush habitat was generally lower in density and height compared to in core areas (e.g., Colorado, Montana, and Wyoming). I suggest that sage-grouse do not use sagebrush habitat differently than in core areas as they used the highest sagebrush canopy cover that was available. However, the mechanisms that regulate sagebrush size and structure in the Dakotas appear to be different than in core sagebrush habitats. I suggest that growth conditions for Wyoming big sagebrush limit the potential of sagebrush to exist at levels comparable to core areas. Most of the precipitation in the Dakotas occurs in April through July and is likely evaporated before it reaches the deep root system of Wyoming big sagebrush plants. Thus, soil moisture may be low and sagebrush growing conditions are likely marginal in this region. Wyoming big sagebrush is uniquely adapted to take advantage of good soil moisture conditions by retaining about one-third of its leaves in winter and by developing ephemeral leaves early in the spring. This allows Wyoming big sagebrush to begin photosynthesis and growth when soil moisture conditions are optimal (DePuit and Caldwell 1973, Miller and Schultz 1987). I suggest that sagebrush in this region may be limited from good growth conditions and will likely continue to occur at lower densities and smaller size structure than in areas that receive most of their precipitation during the winter. Therefore, I recommend that regional management strategies be developed to address the annual requirements of sagebrush and sage-grouse in this region. Additional research that evaluates different strategies for retaining soil moisture could be important for increasing sagebrush structure in this region.

At a minimum, managers should maintain areas that I identified as core winter range. Winter habitat had the highest amount of sagebrush canopy cover in the region which provides important physiological benefits (e.g., increased body mass) and sage-grouse concentrated in these habitats which improved their survival. I recommend that future habitat selection studies on sage-grouse evaluate habitat fragmentation metrics (e.g., patch size, juxtapostition) using high-resolution land cover maps to assess the importance of scale of habitat used. This may also be important to identify migration corridors that are necessary to link sage-grouse populations at the edge of their range with neighboring core populations. A future study could use transmitters that have the capability of collecting multiple daily locations (e.g. satellite transmitters) to develop geographic information systems (GIS) models of habitat use based on seasonal movements. Researchers could make predictions regarding future changes in land cover, fragmentation metrics, and anthropogenic disturbances to identify critical habitats and better focus management at the scale sage-grouse select habitats in this region (e.g., Doherty et al. 2008).

Most sage-grouse (~58%) in the Dakotas occupied similar range on an annual basis. I identified 3 periods when migration occurred between seasonal ranges: late spring (15 May – 15 July), late summer (15 August – 15 December), and late winter (1 Feb – 15 April). Thirty-five, 39, and 43% of sage-grouse migrated during the late spring, late summer, and late winter periods. Although both study areas had seasonal ranges that were interspersed, sage-grouse were more likely to be migratory in South Dakota where seasonal ranges were four times larger than in North Dakota where seasonal ranges were smaller and highly concentrated. Timing of migration during late spring was related to lek abandonment for males and age of chicks (e.g., 3-4 weeks) for females. Factors influencing late summer and late winter migration were less obvious, but were likely related to density of sagebrush on winter range and fidelity to leks. Sage-grouse were located about 62% of the time within 3.2 km of active leks from 16 April to 28 February. Further degradation of habitats near leks would likely be detrimental to sage-grouse populations in this region because seasonal ranges were closely interspersed and contained many active leks. Future research that evaluates movements of neighboring populations (e.g., Montana, Wyoming) could provide insight into immigration rates into the Dakotas and genetic exchange of sage-grouse in this region.

This study was conducted during mild winters and I could not determine the effect severe weather (e.g., deep snow and cold temperatures) had on seasonal movements, survival, or winter habitat use. However, based on previous findings in core areas, I hypothesize that most sage-grouse would migrate to the west (e.g., Montana, Wyoming) towards core areas to find suitable habitat, overwinter survival could be 50-

60%, and sage-grouse that remained within the study areas would occupy large windswept flats where snow would not reduce access to sagebrush. Thus, I suggest that future research investigate the effects of winter severity on sage-grouse movement, survival, and winter habitat use.

Timing of natal dispersal was highly variable and was generally separate from brood breakup movements. Average dispersal distance was 12.7 km and the proportion of dispersers was not gender biased. Because few juveniles ($n = 11$) survived long enough to determine dispersal, additional research with larger sample sizes may be important to determine patterns of dispersal in this region. Larger sample sizes would also allow researchers to investigate emigration/immigration rates, which could have important implications for maintaining genetic diversity in this region.

