

**NESTING AND BROOD-REARING HABITAT SELECTION OF
GREATER SAGE-GROUSE AND ASSOCIATED SURVIVAL OF HENS AND
BROODS AT THE EDGE OF THEIR HISTORIC DISTRIBUTION**

BY

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**NESTING AND BROOD-REARING HABITAT SELECTION OF GREATER
SAGE-GROUSE AND ASSOCIATED SURVIVAL OF HENS AND BROODS AT
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This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT**NESTING AND BROOD-REARING HABITAT SELECTION OF GREATER
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Greater sage-grouse (*Centrocercus urophasianus*) once occurred in 12 states and 3 Canadian provinces. Sage-grouse populations have declined over the last 60 years due to extensive habitat alteration and loss. Concerns for the management and conservation of greater sage-grouse and their habitats have resulted in petitions to list them under the Endangered Species Act. In North Dakota, sage-grouse are confined to approximately 800 square miles of sagebrush habitat, which is facing severe habitat fragmentation and habitat loss. Sage-grouse in North Dakota are not isolated, but are contiguous with populations in Montana and South Dakota. Annual rates of change suggest a long-term population decline in North Dakota, declining 2.79% per year from 1965 to 2003. The species is listed as a Priority Level 1 Species of Special Concern in the state. The objectives of this study were to estimate nest survival, hen and brood survival, and associated nest and brood-site habitat selection of sage-grouse in southwestern North Dakota. The study was conducted during the spring and summer of 2005 and 2006 in Bowman County, North Dakota. Nest-sites were monitored to determine nest fate and broods were monitored by tracking radio-marked adults that successfully hatched young.

Habitat selection was characterized by comparing vegetation at nest-sites and brood-sites to vegetation points at randomly selected sites. I found 34 nests from 39 female sage-grouse (21 in 2005, 18 in 2006) that were radio-marked. Vegetation measurements were taken at 34 nest-sites and 50 random points. I collected vegetation measurements from 130 brood-sites and 107 random sites. Nest survival averaged 31% (33% in 2005 and 30% in 2006). The best model of nest survival included daily precipitation. Models that contained percent grass cover and grass height from the Robel pole also had substantial support (i.e., < 2 AIC units) to explain nest survival. One model strongly supported characteristics associated with selection of nest-sites that included percent total cover, 1-m VOR, and sagebrush density. Sage-grouse nests were positively associated with more total cover, 1-m VOR, and sagebrush density than were present at random sites. In 2005, hen survival was 84% (95%CI: 0.67 to 1.00, $n = 20$) from capture date through the brood-rearing season, and 60% (95%CI: 0.44 to 0.76, $n = 39$) in 2006. I monitored 7 broods in 2005, with an average of 6.86 ± 0.95 chicks/hen at hatch. At 3 weeks post hatch, the average brood size was 2.34 chicks/hen representing 34% apparent survival. In 2006, 6 broods averaged 6.67 ± 1.03 chicks/hen at hatch. At 3 weeks post hatch, the average brood size was 2.83 chicks/hen representing 42% apparent survival. A total of 38 sage-grouse chicks were radio-marked (13 in 2005, and 25 in 2006). Chick survival from hatch date to 3 weeks post hatch, combined with those that survived to 5-6 weeks of age and were able to be captured, 17% of the chicks were estimated to recruit into the population in December 2005 and 13% in December 2006. The majority of identifiable predation events on radio-marked sage-grouse chicks were from canids. One model of

brood site selection was positively associated with more total forb, total grass, and total sagebrush than was present at randomly selected sites, and negatively associated to percent bareground, sagebrush height and sagebrush width. Brood sites consisted of 6-16% forb cover, 29-34 % grass cover, 5% sagebrush cover and approximately 30-38 cm tall sagebrush plants, and 50-53 cm wide sagebrush plants. Percent bareground cover consisted of 11-25% at brood sites. I recommend that managers develop strategies to preserve the integrity of shrubsteppe habitat in southwestern North Dakota. Herbaceous cover in sagebrush habitats is an important component of nesting and brood-rearing habitat for sage-grouse. Thus I recommend management activities that maintain or restore dense, taller residual grass within sage-grouse habitat.

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CHAPTER 1-GENERAL INTRODUCTION

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) populations were once distributed throughout 12 states in western North America, and 3 Canadian provinces. Populations of sage-grouse have undergone long-term population declines due to extensive alteration and loss of sagebrush (*Artemisia* spp.) habitats (Schroeder et al. 2004). Sage-grouse started to decline during the early twentieth century, corresponding with the American westward movement and the arrival of European settlers in the 1800s, increasing numbers of livestock, and intense agriculture practices (Patterson 1952, Gill 1966). Estimates of regional declines in sage-grouse have ranged from 17 to 47% (Connelly and Braun 1997). There was a corresponding decline in sagebrush habitat quality and quantity due to agriculture, invasive exotics (i.e., cheatgrass), overgrazing, energy development, drought, fire, and herbicides (Patterson 1952, Homer et al. 1993, Gregg et al. 1994, Connelly and Braun 1997, Braun 1998, Connelly et al. 2000, Hemstrom et al. 2002). Greater sage-grouse currently occupy 56% of their historic range (Schroeder et al. 2004), and 17% of their prehistoric range in North Dakota.

Greater sage-grouse are obligates of sagebrush ecosystems that dominate most of western North America. Sagebrush is required for food, shelter, and as a water source for sage-grouse (Swenson 1987, Fischer et al. 1996, Schroeder et al. 1999). During the winter months, sagebrush is the only source of food (Hupp and Braun 1989, Welch et al. 1991) with the sage-grouse's diet consisting of leaves and buds (Welch et al. 1991, Homer et al. 1993, Connelly et al. 2000). Sage-grouse are unique among the Galliformes

because they lack a well developed gizzard, which makes their dependence on soft vegetation critical. Since their diet is based mostly on herbaceous leaves of sagebrush, there is no need for a highly developed gizzard (McCarthy and Kobriger 2005).

Sagebrush steppe is important as a management indicator for sage-grouse in all shrub-steppe vegetation communities. Sagebrush coexists with understory forbs that are important for female sage-grouse during nesting and brood-rearing (Drut et al. 1994a, Crawford 1997, Connelly et al. 2000). Greater sage-grouse nest beneath sagebrush (Patterson 1952, Gill 1966, Connelly et al. 1991, Musil et al. 1994, Sveum et al. 1998), where females may show nest-site fidelity from year to year (Fischer et al. 1993). Klebenow (1969) and Wallestad (1975) found that sagebrush provided female sage-grouse with nesting cover and early brood-rearing habitat. Females typically chose nest-sites with horizontal cover of greater than 73% (Musil et al. 1994, Connelly et al. 2000), and tall residual grasses of greater than 18 cm and medium shrubs from 40-80 cm of height (Gregg et al. 1994, Sveum et al. 1998, Connelly et al. 2000).

Recent research of nesting sage-grouse emphasizes the importance of herbaceous cover in determining nest fate. Nest-sites coexist in areas of greater than 38% sagebrush cover because of greater amounts of forbs (Klebenow 1969, Connelly et al. 2000). Presence of forbs increased initiation rates of hens and nutrient acquisition by chicks (Johnson and Boyce 1990, Barnett and Crawford 1994, Drut et al. 1994b, Crawford 1997, Sveum et al. 1998, Gregg 2001).

The decline of sage-grouse throughout their range has caused them to be listed as a Priority Level 1 Species of Special Concern in North Dakota. Immediate research and conservation action is necessary for sage-grouse and their habitats (Wambolt et al. 2002, Schroeder et al. 2004). Similar concerns nationally also have led to petitioning the U.S. Fish and Wildlife Service to protect the greater sage-grouse under the Endangered Species Act (ESA), which would have a significant impact on private and federal land management practices within the United States. North Dakota is situated on the eastern edge of distribution of sage-grouse and sagebrush steppe communities; thus this species may not utilize habitats as predictably as in the interior areas of sagebrush country (Smith 2003, Lewis 2004).

Little is known about the finite habitat use or seasonal movements of sage-grouse in North Dakota. Sage-grouse have never been widespread in North Dakota and are currently confined to the southwestern portion of the state, in western Bowman, Slope, and Golden Valley counties (Johnson and Knue 1989, McCarthy and Kobriger 2005). The North Dakota population is contiguous with sage-grouse populations in South Dakota and Montana (McCarthy and Kobriger 2005). My study was conducted to gather data on seasonal habitat use during nesting and brood-rearing, and survival rates of female sage-grouse and chicks in southwestern North Dakota. In North Dakota and other areas of western United States, sage-grouse inhabit areas where *Artemisia tridentata* *wyomingensis* and other related forbs and grasses occur (McCarthy and Kobriger 2005). Nesting studies are important to ascertain data in regards to nest success, nesting habitat,

and to quantify nest-site vegetation to guide management and conservation activities for sage-grouse habitats.

The objectives of this study were to (1) determine and quantify nesting and brood-rearing habitat selection of radio marked sage-grouse in North Dakota; (2) estimate survival of radio-marked female sage-grouse in southwestern North Dakota and (3) investigate and determine specific causes for observed sage-grouse mortalities. Other objectives were to (4) estimate nest success of radio-marked female sage-grouse in North Dakota, (5) evaluate the cause and timing of nest failures (e.g., abandonment, predation), (6) estimate brood survival of radio-marked female sage-grouse in southwestern North Dakota, and (7) investigate the cause(s) of brood/chick mortality. Addressing these objectives will help resource managers in the development of management recommendations to benefit state and federal wildlife and habitat management agencies that coordinate management of greater sage-grouse and their habitats. These comparisons will benefit managers by providing a measure of management success and failures for sage-grouse. This research also will aid in providing information on habitat selection, movements, and survival of sage-grouse at the eastern fringe range of existence; an area where basic reproductive ecology of the species has not been studied. Data from this study when compared to those from stable populations in the heart of sagebrush range can help elucidate ultimate factors required by sage-grouse.

STUDY AREA

The study area was located in Bowman and Slope counties in southwestern North Dakota (Figure 1). Topography was flat to unglaciated gently-rolling prairie with few buttes and intermittent streams. Soil orders consisted of Entisols, Alfisols, Mollisols, Inceptisols, Mollisols, and Aridisols (Johnson 1976, Kalvels 1982, Johnson 1988, Smith 2003). Annual precipitation ranged from 35.6 cm to 40.6 cm with a majority falling from April to September. Annual summer and winter temperatures ranged from 9.9°C to 27.5°C and from -15.6°C to 0.2°C, respectively (Opdahl et al. 1975, Thompson 1978, Smith 2003). Precipitation for 2005 was 35.88 cm and average January and July temperatures were -10°C and 21°C, respectively (North Dakota Agricultural Weather Network, 2006).

Vegetation was a mixture of shrubland, with an understory of perennial and annual forbs and grasses, with open grassland (Johnson and Larson 1999). Dominant shrub species included silver sagebrush (*A. cana*), big sagebrush (*A. tridentata*), western snowberry (*Symphoricarpos occidentalis*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and greasewood (*Sarcobatus vermiculatus*) (Johnson and Larson 1999).

Dominant grasses in the area consisted of kentucky bluegrass (*Poa pratensis*), western wheatgrass (*Pascopyrum smithii*), japanese brome (*Bromus japonicus*), needle and thread (*Stipa comata*), and junegrass (*Koeleria macrantha*). Dominant forbs were common yarrow (*Achillea millefolidium*), common dandelion (*Taraxacum officinale*), and textile onion (*Allim textile*) (Johnson and Larson 1999).

The majority of the land in the study site was publicly owned and under the jurisdiction of the Bureau of Land Management (BLM). The normal stocking rate for grazing in Bowman County is 4-10 acres per AUM, but in areas with rough terrain/poor soils it can be as high as 14 acres per AUM. Allotments differ from low management intensity areas, because they are small tracts of public land surrounded by large blocks of private land, to high intensity areas, which are large blocks of land, with livestock numbers reported accordingly to land availability. Livestock may or may not be rotated on low management areas, but are rotated through grazing pastures on a schedule in larger blocks of public land. Most ranchers do not use the federal land year round, but year-round grazing is allowed on federal lands to provide flexibility to lessee grazing needs (Mitch Iverson, BLM personal communications).

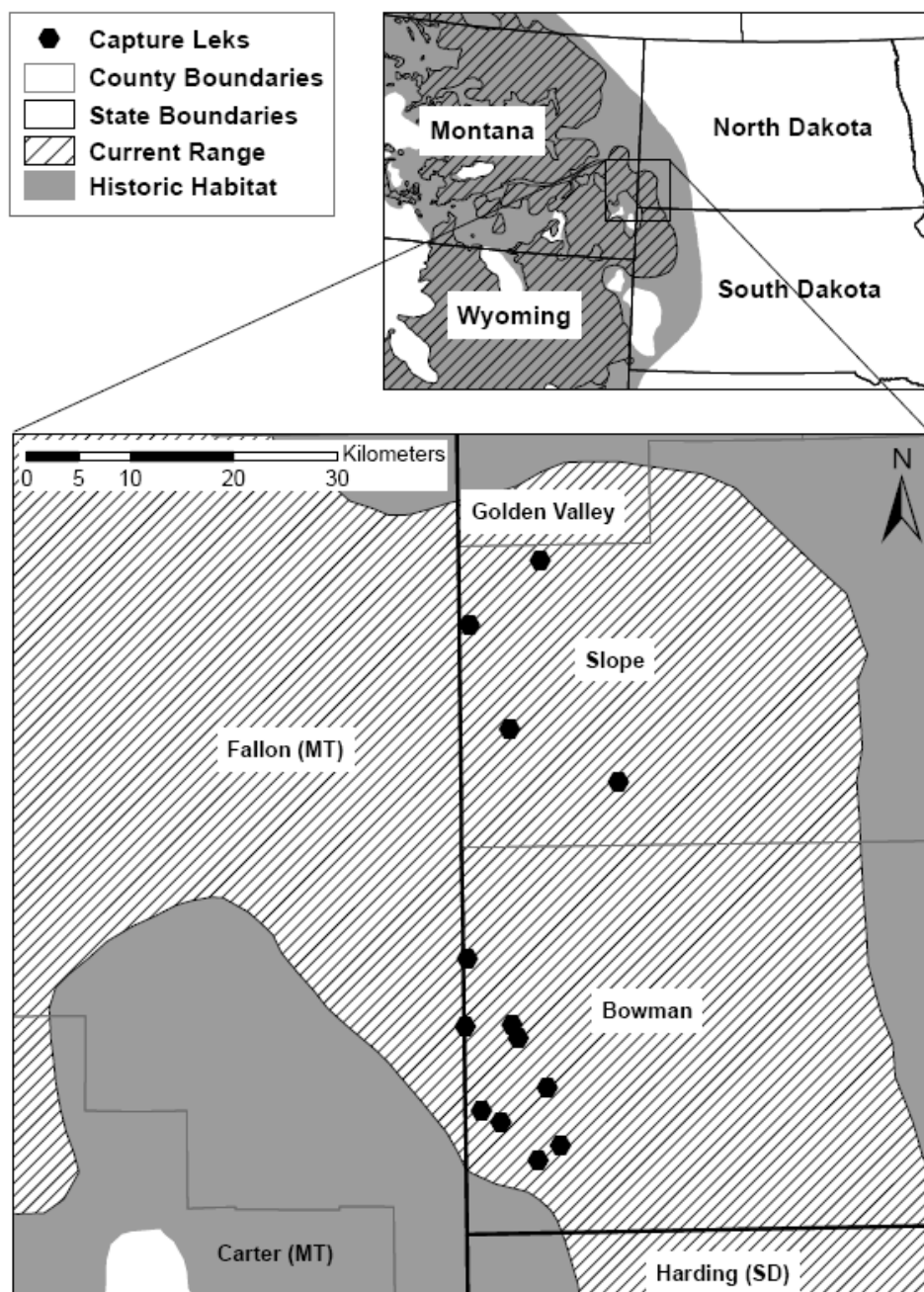


Figure 1. Study area of Bowman, Slope, and Golden Valley counties with capture leks documented during 2005 and 2006.