Prior to this study, limited information existed on the timing and movement patterns associated with brood breakup in sage-grouse (Patterson 1952, Browers and Flake 1985). Also, no studies had evaluated survival of juveniles after brood breakup occurred to recruitment. My results indicated that brood hens typically initiated brood breakup by separating from the juveniles in the brood. Remaining juveniles generally dispersed away from their siblings immediately following breakup. Brood breakup occurred during late summer and timing was independent of gender, juvenile age, brood female age, or study area. Juvenile survival from 10 weeks to 1 March was lower for orphaned juveniles (31.8 ± 0.10%) compared to juveniles (72.2 ± 0.11%) from broods that stayed with the female until brood breakup. Although many orphaned juveniles were located in gang broods (several breeding-age females with many juveniles) following the death of the brood hen, it was unknown whether some of the orphaned juveniles were adopted by other females. I suggest that future research investigate the effects of population density on adoption rates and survival of juveniles to recruitment. Based on my study, I hypothesize that adoption rates are lower in low density populations (e.g. North Dakota, South Dakota) because there are fewer breeding-aged females available to adopt orphaned juveniles. Knowledge of juvenile survival associated with adoption rates could be important for estimating recruitment rates among varying population densities.

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Appendix 2-A. Survival estimates of greater sage-grouse by age and gender during the nesting season in North Dakota, 2005 and 2006 and in South Dakota, 2006 and 2007.

| Type | State | Year | # Birds | # Dead | # Censor | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| Adult female | ND | 2005 | 9 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult female | ND | 2006 | 17 | 2 | 0 | 0.882 | 0.078 | 0.729 | 1.000 |
| Adult female | SD | 2006 | 20 | 3 | 0 | 0.850 | 0.080 | 0.694 | 1.000 |
| Adult female | SD | 2007 | 31 | 4 | 0 | 0.871 | 0.060 | 0.753 | 0.989 |
| Yearling female | ND | 2005 | 10 | 1 | 0 | 0.901 | 0.087 | 0.739 | 1.000 |
| Yearling female | ND | 2006 | 8 | 1 | 0 | 0.875 | 0.117 | 0.646 | 1.000 |
| Yearling female | SD | 2006 | 17 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | SD | 2007 | 10 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Adult male | ND | 2006 | 10 | 2 | 1 | 0.800 | 0.135 | 0.535 | 1.000 |
| Adult male | SD | 2006 | 15 | 2 | 1 | 0.867 | 0.091 | 0.688 | 1.000 |
| Adult male | SD | 2007 | 15 | 2 | 0 | 0.867 | 0.088 | 0.695 | 1.000 |
| Yearling male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | ND | 2006 | 3 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling male | SD | 2006 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | SD | 2007 | 10 | 1 | 0 | 0.900 | 0.095 | 0.714 | 1.000 |
| All hens | ND | 2005 | 19 | 1 | 0 | 0.947 | 0.051 | 0.847 | 1.000 |
| All hens | ND | 2006 | 25 | 3 | 0 | 0.880 | 0.065 | 0.753 | 1.000 |
| All hens | SD | 2006 | 37 | 3 | 0 | 0.919 | 0.045 | 0.831 | 1.000 |
| All hens | SD | 2007 | 41 | 4 | 0 | 0.902 | 0.046 | 0.812 | 0.993 |
| All males | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| All males | ND | 2006 | 13 | 2 | 2 | 0.833 | 0.113 | 0.611 | 1.000 |
| All males | SD | 2006 | 15 | 2 | 1 | 0.867 | 0.091 | 0.688 | 1.000 |
| All males | SD | 2007 | 25 | 3 | 0 | 0.880 | 0.065 | 0.753 | 1.000 |
| Nesting hen | ND | 2005 | 18 | 1 | 0 | 0.944 | 0.054 | 0.839 | 1.000 |
| Nesting hen | ND | 2006 | 19 | 1 | 0 | 0.947 | 0.051 | 0.847 | 1.000 |
| Nesting hen | SD | 2006 | 36 | 3 | 0 | 0.917 | 0.046 | 0.826 | 1.000 |
| Nesting hen | SD | 2007 | 35 | 2 | 0 | 0.943 | 0.039 | 0.866 | 1.000 |
| Non-nesting hen | ND | 2005 | 1 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Non-nesting hen | ND | 2006 | 6 | 2 | 0 | 0.667 | 0.192 | 0.289 | 1.000 |
| Non-nesting hen | SD | 2006 | 1 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Non-nesting hen | SD | 2007 | 6 | 2 | 0 | 0.667 | 0.192 | 0.289 | 1.000 |