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CHAPTER 2- NESTING ECOLOGY OF GREATER SAGE-GROUSE AT THE EASTERN EDGE OF THEIR HISTORIC DISTRIBUTION

INTRODUCTION

Following the arrival of European settlers in the 1800s, greater sage-grouse (*Centrocercus urophasianus*) habitat has been changing continuously (Girard 1937, Patterson 1952). Greater sage-grouse experienced population declines from 45- 80% across their range by the 1950s (Braun 1998) and during the 10-year period from 1985-1995 sage-grouse populations declined 33% (Connelly and Braun 1997). Historically, sage-grouse range is limited to sagebrush (*Artemisia* spp.) vegetation types in at least 12 states and 3 Canadian provinces, but currently they reside in 11 states and 2 Canadian provinces (Schroeder et al. 2004). Sage-grouse are sagebrush obligates and degradation and loss of sagebrush resulted in population declines and constriction of the range (Wisdom et al. 2005, Welch 2005).

Discovery of oil and gas throughout the United States in the 1930s and 1940s impacted wildlife habitats in numerous ways. In Colorado, the initial impacts of oil and gas development caused sage-grouse populations to decline drastically from noise, habitat loss, infrastructure and human activities (Braun 1987). The long-term effects is unknown, but there is no evidence that populations of sage-grouse will recover to pre-disturbance populations, and the length of recovery time for these habitats is estimated to range from 2-30 years (Braun 1998). Grazing by domestic livestock, fire, construction, power lines, fences, and drought also contributed to loss of sagebrush (Braun 1998, Schroeder et al. 1999, Welch 2005). These changes have affected nest-site and brood

rearing habitats by fragmenting the landscape and causing habitat loss (Connelly and Braun 1997, Beck et al. 2003, Crawford et al. 2004).

The importance of sagebrush for nesting habitat of sage-grouse is well documented (Girard 1937, Patterson 1952, Gill 1965, Wallestad and Pyrah 1974, Gray 1967, Petersen 1980, Autenreith 1981, Connelly et al. 1991, Musil et al. 1994). Understanding which characteristics are important for nest-site habitat selection and the associated factors that affect nest success is critical management, conservation, or rehabilitation of sagebrush habitats to benefit sage-grouse. Braun et al. (1977) reported that female sage-grouse typically nested in stands of medium density sagebrush within 3 km of leks. Dense understory vegetation and overstory cover at nest-sites were critical factors determining nest-site selection (DeLong et al. 1995). Vegetation characteristics at successful nest-sites included shrubs greater than 18 cm tall and > 31% canopy cover (Barnett and Crawford 1994). Despite well understood nesting habitat in the core of sage-grouse range, knowledge of reproductive ecology and habitat selection by sage-grouse occurring at the eastern range of their distribution is limited.

The sage-grouse population in North Dakota is contiguous with populations in Montana and South Dakota (McCarthy and Kobriger 2005). Annual rates of change suggest a long-term population decline of about 2.79% per year from 1965 to 2003 (McCarthy and Kobriger 2005). Current breeding populations in North America are estimated to be 3 to 6 times lower than occurred in the late 1960s to early 1970s (Connelly et al. 2004). Sage-grouse are a Priority Level 1 Species of Special Concern in North Dakota. With this listing, it is recommended that immediate research and

conservation actions be taken. Thus, population declines may be related to declining habitat quality which may result in decreased survival and productivity; however, the significance of these factors is unknown. The fragmentation of sagebrush habitats could render them unsuitable as nesting habitat and could contribute to population declines by reducing nest success and overall population productivity.

My objectives were to determine and quantify nest-site habitat selection of sage-grouse in North Dakota, and estimate specific factors that affect sage-grouse nest survival. Other objectives were to estimate nest survival of radio-marked female sage-grouse in North Dakota and evaluate the cause and timing of nest failures (e.g., abandonment, predation), followed by development of models to best explain nest survival and nest-site habitat selection. This data will help in the development of management recommendations to assist state and federal wildlife and habitat management agencies that coordinate management of greater sage-grouse and their habitats.

METHODS

Data Collection

Capture and Marking. – I captured birds at night on or near leks from 31 March – 23 April 2005 and 27 March – 27 April 2006. I used hand-held spotlights to locate birds and approached them while shining the spotlight to confuse them and then used long-handled nets to capture the hens (Giesen et al. 1982). I recorded age, sex, weight, and placed leg-bands and 20-gram necklace type radio transmitters with mortality sensors on

each bird (Advanced Telemetry Systems, Isanti, Minnesota). Each bird was released at the point of capture. The transmitters were less than 2% of the bird's body weight.

Monitoring Radio-marked Hens. - I located radio-marked hens from aerial and ground radiotelemetry. Ground telemetry locations were made weekly using a hand-held 3-element yagi antenna. I recorded locations using a hand-held GPS unit when a nest was initiated. I monitored the hen ≥ 2 times each week to determine nest fate. I marked each nest with flagging approximately 20-40 m south. After the hen began incubation, I flushed her from the nest and determined incubation stage by floating (Hays and LeCroy 1971; Appendix A). If the hen was absent from the nest, the nest was examined to determine nest fate. Nests that were predated, I searched the immediate area for hair, tracks, scat, or any other sign that would indicate the species of predator (Sargeant et al. 1998). Successfully hatched nests were determined by membrane conditions of the egg or visual observation of a brood with the radio-marked hen. Nests were considered successful if ≥ 1 egg hatched. I estimated egg hatchability as percentage of eggs present at the time of hatching which produced chicks. I classified nests with eggshell fragments firmly attached to shell membranes or missing eggs as unsuccessful.

Habitat Measurements. - I recorded vegetation measurements at nest-sites and random locations ≤ 3 km of leks during May and June of 2005 and 2006. Coordinates of nests and random sites were entered into a GPS to locate the point in the field. The accuracy of GPS units was usually less than ± 10 m. Because nests are usually located beneath a shrub, the random site was then centered over the nearest shrub. I recorded slope and aspect for each nest-site using a linometer and compass, respectively as the

downhill direction from each nest. At each nest and random site, I established four 50-m transects which were centered over the nest or random site. I recorded species, height, length, and width of sagebrush at each nest and random site. At each 10-m interval ($n = 20$) along each transect I recorded the distance to the nearest sagebrush using the point-centered-quarter method (Cottam and Curtis 1956). For every sagebrush encountered, I also recorded the height, length, width of the sagebrush, and height of grass growing beneath the shrub. I estimated visual obstruction and height of grass using a modified Robel pole delineated in 2.54 cm increments (Robel et al. 1970, Benkobi et al. 2000). In order to avoid trampling on the vegetation, I viewed the pole from 3 directions for the 1 to 5 m measurement intervals. Herbaceous canopy cover was estimated at the nest or random point, and at 10-m intervals along 50-m transects in 0.10 m² quadrats (see Appendix B for species identification; Daubenmire 1959). I recorded total cover, total sagebrush, total grass, total forb, litter, bareground and dominant species of grasses and shrubs in each quadrat. I obtained measures of maximum and minimum daily temperature, and daily precipitation from the closest weather station in Bowman County (North Dakota Agricultural Weather Network). Additionally, I assessed the road density in a minimum convex polygon using sage-grouse locations from 2005 to 2007 in North Dakota to estimate road miles per square km of sage-grouse habitat as an index of fragmentation (ESRI, Inc. ArcGIS 9.1, Redlands, CA.).

Data Analyses

Distance. - The distance from each random site to the nearest lek, and from each nest to nearest lek and the distance from each nest to the lek nearest to where the hen was captured (if the hen was captured that year) were calculated, along with distance from nest to nearest lek between successful and unsuccessful nests. To examine nest-site fidelity to specific nesting areas, I compared distances between consecutive-years' nests, and between those that were successful or unsuccessful in 2005 to their distances moved in 2006. I tested the hypotheses that there was no difference in distribution between the distances from random sites to nearest lek, nests to nearest lek and lek of capture, or between successful and unsuccessful nests using multiple response permutation programs (MRPP; Mielke and Berry 2001). Statistical significance was determined at $\alpha \leq 0.05$ for these univariate tests.

Habitat Selection. - Canopy cover values were recoded to mid-point values of the categories and I summarized data to an average value for each variable for the site. In addition, I summarized visual obstruction (VOR) values from the nest and 1-m to 5-m intervals; I also calculated the average VOR for the site. Estimates of sagebrush density were made from maximum likelihood estimates (Pollard 1971). I then used MRPP (Mielke and Berry 2001) to test the distributions of vegetation variables between nests and random sites, and used this as a screening process to distinguish important variables for future analysis with a critical value of $\alpha \leq 0.05$. The variables evaluated included percent total vegetative cover, percent grass cover, percent forb cover, percent sagebrush cover, percent bareground, percent litter, sagebrush height, average sagebrush width, site-

VOR and 1-m intervals to 5-m, grass height as measured on the Robel pole (max-VOR), and sagebrush density (Appendix C). I also tested these variables for similarities in distributions at successful and unsuccessful nests, nests of adults and yearlings, and between years using MRPP as initial screening of variables to be included in other analyses at the critical value for $\alpha \leq 0.05$.

I used information theoretic approach (Burnham and Anderson 2002) with logistic regression to estimate variables selected for by female sage-grouse at nest-sites using SAS JMP (2005 SAS Institute Inc). I developed 10 *a priori* models including variables from the previous MRPP test to predict nest-sites. The candidate models included vegetative variables of percent vegetative cover, percent grass cover, percent forb cover, percent sagebrush cover, sagebrush height, site-VOR, nest-VOR and 1-m VOR, grass height from the Robel pole, and sagebrush density. The variable year was considered as a design variable and was included in all candidate models. Thus, any difference among the models in the candidate sets were due to differences in the vegetative variables. For ease of interpretation, I did not include year in the tables. I tested the strength of the model to predict nest-sites using receiver operating characteristic curve (ROC) used as model fit or discrimination diagnostics (SAS JMP). Receiver operation characteristic values between 0.7 and 0.8 were considered acceptable discrimination, and ROC values between 0.8 and 0.9 were considered excellent discrimination (Hosmer and Lemeshow 2000).

To prevent underfitting or overfitting, Akaike's Information Criterion (AIC) was used as the basis for model selection. Using the log-likelihood values and number of parameters (k) provided in the output file from the 10 models within Program JMP. The models were ranked using the equation: $AIC = -2(\log\text{-likelihood}) + 2k$. The two components of AIC include; $-2(\log\text{-likelihood})$, which measures discrepancy of the fit between the data and the model, and (k) is a penalty for the number of parameters included in the model to prevent overfitting the models. Unless the sample size is large with respect to the number of parameters estimated, the use of $AICc$ is recommended; $AIC + 2K(K + 1)/n - K - 1$. The models were ranked using $\Delta AICc$ (Burnham and Anderson 1992).

Nest Survival and Modeling.- I estimated daily survival rate (DSR) of nests using program MARK (White and Burnham 1999) for the 27 day incubation period. I standardized May 6 as day 1 and numbered all nest check dates sequentially thereafter. Estimates of nest survival between adult and yearling hens and nest survival rates between years were compared using Program MARK.

Factors Influencing Nest Survival.- Nest survival probabilities were estimated as a function of continuous and categorical habitat variables using nest survival analyses in program MARK (White and Burnham 1999). Continuous variables included percent vegetative cover, grass cover, forb cover, sagebrush cover, max-VOR, site-VOR, sagebrush height, and sagebrush density. Categorical variables included bird age, nest age, and year. Time-dependent variables included maximum and minimum daily temperatures and precipitation during the interval since the nest status was determined.

Continuous covariates were standardized as deviations from a mean of 0. Categorical and time-dependent covariates were coded with the actual values so they would not hamper numerical optimization of likelihood (Burnham and Anderson 2002). The nesting period was 54 days beginning on 6 May each year. Nest age (in days) was then coded relative to 6 May. Thus, the covariate nest age had values from -17 to 17 and was modeled as a continuous variable.

Variables combined with constant DSR were compared using Akaike's Information Criterion corrected for a small sample size ($AICc$; Akaike 1973, Burnham and Anderson 2002). Models within 2 units of the minimum $AICc$ model were considered best approximating models to explain variation of nest survival (Burnham and Anderson 1998). Variable weights were calculated by adding $AICc$ weights of all models that included variables of interest to assess relative importance of single variables (Burnham and Anderson 2002). I used beta estimates of continuous variables in each set of candidate models to determine direction of effect of that variable on DSR. Because the saturated model fits the data perfectly, there is no need for a goodness-of-fit test between models (Cooch and White 2006).

Hen Survival. - Hen survival was estimated using Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) throughout the nesting and brood-rearing periods.