Appendix 2-B. Survival estimates of greater sage-grouse by age and gender during the early brood-rearing season in North Dakota, 2005 and 2006 and in South Dakota, 2006 and 2007.

| Type | State | Year | # Birds | # Dead | # Censor | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| Adult female | ND | 2005 | 9 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult female | ND | 2006 | 16 | 2 | 0 | 0.875 | 0.083 | 0.713 | 1.000 |
| Adult female | SD | 2006 | 18 | 1 | 0 | 0.944 | 0.054 | 0.839 | 1.000 |
| Adult female | SD | 2007 | 27 | 1 | 0 | 0.963 | 0.036 | 0.892 | 1.000 |
| Yearling female | ND | 2005 | 9 | 1 | 0 | 0.889 | 0.105 | 0.684 | 1.000 |
| Yearling female | ND | 2006 | 12 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | SD | 2006 | 17 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | SD | 2007 | 10 | 1 | 0 | 0.900 | 0.095 | 0.714 | 1.000 |
| Adult male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Adult male | ND | 2006 | 7 | 1 | 0 | 0.857 | 0.132 | 0.598 | 1.000 |
| Adult male | SD | 2006 | 13 | 1 | 0 | 0.923 | 0.074 | 0.778 | 1.000 |
| Adult male | SD | 2007 | 11 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | ND | 2006 | 7 | 2 | 0 | 0.714 | 0.171 | 0.380 | 1.000 |
| Yearling male | SD | 2006 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | SD | 2007 | 9 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| All hens | ND | 2005 | 18 | 1 | 0 | 0.947 | 0.051 | 0.846 | 1.047 |
| All hens | ND | 2006 | 28 | 2 | 0 | 0.923 | 0.049 | 0.833 | 1.000 |
| All hens | SD | 2006 | 35 | 1 | 1 | 0.971 | 0.029 | 0.915 | 1.000 |
| All hens | SD | 2007 | 37 | 2 | 0 | 0.946 | 0.037 | 0.873 | 1.000 |
| All males | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| All males | ND | 2006 | 14 | 3 | 0 | 0.786 | 0.110 | 0.571 | 1.000 |
| All males | SD | 2006 | 13 | 1 | 0 | 0.923 | 0.074 | 0.778 | 1.000 |
| All males | SD | 2007 | 20 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| Brood hens | ND | 2005 | 6 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Brood hens | ND | 2006 | 8 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Brood hens | SD | 2006 | 12 | 1 | 0 | 0.917 | 0.080 | 0.760 | 1.000 |
| Brood hens | SD | 2007 | 16 | 1 | 0 | 0.938 | 0.061 | 0.819 | 1.000 |
| Broodless hens | ND | 2005 | 12 | 1 | 0 | 0.917 | 0.080 | 0.760 | 1.000 |
| Broodless hens | ND | 2006 | 20 | 2 | 0 | 0.900 | 0.067 | 0.769 | 1.000 |
| Broodless hens | SD | 2006 | 23 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| Broodless hens | SD | 2007 | 21 | 1 | 0 | 0.952 | 0.046 | 0.861 | 1.000 |

Appendix 2-C. Survival estimates of greater sage-grouse by age and gender during the late brood-rearing season in North Dakota, 2005 and 2006 and in South Dakota, 2006 and 2007.

| Type | State | Year | # Birds | # Dead | # Censor | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| Adult female | ND | 2005 | 9 | 2 | 0 | 0.750 | 0.139 | 0.506 | 1.000 |
| Adult female | ND | 2006 | 16 | 4 | 4 | 0.718 | 0.135 | 0.454 | 0.982 |
| Adult female | SD | 2006 | 19 | 3 | 0 | 0.842 | 0.084 | 0.678 | 1.000 |
| Adult female | SD | 2007 | 30 | 15 | 1 | 0.500 | 0.094 | 0.315 | 0.685 |
| Yearling female | ND | 2005 | 13 | 2 | 1 | 0.833 | 0.108 | 0.622 | 1.000 |
| Yearling female | ND | 2006 | 15 | 3 | 1 | 0.794 | 0.109 | 0.582 | 1.000 |
| Yearling female | SD | 2006 | 16 | 2 | 0 | 0.875 | 0.083 | 0.713 | 1.000 |
| Yearling female | SD | 2007 | 9 | 4 | 0 | 0.556 | 0.166 | 0.231 | 0.880 |
| Adult male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Adult male | ND | 2006 | 6 | 4 | 1 | 0.222 | 0.196 | 0.020 | 0.606 |
| Adult male | SD | 2006 | 11 | 5 | 1 | 0.500 | 0.158 | 0.190 | 0.810 |
| Adult male | SD | 2007 | 10 | 7 | 0 | 0.300 | 0.145 | 0.016 | 0.584 |
| Yearling male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | ND | 2006 | 5 | 3 | 2 | 0.000 | 0.000 | 0.000 | 0.000 |
| Yearling male | SD | 2006 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | SD | 2007 | 9 | 3 | 0 | 0.667 | 0.157 | 0.359 | 0.975 |
| All hens | ND | 2005 | 22 | 4 | 1 | 0.810 | 0.086 | 0.642 | 0.977 |
| All hens | ND | 2006 | 31 | 7 | 5 | 0.757 | 0.086 | 0.589 | 0.925 |
| All hens | SD | 2006 | 35 | 5 | 0 | 0.857 | 0.059 | 0.741 | 0.973 |
| All hens | SD | 2007 | 39 | 19 | 1 | 0.512 | 0.082 | 0.352 | 0.674 |
| All males | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| All males | ND | 2006 | 11 | 7 | 3 | 0.182 | 0.164 | 0.000 | 0.504 |
| All males | SD | 2006 | 11 | 5 | 1 | 0.500 | 0.158 | 0.190 | 0.810 |
| All males | SD | 2007 | 19 | 10 | 0 | 0.474 | 0.115 | 0.249 | 0.698 |
| All breeding-age | ND | 2005 | 22 | 4 | 1 | 0.810 | 0.086 | 0.642 | 0.977 |
| All breeding-age | ND | 2006 | 42 | 14 | 8 | 0.629 | 0.086 | 0.461 | 0.797 |
| All breeding-age | SD | 2006 | 46 | 10 | 1 | 0.778 | 0.062 | 0.656 | 0.899 |
| All breeding-age | SD | 2007 | 58 | 29 | 1 | 0.500 | 0.067 | 0.369 | 0.631 |
| All juvenile | ND | 2005 | 9 | 3 | 0 | 0.667 | 0.157 | 0.359 | 0.975 |
| All juvenile | ND | 2006 | 16 | 7 | 0 | 0.563 | 0.124 | 0.319 | 0.806 |
| All juvenile | SD | 2006 | 23 | 15 | 0 | 0.348 | 0.099 | 0.153 | 0.542 |
| All juvenile | SD | 2007 | 20 | 14 | 0 | 0.316 | 0.107 | 0.107 | 0.525 |
| Brood hens | ND | 2005 | 6 | 1 | 0 | 0.833 | 0.152 | 0.535 | 1.000 |
| Brood hens | ND | 2006 | 7 | 4 | 0 | 0.429 | 0.187 | 0.062 | 0.795 |
| Brood hens | SD | 2006 | 9 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Brood hens | SD | 2007 | 15 | 12 | 0 | 0.200 | 0.103 | 0.000 | 0.402 |
| Broodless hens | ND | 2005 | 16 | 3 | 1 | 0.800 | 0.103 | 0.598 | 1.000 |
| Broodless hens | ND | 2006 | 24 | 3 | 5 | 0.895 | 0.060 | 0.777 | 1.000 |
| Broodless hens | SD | 2006 | 26 | 5 | 0 | 0.808 | 0.077 | 0.656 | 0.959 |
| Broodless hens | SD | 2007 | 24 | 8 | 1 | 0.708 | 0.093 | 0.526 | 0.890 |

Appendix 2-D. Survival estimates of greater sage-grouse by age and gender during the winter season in North Dakota, 2005 and 2006 and in South Dakota, 2006 and 2007.