RESULTS

Capture and Marking Female Sage-Grouse. - Thirty-nine hens were captured and fitted with radio-collars during spring and summer 2005 and 2006 (21 during 2005, 18 during 2006); 36% (14/39) were adults. Twenty female sage-grouse were included in analyses of nests in 2005, and nine additional female sage-grouse were used during spring 2006 analyses, for a total of 29 hens to model nest survival.

Monitoring Radio-collared Hens. - Based on morning lek counts and capture data during 2005 and 2006, peak hen visitation to leks occurs between 5 April – 11 April (Figure 2). Sage-grouse began laying eggs on 9 April, 2005 and 11 April, 2006 based on the 27 day incubation and the assumption of 1 egg laid every 1.3 days (Patterson 1952). Average nest initiation date during 2005 and 2006 was 23 April (range 21 April to 25 April) ($n = 36$). Adults initiated nests approximately 5 days earlier than yearlings. There were 2 renests in 2005; average date of renests on 21 May (Table 1). Average clutch size was 8 eggs per nest ($n = 36$). Clutch size for 12 successful nests averaged 7.58 ± 0.63 eggs, and 20 unsuccessful nests averaged 8.1 ± 0.49 . Clutch size was not significantly different between successful and unsuccessful nests ($P = 0.699$, MRPP), therefore, I pooled data for further analyses. There was no difference in clutch size between adults and yearlings ($P = 0.858$, MRPP). Overall probability that an egg present at hatching produced living young (Mayfield Egg Hatchability) was 0.34 ($n = 258$). Most eggs were predated, abandoned, or infertile (74%).

Nest Attempts .- All radio-marked hens initiated a nest in 2005. In 2006, 13 of 14 adults (93%), and 5 of 7 yearlings (71%) initiated nests. There was no difference in nest initiation rates between years ($P = 0.105$, MRPP), thus data were pooled. Overall nest initiation for adult hens ($n = 20$) averaged 95% and was not significantly different ($P = 0.578$, MRPP) from yearling hens ($n = 16$) which averaged 88%. Overall nest initiation was 92% for adults and yearlings with both years combined (Table 2). I found that 90% of nest failures of first nest attempts were depredated or abandoned after ≥ 1 week of incubation (Figure 3). Renesting rate during my study was 2 of 21 (10%) during both field seasons. Adults initiated nests approximately 5 days earlier than yearlings, however, there was no significant difference ($P = 0.07$, MRPP).

Distance Between Nests . - Average distance between individual nests in 2005 to subsequent nests in 2006 for 9 birds was 2.35 ± 0.10 km. Distance between unsuccessful nests in 2005 to subsequent nests in 2006 averaged 2.06 ± 0.99 km ($n = 4$), and distance between successful nests in 2005 to subsequent nests in 2006 averaged 2.58 ± 1.73 km ($n = 5$). Hens that were unsuccessful their first nesting season did not move farther from their nests in 2005 than hens that were successful their first year ($P = 0.457$, MRPP).

Average distance from nests to the lek where a hen was captured was 4.94 ± 4.06 km and average distance from nests to nearest lek was 2.66 ± 2.35 km. Unsuccessful nests averaged 2.75 ± 2.85 km ($n = 13$) and successful nests averaged 2.53 ± 1.52 km ($n = 9$) from the nearest lek. Sixty-eight percent of nests were ≤ 3 km from a lek (Figure 4). There was no difference in distribution of distances from nests to nearest leks

between unsuccessful and successful nests ($P = 0.457$, MRPP) or between years ($P = 0.449$, MRPP), and no difference between age classes ($P = 0.767$, MRPP).

Nest Survival and Modeling. - Nest survival was 33% in 2005 ($n = 14$) and 30% in 2006 ($n = 15$). Overall nest survival was 31%, including 1 successful re-nest. Constant DSR was the most parsimonious model; thus data were pooled because there was no difference between years or age category of nest survival (Table 3).

Estimates of variables screened from MRPP between successful and unsuccessful nests indicated certain variables might have more explanatory power to model nest survival. Competitive variables incorporated in nest survival models included percent grass cover, percent forb cover, nest-VOR, sagebrush density, and sagebrush height (Table 4). The relationship of each variable in relation to nest survival is incorporated in Table 4. There was little evidence that a particular vegetation characteristic or combination of two characteristics influenced nest survival. Single variable models including percent grass cover and height of grass from Robel pole had about equal weight. Models including percent sagebrush cover, percent grass, percent forb, nest-VOR, and sagebrush density were a second group of models with less influence on nest survival than the previous variables. The model that incorporated daily precipitation was the best predictive model of nest survival (Table 5). After model averaging, DSR was best explained by the most parsimonious model of daily precipitation (Figure 5).

Nest-site Selection. - Most nests were beneath a shrub and 88% were located beneath sagebrush. One sage-grouse nest was beneath four-wing saltbush (*Atriplex canescens*), one nest was beneath eastern red cedar (*Juniperus virginiana*), two nests were

in residual cover of sweet clover (*Melilotus officinalis*) from the previous year, and one nest was in wheat stubble (*Triticum* spp.).

The distribution of percent total cover, grass cover, forb cover, sagebrush cover, litter, nest-VOR, 1-m VOR, and sagebrush density differed ($P \leq 0.05$, MRPP) between nests and random sites. Averages for these variables were greater at nests than at random sites (Table 6). Distributions of percent forb cover, sagebrush cover, bareground, grass beneath the sagebrush differed ($P \leq 0.05$, MRPP) between years at both nest and random sites. In addition, all VOR measurements extending out from nests differed between years at random sites. Average values for all these variables were greater in 2005 than 2006. All logistic models included the design variable year (Table 7).

One model strongly was supported with selection of nests that included percent total cover, 1-m VOR, and sagebrush density (Table 8). Sage-grouse nests were positively associated with more percent total cover, 1-m VOR, and sagebrush density than were present at random sites. In the model, increasing VOR by 2.54 cm increased the probability of the site to be a nest by a multiplicative factor of 0.281 ± 0.275 (CI 95%). Increasing total vegetative cover by 10%, increased the probability of the site to be a nest by a multiplicative factor of 0.60 ± 0.52 (CI 95%), and increasing sagebrush density by 50 shrubs/hectare, increased the probability of the site to be a nest by a multiplicative factor of 4.3 ± 0.85 (CI 95%) (Table 9). Classification accuracy of the model was acceptable with an ROC value = 0.76.

Habitat fragmentation. - In North Dakota, I estimated 1.45 km of roads/km² in approximately 900 km² area of sage-grouse habitat.

Hen Survival.- Hen survival was evaluated throughout nesting and brood rearing periods from time of capture (March – April) through August. In 2005, hen survival was 84% (95%CI: 0.67 to 1.00, $n = 20$) (Figure 6). In 2006, hen survival was 60% (95%CI: 0.44 to 0.76, $n = 39$) (Figure 7).

DISCUSSION

Breeding Chronology and Nesting. - Peak hen attendance at leks by greater sage-grouse in southwestern North Dakota was later than in the Columbia Basin and Great Basin states (Bradbury et al. 1989, Schroeder 1997, Connelly et al. 2004), but similar to sage-grouse ranges on the western edge of the Great Plains (Jenni and Hartzler 1978, Aldridge and Brigham 2001, Hausleitner 2003). This effect may be mitigated by milder temperatures and different precipitation between my study area and that at the Great Basin or Columbia Basin. Precipitation in the latter areas occurs most during the fall, winter, and spring and by July most of the Great Basin and Columbia Basin have little green herbaceous vegetation remaining (Bailey 1980). In North Dakota, about 60% of the precipitation occurs between April and July (North Dakota Agricultural Weather Network, 2006). Even though peak hen attendance was later in North Dakota; initiation of incubation in my study was similar to those found in the Columbia and Great Basin states (Schroeder 1997) suggesting that peak attendance was not synchronize with nest initiation.

All of the radio-marked hens attempted to nest in 2005. In 2006, some hens did not nest. In 2006, I had a larger sample size which could account for a greater probability of some hens to not initiate a nest. Reported nest initiation rates vary by region. Averaged across 11 studies, nest initiation rates of hens was 80%. Competition for nest-sites by female sage-grouse in populations that are dense could cause some hens not to nest. However, where populations are low, competition for nest-sites is less likely, and most hens will initiate a nest (Aldridge and Brigham 2001). The observed nest initiation rate may also be influenced by the abundance and distribution of suitable habitat for all aspects of sage-grouse's life history.

Renesting by hens varies regionally from 6–87% (Hanf et al. 1994, Schroeder 1997, Aldridge and Brigham 2001). Renesting in wild turkeys has been related to habitat quality (Rumble and Hodorff 1993, Rumble et al. 2003). My low renesting rates may suggest low habitat quality. Female sage-grouse nested 3 times in Washington, with adults more likely to reneest than yearlings (Sveum 1995, Schroeder 1997). Protein may be an important variable for renesting because it is a major nutrient found in eggs (Carey 1996) and could be a limiting factor for egg production in sage-grouse (Moss 1972, Thomas and Popko 1981, Thomas 1982). Protein resources necessary for reproduction originate from the diet (i.e., exogenous sources; Beckerton and Middleton 1982, Carey 1996). Daily intake of proteins during spring, age, date of first nesting attempt, and incubation stage of the lost nest could affect renesting abilities of sage-grouse (Seubert 1952, Gates 1962, Sopuck and Zwickel 1983, Bergerud 1988, and Grand and Flint 1996). Gregg et al. (2006) documented that renesting rates decreased when hens initiated nests

later in the nesting season or lost nests later during incubation. Bergerud (1988) suggested that adult hens reneest more frequently than yearlings because they tend to nest earlier in the season, and therefore have enough time to initiate a second nest and hatch a successful brood and raise a brood.

Habitat quality and quantity may also be responsible for low nest success by decreasing amount of protein available during early spring nesting seasons. The age of nest at termination could be a factor associated with the lack of reneesting in southwestern North Dakota. Hen age did not appear to be an important variable for distinguishing between reneesting and non-reneesting sage-grouse because 40% of nest failures were by adults, and 50% were yearlings.

Adult hens tend to nest earlier than yearlings (Batterson and Morse 1948, Schlatterer 1960, Petersen 1980, Schroeder 1997), and I noted a similar pattern. Earlier nesting by adults is attributed to adults being more biologically ready to nest than yearlings (Schroeder 1997). I found adults initiated nests approximately 5 days earlier than yearlings.

Average clutch size in my study was consistent with other studies (Wallestad and Pyrah 1974, Sveum 1995). Despite predictions of age-specific differences in clutch size (Wallestad and Pyrah 1974, Petersen 1980), clutch size of adult and yearling nests was similar during my study.

Nest Survival. - Connelly et al. (2004) reported that nest success of female sage-grouse across their range varied from 14-86%. Average nest success across the range was 47.7% (Trueblood 1954, Gregg 1991). Nest success during my study was lower than

previous studies; most nests were lost to predation or weather. Nest predation can be higher in fragmented landscapes (Andre'n et al. 1985, Andre and Angelstam 1988, and Kurki et al. 1997). My study area had 1.45 km of roads/km² resulting in fragmentation. In the Powder River Basin there have been large-scale modifications of sagebrush habitat associated with oil and gas development that could have important impacts on habitat use or survival rates of sagebrush obligate species (Walker, unpublished data 26th Meeting of the Western Agencies Sage and Columbian Sharp-tailed Grouse Technical Symposium, abstract). Since I was not able to demonstrate that vegetation characteristics surrounding nests influenced nest survival at the scale at which I measured vegetation, predation and other factors that caused nest loss may be random events. Alternatively, the protective quality of habitat could be homogeneously poor (see habitat selection). Due to the limited distribution of dense sagebrush, sage-grouse could be constrained to remaining sagebrush habitats for nest-sites. There was support for models of nest survival that included precipitation (random) and vegetation (nonrandom).

Within fragmented ecosystems, it has been hypothesized that increased levels of moisture during incubation increased nest depredation in wild turkeys (*Meleagris gallopavo*; Roberts et al. 1995, Roberts and Porter 1998, Lehman 2005). My models indicated that precipitation was the best variable to explain nest success in 2005 and 2006. Predators with a keen sense of smell use olfactory cues to locate nests (Storaas 1988), which makes following scent easier during moist conditions supporting the hypothesis that hens are more vulnerable to predation during wet periods than under dryer conditions (Roberts and Porter 1998). Syrotuck (1972) hypothesized that water

activated bacteria on the skin of turkeys, and allowed predators to locate incubating hens efficiently, which could be a similar hypothesis for female sage-grouse.

Habitat Selection. - Female sage-grouse in North Dakota selected nests in areas with more vegetative cover and higher sagebrush density than occurred elsewhere in the study area. Within these areas the actual nest-site that was selected was rather small as evidenced by inclusion of 1-m VOR and no other VOR intervals. Both nest and random sites were centered over sagebrush, so it is not surprising nest-VOR was not important. Several studies have established the importance of sagebrush canopy cover (Patterson 1952, Wallestad and Pyrah 1974, Wakkinen 1990, Fischer 1994, Sveum et al. 1998) and herbaceous canopy cover (Wakkinen 1990, Connelly et al. 1991, Sveum et al. 1998) to sage-grouse nesting habitat.

Visual obstruction surrounding more than the bush itself can provide additional concealment from predators. I found average total vegetative cover around nests > 66%. These variables contribute to successfully camouflaging the nest-site (Autenrieth 1981). I found hens selected for more dense sagebrush habitat than what was available. However, sage-grouse habitat includes a wide range of sagebrush density. Sagebrush density at nest-sites in my study was about ½ that reported in Nevada (Klebenow 1969) and 1/3 that reported for Montana (Wallestand and Pyrah 1974), while in south-central Idaho sagebrush density (Connelly 1991) was only slightly greater than in my study. Sagebrush density varies with local conditions and sagebrush species (Davies et al. 2006). Despite low sagebrush density and cover in my study, the amount of grass cover around nests suggests that grass is an important contributor to cover of sage-grouse nests.

Across their range, female sage-grouse usually select sagebrush patches for nests with shrub canopy cover of 15-25%, and avoid sparse or excessively dense patches (Connelly et al. 2000). However, in southwestern North Dakota, hens may have to select different nest-site characteristics to maintain adequate cover because of restricted patches of remaining sagebrush habitats, all of which are similar in habitat quality. This is a topic of high priority for future studies in North Dakota.

Previous studies have noted that hens select nest-sites with the tallest available bush, with the greatest diameter to initiate a nest (Gray 1967, Klebenow 1969, Wallestand and Pyrah 1974, Autenreith 1981). In my study, hens did not select for taller bushes at nests. The lack of selection for tall sagebrush may reflect homogeneity among sagebrush plants in the area. Sage-grouse can inhabit areas of lower sagebrush height and density than reported in the literature if additional cover from grasses is available. Previous studies have also documented the importance of cover from grasses within shrub stands (Wakkinen 1990, Connelly et al. 1991) which is associated to higher nest success rates (Gregg et al. 1994), and can offer additional nest protection. Hens selected nest-sites with grass cover consisting of half the total cover around the nest-site. It is likely that graminoid cover provides alternative nest cover than sagebrush.

Distance.- Most grouse species display fidelity to their nesting areas. The distance between consecutive nests varies from 0.7 to 2.8 km (Fischer et al. 1993, Schroeder 1997). The fidelity of hens in my study was typical of other studies. In my study, successful hens nested farther from their previous nest than unsuccessful hens. However, Fisher et al. (1993) found that unsuccessful hens nested further between

consecutive years than successful hens. Although fidelity to breeding areas may be advantageous for grouse (Bergerud and Gratson 1988), fidelity to nest-sites could decrease nest success following habitat alterations that make the areas less secure. Habitat fragmentation and habitat alteration throughout southwestern North Dakota from associated agriculture and oil and gas development alter the landscape for sage-grouse every year. Increased fragmentation and low connectivity of sagebrush habitats may explain why some hens are moving exceptionally large distances between nesting attempts in North Dakota.

Previous studies have documented that hens select nest-sites independent of proximity to leks. Nonetheless, most nests occur within 2.5-3.2 km of leks (Wallestad and Pyrah 1974, Bradbury et al. 1989, Wakkinen et al. 1992). During my study, average distance from nests to lek of capture was 4.94 ± 4.06 km. Sixty-eight percent of nests in my study were within 3.2 km of the nearest lek. Autenrieth (1981) suggested that lek to nest distances were inversely correlated to habitat quality. However, the limited distribution and patchiness of sagebrush in North Dakota restrict nesting which is mostly confined to sagebrush to occur near leks which are associated with sagebrush.

Hen Survival. -Survival of female sage-grouse is normally presented on an annual basis. Because there are numerous ways of evaluating survival (i.e., leg-bands, radio transmitters, brood observations), estimates of survival are hard to obtain that are comparable between studies. Previous estimates of annual survival range from 57-78% (Connelly et al. 1991, Aldridge and Brigham 2001, Wik 2002, and Hausleitner 2003),

suggesting that mortality of hens during nesting and brood-rearing seasons was not a primary factor affecting the sage-grouse population in North Dakota.

MANAGEMENT IMPLICATIONS

Vegetative trends in sagebrush habitat found in North Dakota are similar to the rest of the sagebrush range. I recommend that managers develop strategies to preserve the integrity of shrubsteppe habitat in southwestern North Dakota. Herbaceous cover in sagebrush habitats is an important component of nesting habitat for female sage-grouse. Thus, I recommend management activities that maintain or restore dense, taller residual grass within nesting habitat. There is little direct evidence associating livestock grazing practices to sage-grouse population levels. However, my results suggest excessive annual grazing within suitable nesting habitat could have a negative impact on the following year's nesting success by reducing residual grass cover, thereby reducing the quality of habitat for nesting birds. Factors such as timing, density, and spatial distribution of grazing should be reevaluated to maximize the protective cover value of the sagebrush. Ensuring proper grazing management on federal and state lands and encouraging participation from local land owners to participate in similar grazing practices with considerations for sage-grouse will help maintain adequate herbaceous understory throughout the nesting season.

I suggest expanding the current 3.2 km rule of the 1988 Resource Management Plan guideline initiated by the BLM in relation to habitat quality around known leks to a 5 km buffer, and encourage strict enforcement of these guidelines. This increased distance under special management would include 86% of nests versus 68% with the

current 3.2 km buffer. There currently are no management regulations pertaining to sage-grouse on state owned land in North Dakota. Consequently, activities associated with oil and gas development can occur year round anywhere. I recommend that states implement the same regulation as the BLM and apply it to a 5 km buffer around leks.

The relatively random distribution of nests in relation to leks indicates that habitat management should focus on providing suitable sagebrush habitats wherever possible regardless of their distance to active leks. Efforts should focus on constructing a habitat suitability index to aid in assessing habitat quality of sage-grouse throughout North Dakota. Additionally, future research should identify movement corridors, and assess distribution and quality of sagebrush habitats throughout North Dakota.

Table 2. Nest initiation rate of radio-marked adult and yearling sage-grouse in southwestern North Dakota, USA, 2005-2006.

Year	Adults	<i>N</i>	Yearlings	<i>N</i>	Total
2005	100%	6	100%	9	100% (15 of 15)
2006	93%	14	71%	7	86% (18 of 21)
Total	95%	20	88%	16	92% (33 of 36)

Table 3. Summary of model selection results for nest survival between year and age of greater sage-grouse in southwestern North Dakota, USA, 2005-2006.

Model	AICc^a	Δ AICc^b	AICc Weight^c	K^d
(.)	112.572	0.00	0.5422	1
(Year)	114.565	1.99	0.20028	2
(Age)	114.590	2.02	0.19770	2
(Year * Age)	116.978	4.41	0.05989	4

^a Akaike's Information Criterion adjusted for small sample size (*AICc*)

^b Difference in *AICc* (Δ *AICc*)

^c Akaike weights (*w_i*)

^d Number of parameters (*K*).

Table 4. Summary of model selection results for nest survival between habitat variables of greater sage-grouse in southwestern North Dakota, USA, 2005-2006.

Model	AICc^a	Δ AICc^b	AICc Weight^c	<i>K</i>^d
(.)	112.572	0.00	0.1535	1
TOGR (-)	112.651	0.08	0.1467	2
Grass Hgt within shrubs (-)	113.181	0.61	0.1125	2
TOFO (+)	113.545	0.97	0.0938	2
TOSH (+)	113.618	1.05	0.0903	2
TOFO (+) + TOGR (-)	113.725	1.15	0.0857	3
Nest VOR (-)	113.782	1.21	0.0833	2
Shrub Density (+)	113.912	1.34	0.0780	2
Shrub Hgt (-)	114.706	2.13	0.0739	3
Grass Hgt within shrub (-) + Shrub Hgt (-)	114.706	2.13	0.0525	3
TOCO (+) + Nest VOR (-)	115.766	3.19	0.0308	3
Nest Age (+)	162.733	50.16	0.0000	1

^a Akaike's Information Criterion adjusted for small sample size (AICc)

^b Difference in AICc (Δ AICc)

^c Akaike weights (*w_i*)

^d Number of parameters (*K*).

Table 5. Summary of model selection results for nest survival between time-dependent variables of greater sage-grouse in southwestern North Dakota, USA, 2005-2006

Model	AICc^a	Δ AICc^b	AICc Weight^c	K^d	Log-likelihood
Daily Precip	107.467	0.00	0.3374	2	103.436
Daily Precip + TOGR	107.608	0.14	0.3145	3	101.545
Daily Precip + Grass height with Robel pole	109.051	1.58	0.1528	3	102.988
Year + Daily Precip	109.480	2.01	0.1233	3	103.417
(.)	112.572	5.10	0.0263	1	110.562
Max Temp	112.947	5.48	0.0218	2	108.915
Year + Max Temp	113.896	6.43	0.0136	3	107.833
Min Temp	114.392	6.92	0.0106	2	110.360

^a Akaike's Information Criterion adjusted for small sample size (AICc)

^b Difference in AICc (Δ AICc)

^c Akaike weights (w_i)

^d Number of parameters (K).

Table 6. Combined average distributions of vegetation characteristics for nest-sites and random sites of sage-grouse in southwestern North Dakota using MRPP, 2005-2006.

Variable	Nest \bar{x} (<i>n</i> = 34)	Random \bar{x} (<i>n</i> = 50)	p-value
Total cover (%)	70	54	< 0.001
Total grass (%)	27	19	0.0111
Total forb (%)	15	11	< 0.001
Total sagebrush (%)	10	7	0.003
Bareground (%)	21	33	0.0058
Litter (%)	13	8	< 0.001
Sagebrush density/hectare	2,576.1	1,399.4	< 0.001
Nest-VOR	9.3	7	0.0019

Table 7. Average vegetation characteristics of nest-site and random sites between years for sage-grouse in southwestern North Dakota using MRPP, during 2005-2006.

Variable	Nest 2005 (n = 17)	Nest 2006 (n = 17)	p-value	Random 2005 (n = 17)	Random 2006 (n = 33)	p-value
Total Forb (%)	23	8	< 0.001*	16	8	< 0.001*
Total Sage (%)	11	8	0.0242*	9	6	0.0238*
Bareground (%)	27	16	0.0269*			
Grass hgt. in shrub (cm)	35.1	29.9	0.0185*	41.5	32.2	0.0041*
Avg. width of shrubs (cm)	41.5	53	0.0061*	48.5	31.8	< 0.001*
Nest VOR (in)	9.7	8.9	0.6525	23.6	6.7	< 0.001*
VOR 1m	4.1	3.7	0.7094	9.9	2.4	< 0.001*
VOR 2m	3.4	2.5	0.3131	7.8	2.2	< 0.001*
VOR 3m	2.6	2.4	0.2705	6.6	2.1	< 0.001*
VOR 4m	2.2	2.6	0.6016	7.1	2.1	< 0.001*
VOR 5m	2.3	2.1	0.9263	7.3	2.2	< 0.001*
VOR 10m	2.2	2.2	0.8988	8.4	1.8	< 0.001*
VOR 20m	1.6	2.2	0.1289	6.8	1.4	< 0.001*
VOR 30m	2.2	2.2	0.7868	7.3	1.5	< 0.001*
VOR 40m	2.1	2.2	0.6366	6.6	1.5	< 0.001*
VOR 50m				5	1.1	< 0.001*

Asterisks (*) indicates significant difference between nests of 2005 and 2006, and significant differences between random sites compared between 2005 and 2006.

Table 8. Logistic regression models predicting greater sage-grouse nest-sites ($n = 34$) versus random sites ($n = 50$) using vegetal data collected in North Dakota, USA, 2005-2006. Log-likelihood ($-2 \ln [L]$), number of parameters including year indicator variable plus 2 (intercept + SE) (K), Akaike's Information Criterion adjusted for small sample size (AICc), difference in AICc (Δ AICc), and Akaike weights (w_i). Models with Δ AICc < 2 are highlighted.

Model	Log-likelihood	K	AICc	Δ AICc	Wi
TOCO + VOR 1-M + SHRUB DEN	-45.937434	6	91.8749	0	0.873
TOCO + GRASS HGT + SHRUB HGT + SHRUB DEN	-40.570508	7	96.78808	4.913	0.075
TOCO + GRASS HGT + SHRUB HGT + VOR 0-M + VOR 1-M	-45.857659	8	97.68791	5.813	0.048
TOCO + COVER + SHRUB DEN	-46.019476	6	103.8773	12.002	0.002
TOFO + TOGR + TOSH + SHRUB DEN + VOR 0-M + VOR 1-M	-46.353773	9	105.6413	13.766	0.001
TOCO + HEIGHT + VOR 0-M + VOR 1-M	-46.863904	7	106.4435	14.569	0.001
TOCO + SHRUB DEN + VOR 1-M + VOR 0-M	-48.530504	7	107.2043	15.330	<0.001
GRASS HGT + SHRUB HGT + VOR 0-M + VOR 1-M	-49.759395	7	107.3624	15.487	<0.001
TOFO + TOGR + TOSH	-51.746931	6	110.2784	18.403	<0.001
GRASS HGT + SHRUB HGT + SHRUB DEN	-45.778607	6	112.7362	20.861	<0.001

^a I included the following habitat variables in my models: total canopy coverage (TOCO), percent forb cover (TOFO), percent grass cover (TOGR), percent sagebrush cover (TOSH), sagebrush height (SHRUB HGT), site-VOR (COVER), 0m-VOR (VOR 0m), and 1-m-VOR (VOR 1m), sagebrush density/hectare (SHRUB DEN), and max grass height surrounding the Robel pole (HEIGHT).

^b To facilitate interpretation, I excluded year indicator variable from model column.

Table 9. Odds ratio and confidence intervals associated with independent variables that best explain nest-sites in southwestern North Dakota, USA, 2005-2006.