| Type | State | Year | # Birds | # Dead | # Censor | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| Adult female | ND | 2005 | 7 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult female | ND | 2006 | 8 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult female | SD | 2006 | 16 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult female | SD | 2007 | 14 | 1 | 0 | 0.929 | 0.069 | 0.794 | 1.000 |
| Yearling female | ND | 2005 | 9 | 1 | 0 | 0.889 | 0.105 | 0.684 | 1.000 |
| Yearling female | ND | 2006 | 11 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | SD | 2006 | 14 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | SD | 2007 | 5 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Adult male | ND | 2006 | 1 | 0 | 1 | n/a | n/a | n/a | n/a |
| Adult male | SD | 2006 | 5 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult male | SD | 2007 | 3 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling male | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | ND | 2006 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | SD | 2006 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | SD | 2007 | 5 | 1 | 0 | 0.800 | 0.179 | 0.449 | 1.000 |
| All hens | ND | 2005 | 16 | 1 | 0 | 0.938 | 0.061 | 0.819 | 1.000 |
| All hens | ND | 2006 | 19 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| All hens | SD | 2006 | 30 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| All hens | SD | 2007 | 19 | 1 | 0 | 0.947 | 0.051 | 0.847 | 1.000 |
| All males | ND | 2005 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| All males | ND | 2006 | 1 | 0 | 1 | n/a | n/a | n/a | n/a |
| All males | SD | 2006 | 5 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| All males | SD | 2007 | 8 | 1 | 0 | 0.875 | 0.117 | 0.646 | 1.000 |
| All breeding-age | ND | 2005 | 16 | 1 | 0 | 0.938 | 0.061 | 0.819 | 1.000 |
| All breeding-age | ND | 2006 | 20 | 0 | 1 | 1.000 | 0.000 | 1.000 | 1.000 |
| All breeding-age | SD | 2006 | 35 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| All breeding-age | SD | 2007 | 27 | 2 | 0 | 0.926 | 0.050 | 0.827 | 1.000 |
| All juvenile | ND | 2005 | 5 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| All juvenile | ND | 2006 | 9 | 2 | 0 | 0.778 | 0.139 | 0.506 | 1.000 |
| All juvenile | SD | 2006 | 8 | 1 | 0 | 0.875 | 0.117 | 0.646 | 1.000 |
| All juvenile | SD | 2007 | 6 | 1 | 1 | 0.800 | 0.179 | 0.449 | 1.000 |

Appendix 2-E. Survival estimates of greater sage-grouse by age and gender during the breeding season in North Dakota, 2006 and in South Dakota, 2006 and 2007.

| Type | State | Year | # Birds | # Dead | # Censor | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| Adult female | ND | 2006 | 19 | 1 | 0 | 0.947 | 0.051 | 0.847 | 1.048 |
| Adult female | SD | 2006 | 22 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult female | SD | 2007 | 31 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | ND | 2006 | 4 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | SD | 2006 | 17 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling female | SD | 2007 | 9 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Adult male | ND | 2006 | 1 | 1 | 0 | 0.000 | 0.000 | 0.000 | 0.000 |
| Adult male | SD | 2006 | 5 | 1 | 0 | 0.800 | 0.179 | 0.449 | 1.000 |
| Adult male | SD | 2007 | 13 | 3 | 1 | 0.750 | 0.119 | 0.518 | 0.982 |
| Yearling male | ND | 2006 | 3 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| Yearling male | SD | 2006 | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Yearling male | SD | 2007 | 7 | 1 | 0 | 0.857 | 0.132 | 0.598 | 1.000 |
| All hens | ND | 2006 | 23 | 1 | 0 | 0.956 | 0.043 | 0.873 | 1.000 |
| All hens | SD | 2006 | 39 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| All hens | SD | 2007 | 40 | 0 | 0 | 1.000 | 0.000 | 1.000 | 1.000 |
| All males | ND | 2006 | 4 | 1 | 0 | 0.750 | 0.217 | 0.326 | 1.000 |
| All males | SD | 2006 | 5 | 1 | 0 | 0.800 | 0.179 | 0.449 | 1.000 |
| All males | SD | 2007 | 20 | 4 | 1 | 0.792 | 0.090 | 0.615 | 0.969 |