Variable	Odds Ratio	Odds Lower CI	Odds Upper CI
TOCO	0.060	0.006	0.502
Sagebrush density	0.086	0.008	0.732
1-m VOR	0.280	0.017	4.013

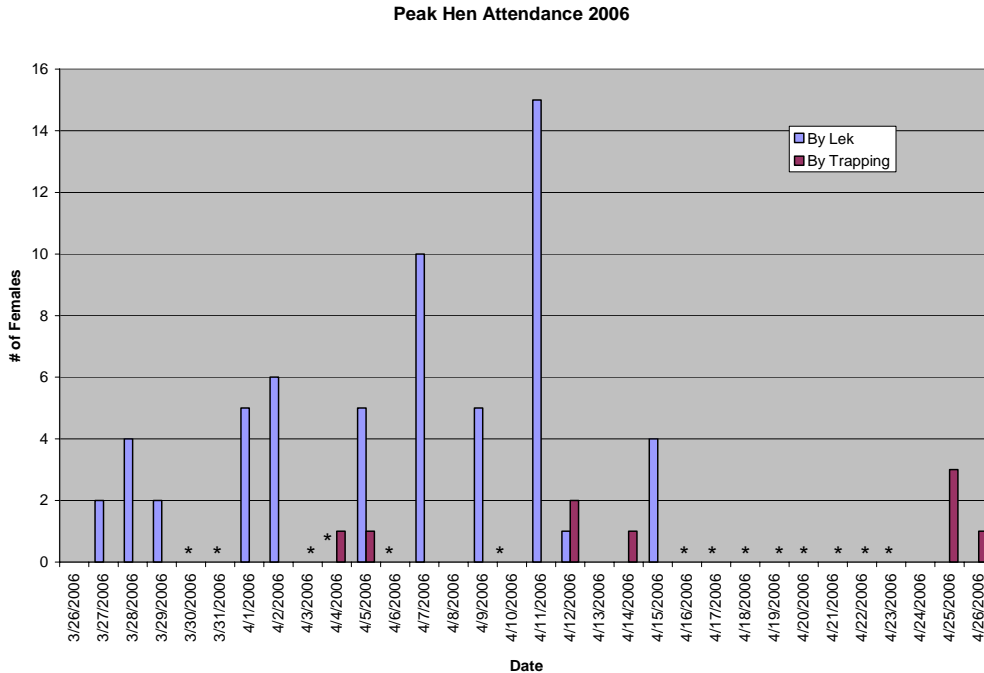
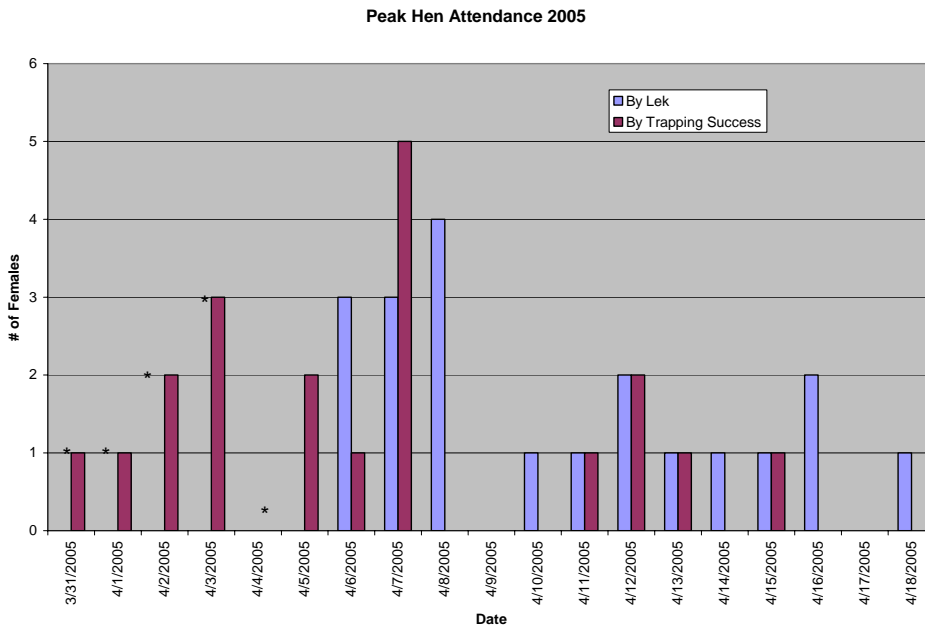


Figure 2. Number of female sage-grouse counted from morning lek counts or trapping success in 2005 and 2006 in relation to date. Asterisks (*) indicates dates lek counts were not conducted.

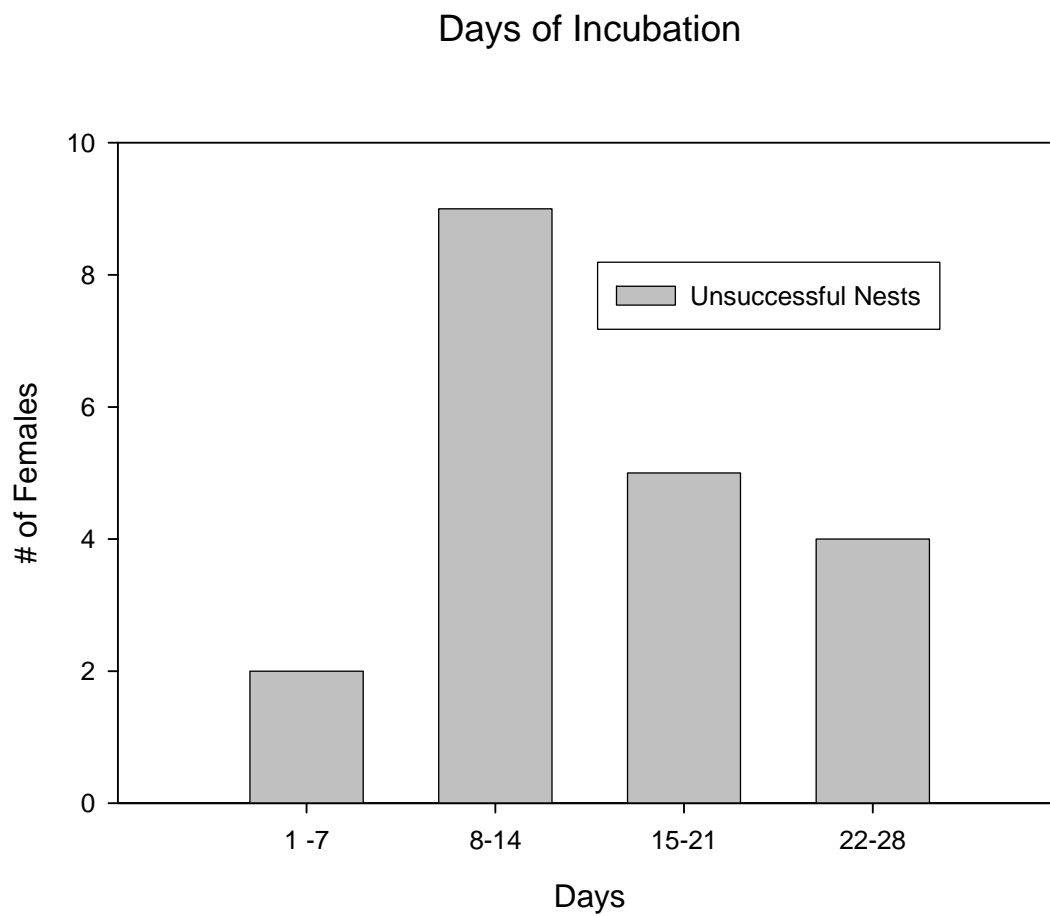


Figure 3. Nest loss period during 4-week incubation for first nesting attempts of greater sage-grouse in southwestern North Dakota, USA, 2005-2006.

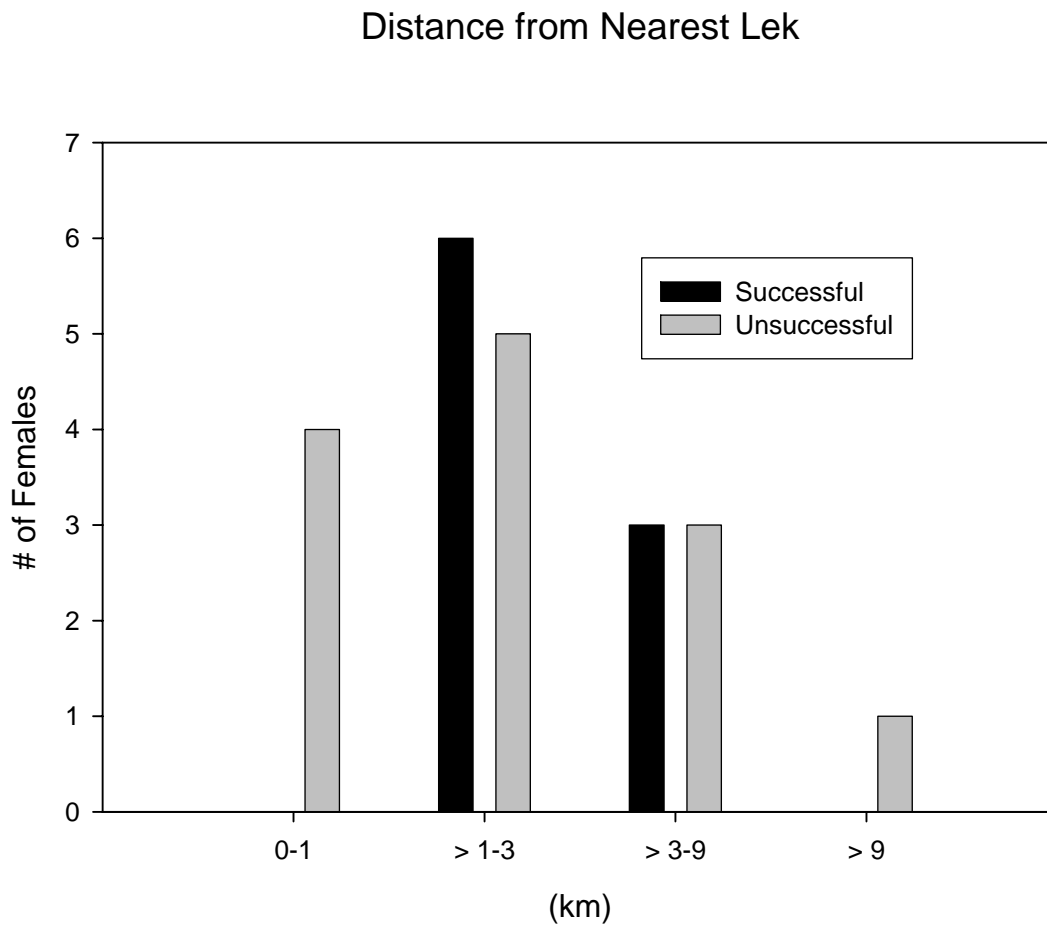


Figure 4. Distribution of distances between 22 pairs of nests to nearest lek distance for greater sage-grouse in southwestern North Dakota, USA, 2005-2006.

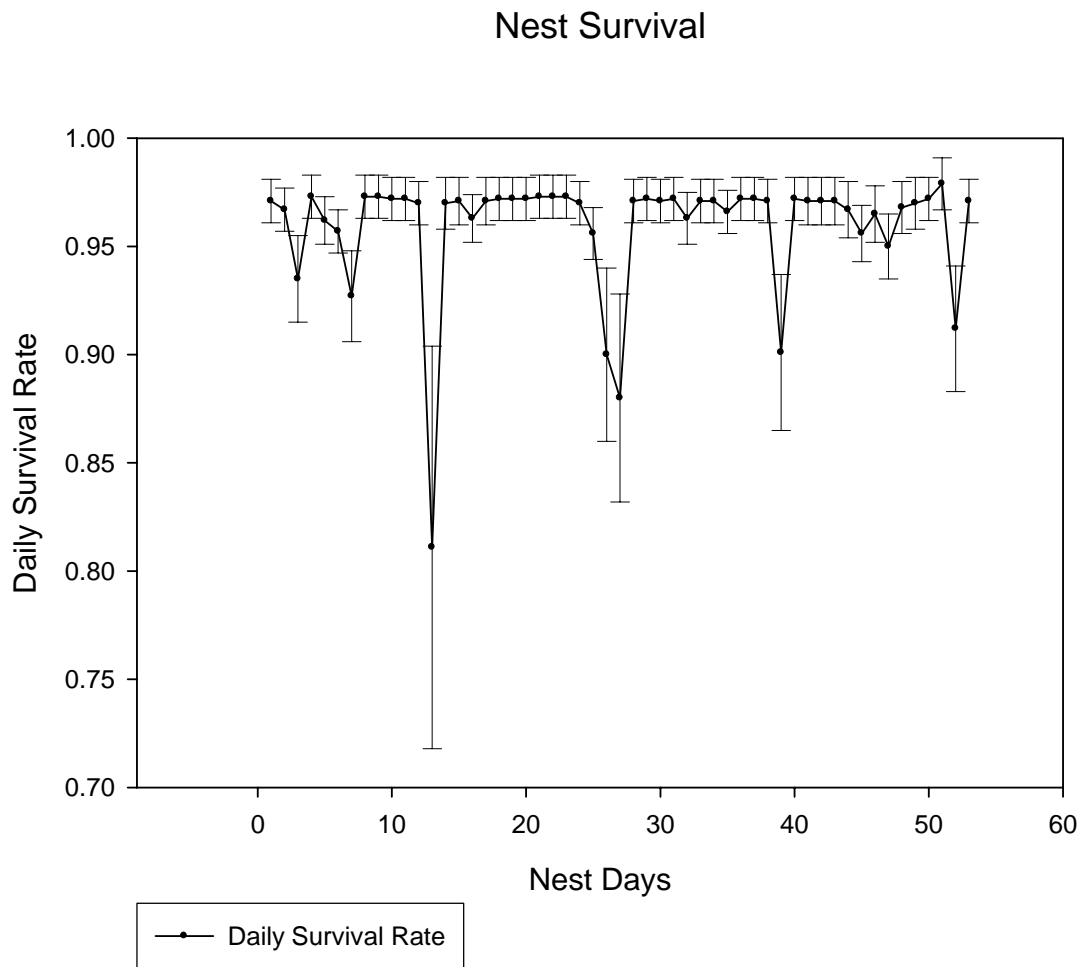


Figure 5. Daily survival rate from model averaging of models $< 2 \Delta AICc$ from the most parsimonious model over the 54 day nesting period used in Program MARK to model nest survival in southwestern North Dakota, 2005-2006. The spikes implicate a rain event, with DSR including average values from percent total grass and grass height from the Robel pole.

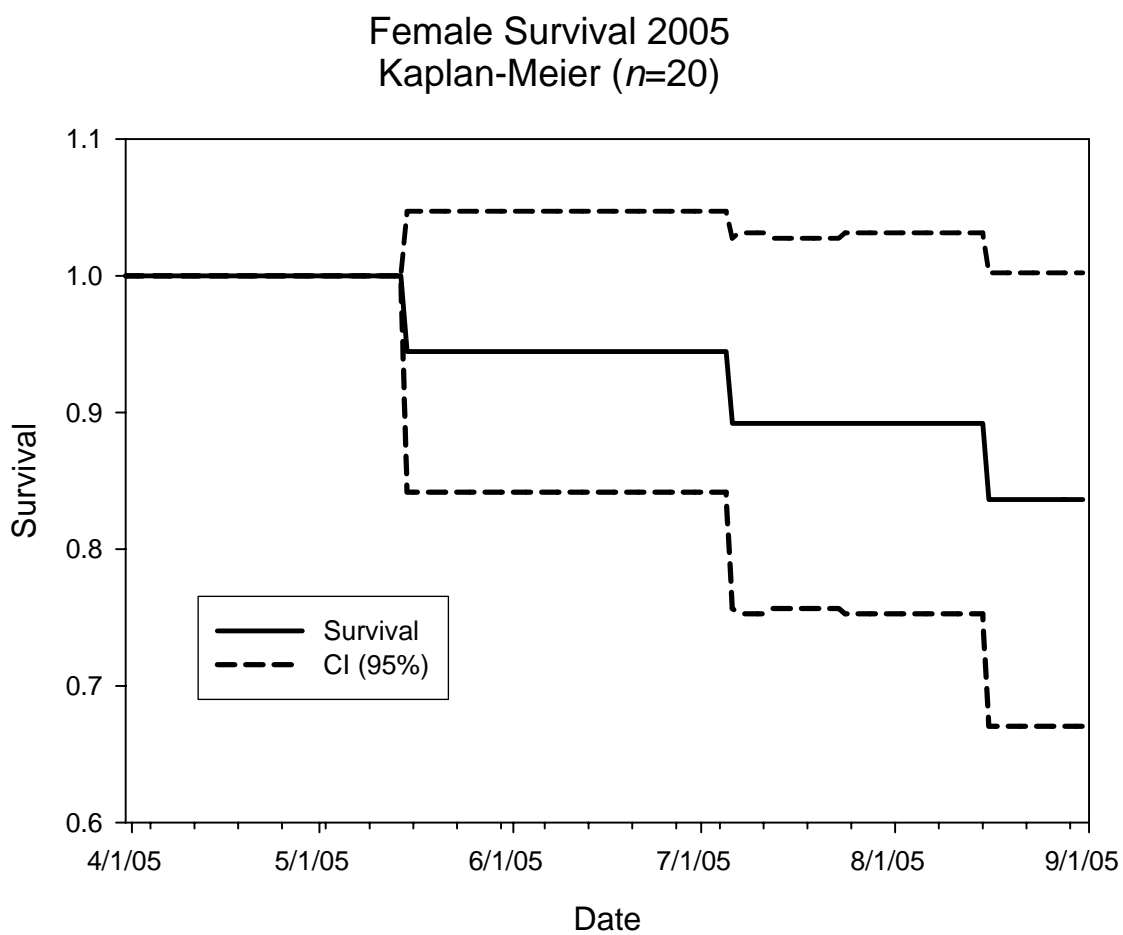


Figure 6. Greater sage-grouse hen survival rate and 95% confidence intervals (dashed lines) during the nesting and brood-rearing season during 2005 in southwestern North Dakota, USA (Kaplan and Meier 1958, Pollock et al. 1989).

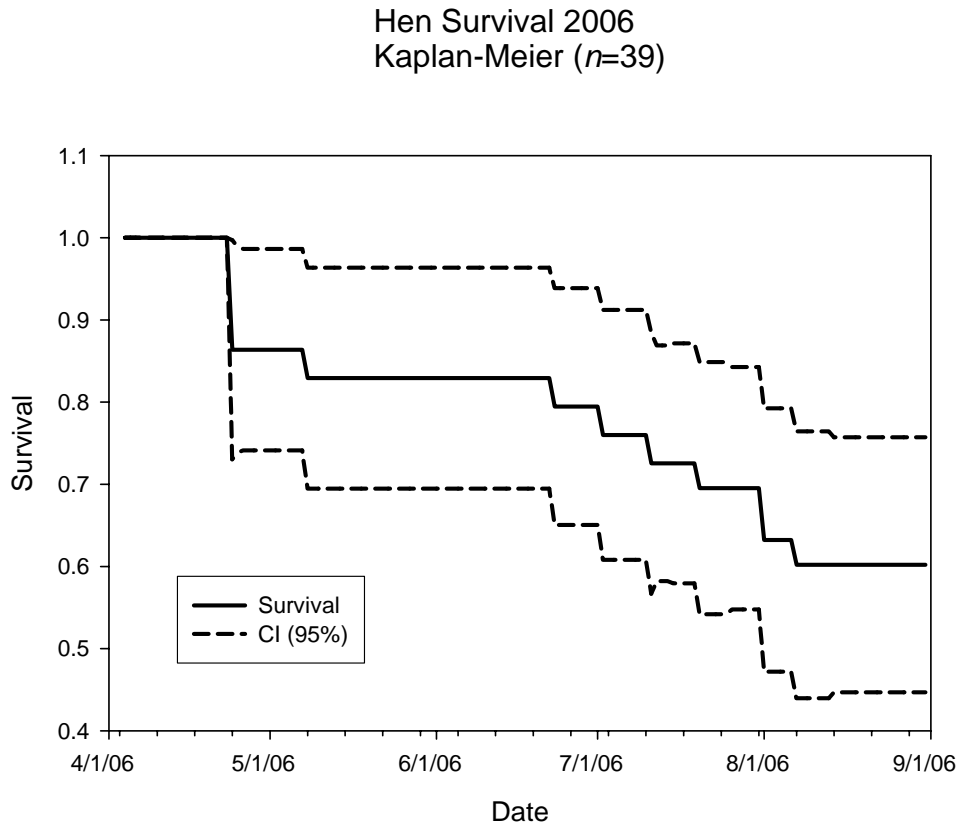


Figure 7. Greater sage-grouse hen survival rate and 95% confidence intervals (dashed lines) during the nesting and brood rearing season from 2006 in southwestern North Dakota, USA (Kaplan and Meier 1958, Pollock et al. 1989).

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Appendix A. Nest ages of greater sage-grouse nests in southwestern, North Dakota, USA, as determined by egg flotation.

Nest age (d)	Mean age (d)	Description
1-4	2	Egg lying flat on bottom
5	5	Large end of egg beginning to float
5-9	7	Egg standing upright on bottom
10-13	12	Egg about to float (middle of water)
14-18	16	Egg floating, top barely breaking water surface
19-23	21	Egg floating high with top out of water surface
24-28	26	Egg floating with noticeable tilt

Note: Ranges for each incubation stage was adapted from Hays and LeCroy 1971, and compared with my own 36 nesting attempts.

Appendix B. Four-digit code, common name and scientific name of plant species identified at nests and random sites in southwestern North Dakota, USA, 2005-2006.

Variable	Name	Scientific Name
acmi	western yarrow	<i>Achillea millefolium</i>
aggl	false dandelion	<i>Hypochoeris radicata</i>
agst	redtop	<i>Agrostis gigantea</i>
alfa	alfalfa	<i>Medicago spp.</i>
arca	silver sage	<i>Artemisia cana</i>
arfi	fringed sagewort	<i>Artemisia frigida</i>
arlu	cudweed sagewort	<i>Artemisia ludoviciana</i>
artr	big sagebrush	<i>Artemisia tridentata wyomingensis</i>
atri	<i>Atriplex spp.</i>	<i>Atriplex spp.</i>
bear	beards tongue	<i>Penstemon spp.</i>
bell	bluebells	<i>Mertensia spp.</i>
bogr	blue grama	<i>Bouteloua gracilis</i>
brin	smooth brome	<i>Bromus inermis</i>
brja	japanese brome	<i>Bromus japonicus</i>
bkbr	buckbrush	<i>Symphoricarpos occidentalis</i>
blue	little bluestem	<i>Vulpia octoflora</i>
buda	buffalo grass	<i>Buchloe dactyloides</i>
cafi	threadleaf sedge	<i>Carex filifolia</i>
calo	prairie sandreed	<i>Calamovilfa longifolia</i>
carr	wild carrot	<i>Daucus carota</i>
cele	wild celery	<i>Apium graveolens</i>
chea	cheatgrass	<i>Bromus tectorum</i>
cone	purple coneflower	<i>Echinacea Moench</i>
crew	crested wheatgrass	<i>Agropyron cristatum</i>
curd	curly doc	<i>Rumex crispus</i>
disp	inland saltgrass	<i>Distichlis spicata</i>
dwrp	dwarf alyssum	<i>Alyssum cuneifolium</i>
ercs	eastern red cedar	<i>Juniperus virginiana</i>
fieb	field bindweed	<i>Convolvulus arvensis</i>
gayf	gayfeather	<i>Liatris spicata</i>
gold	goldenrod	<i>Solidago spp.</i>
gotb	goatsbeard	<i>Tragopogon dubius</i>
gpea	golden pea	<i>Thermopsis rhombifolia</i>
grra	grayragwort	<i>Senecio incanus</i>
gumb	gumbo lily	<i>Oenothera caespitosa</i>
gumw	curlycup gumweed	<i>Grindelia squarrosa</i>
gusa	broom snakeweed	<i>Gutierrezia sarothrae</i>
hoju	foxtail barley	<i>Hordeum jubatum</i>

Appendix B. Continued

hors	horseweed	<i>Conyza</i> spp.
hory	hairy fleabane	<i>Conyza bonariensis</i>
indw	indian wheat	<i>Plantago patagonica</i>
intw	intermediate wheatgrass	<i>Thinopyrum intermedium</i>
koma	junegrass	<i>Koeleria macrantha</i>
long	longleaf wormweed	<i>Artemisa longifolia</i>
must	mustard	<i>Cardaria</i> spp.
navi	green needle	<i>Nassella viridula</i>
nutv	nuttall's violet	<i>Viola nuttallii</i>
pars	wild parsley	<i>Musineon</i> spp.
pasm	western wheatgrass	<i>Pascopyrum smithii</i>
penn	pennycress	<i>Thlaspi arvense</i>
pepp	pepperweed	<i>Lepidium densiflorum</i>
phho	hood's phlox	<i>Phlox hoodii</i>
plan	slender plantain	<i>Plantago heterophylla</i>
prpr	prickly pear	<i>Opuntia</i> spp.
popr	kentucky bluegrass	<i>Poa pratensis</i>
povw	povertyweed	<i>Iva axillaris</i> Pursh
psut	pussytoes	<i>Antennaria</i> spp.
redg	red goosefoot	<i>Chenopodium rubrum</i>
redt	redtop	<i>Agrostis stolonifera</i>
ripg	prairie cordgrass	<i>Spartina pectinata</i>
rose	wild rose	<i>Rosa woodsii</i>
rubb	rubber rabbitbrush	<i>Ericameria nauseosa</i>
sand	sandbergs bluegrass	<i>Poa secunda</i>
scgo	scarlet gaura	<i>Gaura coccinea</i>
scur	scurfpea	<i>Psoralea</i> spp.
side	sideoats grama	<i>Bouteloua curtipendula</i>
silv	silverbladder pod	<i>Lesquerella argyraea</i>
skel	skeletonplant	<i>Lygodesmia</i> spp.
spid	spiderwort	<i>Tradescantia ohiensis</i>
spco	scarlet globemallow	<i>Sphaeralcea coccinea</i>
stic	stickseed	<i>Hackelia</i> Opiz
stco	needle and thread	<i>Stipa comata</i>
sthy	angelita daisy	<i>Hymenoxys acaulis</i>
sunf	sunflower	<i>Eriophyllum</i> spp.
swee	sweetclover	<i>Melilotus</i> spp.
taof	dandelion	<i>Taraxacum officinale</i>
toad	bastard toadflax	<i>Commandra umbellate</i>
this	thistle	<i>Cirsium</i> spp.
txon	textile onion	<i>Allium</i> spp.
vetc	<i>Astragalus</i> spp.	<i>Astragalus</i> spp.

Appendix B. Continued

vuoc	six weeks-fescue	<i>Vulpia octoflora</i>
wewa	western wallflower	<i>Erysimum asperum</i>
wint	winter fat	<i>Krascheninnikovia</i> spp.
yuca	yucca	<i>Yucca glauca</i>

Appendix C. Definition of all acronyms used for vegetative sampling in southwestern North Dakota, USA, 2005-2006.

Acronym	Definition
TOCO	Percent total vegetative cover
TOFO	Percent total forb cover
TOSH	Percent total sagebrush cover
TOGR	Percent total grass cover
Litter	Percent total litter cover (ie. residual grasses, rocks, feces)
Bareground	Percent bareground
Effective Grass Hgt	Grass height beneath sagebrush from Robel pole (in)
Max Grass Hgt	Tallest reading of grass species surrounding Robel pole (in)
Sagebrush Hgt	Sagebrush height (cm)
Sagebrush Width	Sagebrush width (minor and major cord averaged) (cm)
Sagebrush density	Sagebrush density/hectare
Site-VOR	Visual obstruction reading for the site
1-m VOR	Average visual obstruction reading for 1-m around site
2-m VOR	Average visual obstruction reading for 2-m around site
3-m VOR	Average visual obstruction reading for 3-m around site
4-m VOR	Average visual obstruction reading for 4-m around site
5-m VOR	Average visual obstruction reading for 5-m around site
10-m VOR	Average visual obstruction reading for 10-m around site
20-m VOR	Average visual obstruction reading for 20-m around site
30-m VOR	Average visual obstruction reading for 30-m around site
40-m VOR	Average visual obstruction reading for 40-m around site
50-m VOR	Average visual obstruction reading for 50-m around site

CHAPTER 3- BROOD SURVIVAL AND HABITAT SELECTION OF GREATER SAGE-GROUSE AT THE EASTERN EDGE OF THEIR HISTORIC DISTRIBUTION

INTRODUCTION

Following the arrival of European settlers in the 1800s, greater sage-grouse (*Centrocercus urophasianus*) habitat has continuously been changing (Girard 1937, Patterson 1952). Greater sage-grouse experienced population declines from 45- 80% across their range by the 1950s (Braun 1998) and during the 10-year period from 1985-1995 sage-grouse populations declined 33% (Connelly and Braun 1997). Historically, sage-grouse range is limited to sagebrush (*Artemisia* spp.) vegetation types in at least 12 states and 3 Canadian provinces, but currently they are resident in only 11 states and 2 Canadian provinces (Schroeder et al. 2004). Sage-grouse are sagebrush obligates and degradation and loss of sagebrush resulted in population declines and constriction of the range (Wisdom et al. 2005, Welch 2005).

Discovery of oil and gas throughout the United States in the 1930s and 1940s impacted wildlife habitats in numerous ways. In Colorado, the initial impacts of oil and gas development caused sage-grouse populations to decline drastically from noise, habitat loss, infrastructure and human activities (Braun 1987). The long-term effects are unknown, but there is no evidence that populations of sage-grouse will recover to pre-disturbance populations, and the length of recovery time for these habitats is estimated to range from 2-30 years (Braun 1998). Grazing by domestic livestock, fire, construction, power lines, fences, roads, and drought also contributed to loss of sagebrush to sagebrush

ecosystems (Braun 1998, Schroeder et al. 1999, Welch 2005). Habitat fragmentation is of great concern in southwestern North Dakota with an estimate of 1.45 km of roads/km² in approximately 900 km² area of sage-grouse habitat. These changes have affected brood-rearing habitats through habitat alteration and habitat loss (Connelly and Braun 1997, Beck et al. 2003, Crawford et al. 2004).

The sage-grouse population in North Dakota is contiguous with populations in Montana and South Dakota (McCarthy and Kobriger 2005). Annual rates of change suggest a long-term population decline of about 2.79% per year from 1965 to 2003 (McCarthy and Kobriger 2005). Current breeding populations are estimated to be 3 to 6 times lower than occurred in the late 1960s to early 1970s (Connelly et al. 2004). Sage-grouse are a Priority Level 1 Species of Special Concern in North Dakota, and it is recommended that immediate research and conservation actions be taken. Thus, population declines may be related to declining habitat quality which may result in decreased survival and productivity, however, the significance of these factors is unknown. The fragmentation of sagebrush habitats could render North Dakota unsuitable as brood-rearing habitat and could contribute to population declines by reducing nest success and overall population productivity.

Estimates of sage-grouse chick (0-10 weeks of age) or juvenile survival (10-40 weeks of age) is limited and is not based on standardized time periods, thereby making comparisons and drawing conclusions difficult (Beck et al. 2006). In Oregon, only 10% of sage-grouse chicks survived until their first season as of March 1st (Crawford et al.

2004). Typically, only 50-60% of sage-grouse chicks survive through autumn (Bergerud 1988).

Sage-grouse use a variety of habitats throughout the year including grasslands and mosaics of sagebrush or aspen (*Populus* spp.); Paige and Ritter 1999). Sage-grouse productivity depends on brood-rearing habitat quality and availability (Crawford et al. 1992). Food availability and structure of the stand are common characteristics associated with habitat selection of hens with broods (Klebenow 1969, Peterson 1970, Wallestad 1971, Autenrieth 1981). Limited food resources slow growth and survival of sage-grouse chicks (Johnson and Boye 1990). Dunn and Braun (1986) discovered that vegetative cover and the extent of habitat interspersions are important factors that influence summer habitat use of sage-grouse hens and broods.

Key features of sage-grouse brood-rearing habitat are influenced by shrub density, plant composition and vegetation height (Klott and Lindzey 1990). Early brood-rearing areas are relatively close to nest-sites (Connelly 1982, Gates 1983) for the first 2-3 weeks post hatch (Connelly et al. 1988). Hens with broods prefer areas of abundant herbaceous growth surrounding nest-sites (Wallestad 1971, Klebenow 1985). Areas used by hens with broods usually have shrub cover between 8-14% and shrubs tend to have shorter than average stature (Klebenow 1969, Martin 1970, Wallestad 1971).

Although brood-rearing habitat selection for early and late summer use of sage-grouse chicks and juveniles has been well documented throughout western North America, knowledge of habitat selection by juvenile sage-grouse at the eastern edge of their range distribution where sagebrush communities are different than in the core of

sagebrush distribution has not been quantified. Thus, the objectives of my study were to determine brood-rearing habitat selection of sage-grouse, and estimate brood survival for a population of sage-grouse in southwestern North Dakota. I tested the null hypotheses that there were no differences between vegetation composition and structure found at brood and random points. Knowledge of brood habitat use and selection will provide baseline information to develop management recommendations for use by state and federal wildlife and habitat management agencies to improve habitats for sage-grouse.

METHODS

Data Collection

Capture and Marking of Chicks. - I captured birds at night on or near leks from 31 March – 23 April 2005 and 27 March – 27 April 2006. I used hand-held spotlights to locate birds and approached them while shining the spotlight to confuse them and then used long-handled nets to capture hens (Giesen et al. 1982). I recorded age, sex, weight, and placed leg-bands and 20-gram necklace type radio transmitters with mortality sensors on each bird (Advanced Telemetry Systems, Isanti, Minnesota). Each bird was released at the point of capture. The transmitters were less than 2% of the bird's body weight. Each year, I monitored nest completion to estimate initial brood size from egg shells of successful nests.

Monitoring Radio-collared chicks. -Radio-marked hens with broods were located ≥ 2 times/week with a hand-held or vehicle-mounted yagi antenna and portable receiver. To obtain accurate locations and to monitor number of chicks, I obtained visual observations without flushing either the hen or brood. Once per week the hen and chicks

were flushed to obtain an accurate estimate of chick numbers. Each brood location coordinate was recorded in a hand-held GPS unit in Universal Transverse Mercator (UTM).

At 5-6 weeks of age, I captured chicks from each brood by night-spotlighting and a long-handled net. Locating broods was aided by radio-marked hens. Each captured chick was weighed, leg-banded (size 14), and radio-marked with a 10.7-gram necklace type transmitter (Advanced Telemetry Systems, Isanti, Minnesota). Each transmitter was no more than 3% of the bird's body weight, and was fitted with mortality switches.

Chicks were located 2-3 times each week from capture date through August in 2005 and 2006 to determine chick and brood survival and cause-specific mortality. I estimated chick survival from initial number of chicks that hatched from successful nests to the number of chicks that survived 3 weeks post hatch. The initial number of chicks that hatched was estimated by examining condition of egg membranes. Chicks were counted twice each week by searching the area, flushing the radio-marked hen and counting her chicks each week. Chicks > 3 weeks of age were difficult to count accurately, so there is a data gap of survival from 3 weeks of age until chicks could be radio-marked at 5-6 weeks of age to estimate juvenile survival.

Habitat measurements. - I recorded vegetation measurements at brood sites and independent random sites within 10 km of leks from May to August of 2005 and 2006. Coordinates of random sites were entered into a GPS to locate the point in the field, created in ArcGIS 9.1 (ESRI, Inc., ArcGIS 9.1, Redlands, CA). The accuracy of GPS units was usually less than ± 10 m. I recorded slope and aspect for each site using a

clinometer and compass, respectively as the downhill direction from each site. At each brood and random site I established two 50-m transects which were centered over the brood site or nearest to the random point. I recorded species, height, length, and width (cm) of sagebrush at each brood site and random site. At each 10-m interval ($n = 20$) along each transect I recorded the distance to the nearest sagebrush using the point-centered-quarter method (Cottam and Curtis 1956). For every sagebrush encountered, I also recorded the height, length, and width of each sagebrush, and measured grass height with the Robel pole. I estimated visual obstruction and height of grass using a modified Robel pole delineated in 2.54 cm increments (Robel et al. 1970, Higgins and Barker 1982, Benkobi et al. 2000). Herbaceous canopy cover was estimated at the brood or random site, and at additional 10-m intervals along 50-m transects in 0.10 m² quadrats (see Appendix D for species identification at brood sites and random sites; Daubenmire 1959). I recorded total cover, total shrub, total grass, total forb, litter, bareground and common species of grass and shrubs in each quadrat. I obtained measures of maximum and minimum daily temperature, and daily precipitation from a weather station in Bowman County (North Dakota Agricultural Weather Network, 2006).

Data Analysis

Habitat Selection. - Canopy cover values were recoded to mid-point values of the categories and I summarized these data to an average value for each variable for the site. Estimates of sagebrush density were made from maximum likelihood estimates (Pollard 1971). I then used MRPP (Mielke and Berry 2001) to test the distributions of vegetation characteristics at brood sites and random sites, and used this as a screening process to

distinguish important variables for future analysis with a critical value of $\alpha \leq 0.05$.

Vegetation characteristics included in MRPP evaluation were percent total vegetative cover, percent grass cover, percent forb cover, percent sagebrush cover, percent bareground, percent litter, sagebrush height, average sagebrush width, site-VOR and VOR increments of 10-m extending from the brood site to 50-m, grass height from the Robel pole beneath the sagebrush, and sagebrush density (Appendix E). I compared variables between brood sites and random sites, and between years using MRPP as initial screening between significant variables at the critical value of $\alpha \leq 0.05$.

I used Information Theoretic approach (Burnham and Anderson 2002) with logistic regression to estimate variables selected for by hens with chicks at brood sites using SAS JMP (2005 SAS Institute Inc). I developed 10 a-priori models for resource selection of brood sites. Only variables for which distributions differed between brood and random sites from MRPP were considered for inclusion in these models. The candidate models included percent total vegetative cover, percent grass cover, percent sagebrush cover, shrub height, site-VOR, every 10-m intervals of VOR extending from the center point, grass height from the Robel pole, and sagebrush density. Year was considered a dummy variable in all candidate models. Thus, any differences among the models in the candidate sets were due to differences in the vegetative variables. Year was not included in the tables for ease of interpretation.

To prevent underfitting or overfitting, Akaike's Information Criterion (AIC) was used as the basis for model selection. Using the log-likelihood values and number of parameters (k) provided in the output file from the 10 models within Program JMP. The

models were ranked using the equation: $AIC = -2(\log\text{-likelihood}) + 2k$. The two components of AIC include; $-2(\log\text{-likelihood})$, which measures discrepancy of the fit between the data and the model, and (k) is a penalty for the number of parameters included in the model to prevent overfitting the models. Unless the sample size is large with respect to the number of parameters estimated, the use of $AICc$ is recommended; $AIC + 2K(K + 1)/n - K - 1$. The models were ranked using $\Delta AICc$ (Burnham and Anderson 1992).

I tested the strength of the model to predict brood sites using receiver operating characteristic curve (ROC) used as model fit or discrimination diagnostics (SAS JMP 2005). ROC values between 0.7 and 0.8 were considered acceptable discrimination, and values between 0.8 and 0.9 were considered excellent discrimination (Hosmer and Lemeshow 2000).

Chick Survival. -Chicks were radio-marked and located ≥ 2 times/week from capture date through August in 2005 and 2006 to determine chick and brood survival and cause-specific mortality. Chick survival was estimated using Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) throughout the brood-rearing periods. I designated seasons as summer (June-August), autumn (September-November), winter (December-February), and spring (March-May; Leonard et al. 2000).

Differences in distribution of chick survival and average brood size were tested with MRPP between years at the critical value of $\alpha \leq 0.05$. A brood was considered successful if ≥ 1 chicks were observed with a radio-marked hen after 1 August, the

approximate date of brood breakup (Dalke et al. 1960, Oakleaf 1971). I defined recruitment as a chick surviving through December 31; the approximate date when the highest percent of mortality has decreased when there is low winter mortality (Robertson 1991, Wik 2002, Hausleitner 2003, Zablan 2003).

RESULTS

Chick Survival. - I monitored 7 broods in 2005, with an average of 6.86 ± 0.95 chicks/hen at hatch. In 2005, at 3 weeks post hatch, the average brood size from 7 hens was 2.34 chicks/hen representing 34% apparent survival. In 2006, 6 broods averaged 6.67 ± 1.03 chicks/hen at hatch. At 3 weeks post hatch, the average brood size from 6 hens was 2.83 chicks/hen representing 42% apparent survival. Initial brood size at hatch was similar between years ($P = 0.90$, MRPP).

In 2005, 6 hens had at least 1 chick alive on 1 August, and in 2006 only 3 hens had at least 1 chick alive on 1 August. In 2005, 50% (95% CI: 0.23 to 0.58) of chicks radio-marked at 5-6 weeks of age survived to 1 January (Figure 8). In 2006, 32% (95% CI: 0.14 to 0.49) of chicks survived to 1 January (Figure 9). Assuming no mortality from 3 weeks to 5-6 weeks, a very liberal estimate was 17% of chicks recruited into the population in 2005 and 13% recruited in 2006 (Table 10). The majority of identifiable predation events on radio-marked sage-grouse chicks were from canids. Survival of radio-marked chicks between years was similar ($P = 0.32$, MRPP). Combined yearly survival of radio-marked chicks from 5-6 weeks to 1 January was 39% for both field seasons (Figure 10). Brood success in 2005 was the same as in 2006 (75% in 2005 and 75% in 2006).

Brood Site Selection .- I measured vegetative characteristics at 55 and 75 brood sites in 2005 and 2006, respectively. I also measured 107 random sites during the two years (47 in 2005, 60 in 2006). Distributions of percent total vegetative cover, percent forb, percent grass, percent sagebrush, percent litter, site-VOR, and sagebrush density, differed ($P \leq 0.05$) from random sites. Random sites, however, had more bareground and taller grass ($P \leq 0.05$) than brood sites (Table 11). There were also several variables that differed between years for both brood and random sites (Table 12).

Because annual differences between years were evident, one model strongly was supported with selection of brood sites and percent forbs, percent grass, percent sagebrush, percent bareground, sagebrush height and width (Table 13). Sage-grouse brood sites were positively associated with more canopy cover from forbs, grasses, and sagebrush than were present at random sites, and negatively associated to percent bareground, sagebrush height and width. In the model, increasing forb cover by 10%, increased the probability of the site being used by a hen with a brood by a multiplicative factor of 0.09 ± 0.08 (CI 95%). Increasing grass cover by 10% increased the probability of the site being used by a hen with a brood by a multiplicative factor of 0.61 ± 0.56 (CI 95%), and increasing sagebrush cover by 10% increased the probability of the site being used by a hen with a brood by a multiplicative factor of 1.12 ± 0.95 (CI 95%). Increasing the percent of bareground by 10% decreased the probability of the site being used by a hen with a brood by a multiplicative factor of 240.89 ± 32.89 (CI 95%). Increasing sagebrush height by 5 cm decreased the probability of the site being used by a hen with a brood by a multiplicative factor of 22.18 ± 21.42 (CI 95%), and increasing sagebrush

width by 5 cm decreased the probability of the site being used by a hen with a brood by a multiplicative factor of 15.5 ± 14.68 (Table 14). Classification accuracy of the model was acceptable with an ROC value = 0.78.

Brood sites consisted of 6-16% forb cover, 29-34 % grass cover, and 5% sagebrush cover, and sagebrush 30-38 cm tall, and 50-53 cm wide. Percent bareground cover at brood sites ranged from 11-25% (Table 15).

DISCUSSION:

Chick/Brood Survival. - The low chick survival in southwestern North Dakota is typical of other sage-grouse populations (Schroeder et al. 1997). The period of greatest chick mortality occurred from hatch to 3 weeks of age. Canid predation was the largest direct cause of mortality of radio-marked sage-grouse chicks. Exposure to wet and cold weather can also reduce survival of chicks (Patterson 1952). I found high mortality to chicks exposed to rain and cold weather immediately after hatch. Greater precipitation in 2005 resulting in increased herbaceous cover and delayed plant desiccation may have resulted in higher survival of chicks \geq 5-6 weeks to 1 January in 2005 (Oakleaf 1971).

It is difficult to draw conclusions regarding survival rates of juvenile sage-grouse among various studies because methods of data collection and analyses varied among studies. Nonetheless, Crawford et al. (2004) estimated 10% survival for sage-grouse chicks from hatch to the following breeding season. My estimate of chick survival through 1 January of 13-17% is half that required to sustain a population, assuming reasonable levels (40-60%) of nest success and nesting rates (Aldridge and Brigham 2001). However, the 13-17% is a liberal estimate because I do not know what

the mortality was from 3 to 5-6 weeks of age. Poor recruitment could be the limiting factor of population growth (Johnson and Braun 1999). Chick survival could be limited by availability of mesic habitats that contain higher amounts of forbs during 3-4 weeks post hatch (Aldridge 2000). Studies conducted in the Powder River Basin have documented large-scale modification of sagebrush habitat associated with oil and gas development that could have impacts on habitat use or survival rates of sagebrush obligate species (Walker, unpublished data 26th Meeting of the Western Agencies Sage and Columbian Sharp-tailed Grouse Technical Symposium, abstract). Fragmentation of brood rearing habitats results in additional challenges to brood survival and may create travel barriers separating suitable cover from important mesic feeding areas.

Habitat Selection. - A key factor associated with sage-grouse productivity is brood-rearing habitat (Crawford et al. 1992). Availability of food resources such as forbs and insects can limit sage-grouse populations through decreased recruitment of young (Klebenow 1969, Peterson 1970, Wallestad 1975, Autenrieth 1981). The period from 1-10 days is when chick mortality is highest (Patterson 1952, Autenrieth 1981) and they need insects in close proximity to escape cover. Based on the low chick survival in this study, the present availability of high-quality brood-rearing habitat may be an important factor contributing to low survival rates and ultimately to declining populations of sage-grouse in North Dakota.

Hens with broods selected sites with greater herbaceous cover (forbs and grass), greater sagebrush cover, shorter sagebrush, and less bareground. In the Great Basin, hens with chicks also selected for areas of increased forb cover (Klebenow 1969, Autenrieth 1981, Dunn and Braun 1986). Martin (1970) reported heights of sagebrush ranging from 22-38 cm at brood locations in southwestern Montana, which is similar to sage-grouse brood habitat in my study. The primary food for chicks < 10 days old is insects. Chicks require insects for growth and development (Johnson and Boyce 1990) and insect abundance is greater in areas with greater herbaceous biomass (Healy 1985, Rumble and Anderson 1996). Diet and feeding rates of birds have been shown to increase with abundance of food items (Healy 1985, Miller et al. 1994) which may explain why I found that broods selected areas with greater grass and forb abundance.

Sveum et al. (1998) reported that lack of alternate brood-rearing cover types resulted in low chick survival. Unlike many other sage-grouse populations in the core area of sagebrush habitat, hens in my study had little opportunity to choose alternate brood-rearing habitats. Increased food and cover may reduce brood movements, thereby reducing exposure to potential predators. Reduced movement also would result in lower energetic costs associated with obtaining food and higher foraging efficiency, thereby increasing the nutrients available for growth and development resulting in faster rates (Sveum et al. 1998). It is likely that the limited brood-rearing habitat distribution, the lack of alternative habitats, and the disturbance and fragmentation from oil and gas development has a detrimental affect on chick survival and juvenile recruitment.

MANAGEMENT IMPLICATIONS

Low productivity and chick survival rates should be of great concern to managers charged with maintaining viable populations of great sage-grouse (Connelly and Braun 1997, Crawford et al. 2004). Additional research to achieve a better understanding of juvenile survival and understand factors affecting productivity and recruitment is needed. Additional research to verify the effects of oil and gas development in a highly fragmented landscape is warranted.

My results suggest that conservation and/or restoration of native forb and grass communities within sagebrush shrubsteppe dominated habitats would benefit sage-grouse. Vegetative cover and habitat interspersions are also important factors which influence summer habitat use for grouse. Mosaics of patchy sagebrush with openings of native grasses and forbs will sustain brood-rearing habitat.

Trends in sagebrush vegetation in North Dakota are similar to the rest of the sagebrush range. I recommend that managers develop strategies to preserve the integrity of shrubsteppe in southwestern North Dakota. Herbaceous cover in sagebrush habitats is an important component of brood-rearing habitat for sage-grouse. There is little direct evidence associating livestock grazing practices to sage-grouse populations. However, my results suggest excessive grazing within suitable brood-rearing habitats could have a negative impact by reducing grass and forb cover. Improper grazing facilitates invasion by exotic plant species. Additionally, private landowners should be encouraged to participate in programs that are directed at maintaining and improving sage-grouse habitats on private lands.

Oil and gas development in various grouse habitat types has been increasing in southwestern North Dakota. Even though the timing of the increase in oil and gas development has been coincident with the declining trend of sage-grouse populations in southwestern North Dakota, very little is documented about effects this development has on grouse populations. Massive landscape changes within habitats utilized by broods have rarely been documented. Additional research to determine the effects of oil and gas development in relation to survival of great sage-grouse chick habitat selection is needed.

Table 10. Chick recruitment as of 1 January estimated for chick survival from hatch to 3 weeks-post hatch combined with chick survival at 5-6 weeks through recruitment in southwestern North Dakota, USA, 2005-2006.

Year	3 Week Survival (Apparent)	5-6 Week Survival (Kaplan-Meier)	Recruitment
2005	34%	50%	17%
2006	42%	32%	13%

Table 11. Combined average distributions of vegetation characteristics for brood sites and random sites of sage-grouse in southwestern North Dakota using MRPP, 2005-2006.

Variable	Brood (n = 130)	Random (n = 107)	p-value
Vegetative cover (%)	74	55	< 0.001*
Grass cover (%)	32	21	< 0.001*
Forb cover (%)	11	9	< 0.001*
Sagebrush cover (%)	5	4	0.041*
Bareground cover (%)	17	32	< 0.001*
Site-VOR (in)	3	2	0.107 *
Sagebrush density/hectare	2,300	1,546	< 0.001*
Sage (%)	5	3	< 0.001*
Vegetation height/site (in)	12	14	0.065*
Grass height beneath the sagebrush (cm)	41	42	0.431
Sagebrush height (cm)	33	33	0.646
Sagebrush width (cm)	48	48	0.298

Asterisks (*) indicates significance. Definition of each variable in Appendix E.

Table 12. Combined average distributions of habitat characteristics for brood sites compared between years and random sites compared between years of sage-grouse in southwestern North Dakota using MRPP, 2005-2006.

Variable	Brood 2005 (n = 55)	Brood 2006 (n = 75)	p-value	Random 2005 (n = 47)	Random 2006 (n = 60)	p- value
Vegetative cover (%)	67	79	< 0.001*	57	54	0.429
Forb cover (%)	16	6	< 0.001*	13	6	< 0.001*
Grass cover (%)	29	33	0.145	23	19	0.249
Sagebrush cover (%)	5	5	0.334	5	3	0.016*
Bareground cover (%)	25	10	< 0.001*	34	29	0.113
Site-VOR (cm)	6	1	< 0.001*	3	1	< 0.001*
Sagebrush density/hectare	1,619	2,991	0.001*	1,011	1,966	< 0.103*
Sagebrush (%)	5	5	0.4075	4	3	0.220
Grass hgt beneath the sagebrush (cm)	48	36	< 0.001*	49	37	< 0.001*
Sagebrush hgt (cm)	38	30	< 0.001*	38	29	< 0.001*
Sagebrush width (cm)	51	45	0.011*	53	44	< 0.002*

Asterisks (*) indicates significance. Definition of each variable (Appendix E).

Table 13. Logistic regression models predicting greater sage-grouse brood sites ($n = 130$) versus random sites ($n = 107$) using vegetal data collected in North Dakota, USA, 2005-2006. Log-likelihood ($-2 \ln [L]$), number of parameters including year indicator variable plus 2 (*intercept + SE*) (K), Akaike's Information Criterion adjusted for small sample size ($AICc$), difference in $AICc$ ($\Delta AICc$), Akaike weights (w_i). Models with $\Delta AICc < 2$ are highlighted as the best model.

Model	Log-likelihood	K	AICc	Δ AICc	Wi
Togr (+) + Tofo (+) + Tosh (+) + Bare (-) Shrub hgt (-) + Shrub w (-)	-135.97149	9	258.9682	0	0.890
Toco (+) + cover (+) + Shrub hgt (-) + Shrub w (-)	-123.91192	7	263.215	4.247	0.106
Toco (+)	-123.78395	8	271.0118	12.044	0.002
Tofo (+) + Togr (+) + Tosh (+) + Bare (-) + Cover (+)	-140.64085	8	271.943	12.975	0.001
Tofo (+) + Togr (+) + Tosh (+)	-145.71992	6	288.5111	29.543	<0.001
Tofo (+) + Togr (+) + Tosh (+) + Bare (-)	-137.64685	7	288.5452	29.577	<0.001
Toco (+) + Cover (+) + Shrub den (+)	-136.44906	6	289.1771	30.209	<0.001
Tofo (+) + Togr (+) + Cover (+) + Shrub den(+)	-137.97987	7	296.9288	37.961	<0.001
Tofo (+) + Togr (+) + Cover (+)	-146.78395	6	304.6572	45.689	<0.001
Tofo (+) + Togr (+) + Tosh (+) + Bare (-) + Height (-) + Shrub w (-)	-134.0313	9	314.2952	55.327	<0.001

a I included the following vegetation variables in my models: total vegetative cover (TOCO), percent forb cover (TOFO), percent grass cover (TOGR), percent sagebrush cover (TOSH), sagebrush height (SHRUB HGT), sagebrush width (SHRUB W), site-VOR (COVER), percent bareground cover (BARE), sagebrush density/hectare (SHRUB DEN), and grass height around the Robel pole (HEIGHT).

b To facilitate interpretation, I excluded year indicator variable from model column.

Table 14. Odds ratio and confidence intervals associated with independent variables that best explain brood sites or random sites in southwestern North Dakota, USA, 2005-2006.

Variable	Odds Ratio	Site	Odds Lower CI	Odds Upper CI
TOFO	0.009	Brood	0.001	0.100
TOGR	0.061	Brood	0.005	0.728
TOSH	0.112	Brood	0.017	0.684
Bareground	24.088	Random	3.289	198.941
Sagebrush height	4.435	Random	0.152	133.220
Sagebrush width	3.100	Random	0.165	104.172

Table 15. Average vegetation characteristic of sage-grouse brood and random sites used in the best model to explain brood sites in southwestern North Dakota, USA, 2005-2006.

Variable	Broods	Randoms	Broods	Randoms
	2005	2005	2006	2006
	\bar{x}	\bar{x}	\bar{x}	\bar{x}
Forb cover (%)	16	13	6	4
Grass cover (%)	29	23	34	19
Sagebrush cover (%)	5	5	5	3
Bareground cover (%)	25	35	11	29
Sagebrush height (cm)	38	38	30	29
Sagebrush width (cm)	53	55	50	47

**Kaplan-Meier ($n = 13$)
5-6 Week Survival-Recruitment**

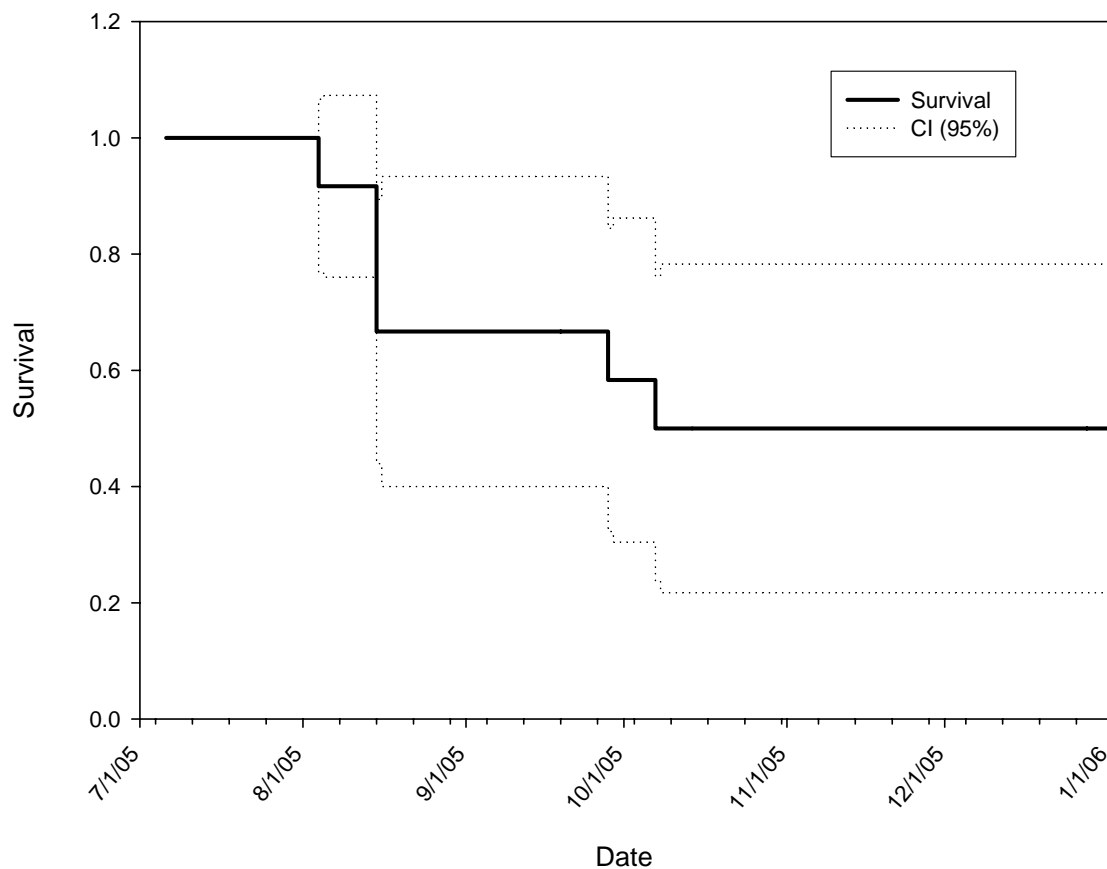


Figure 8. Greater sage-grouse chick survival rate and 95% confidence intervals (dashed lines) of chicks captured at 5-6 weeks of age that recruited into the population as of January 1 2006 in southwestern North Dakota, USA (Kaplan and Meier 1958, Pollock et al. 1989).

Kaplan-Meier ($n = 25$)
5-6 Week Survival-Recruitment

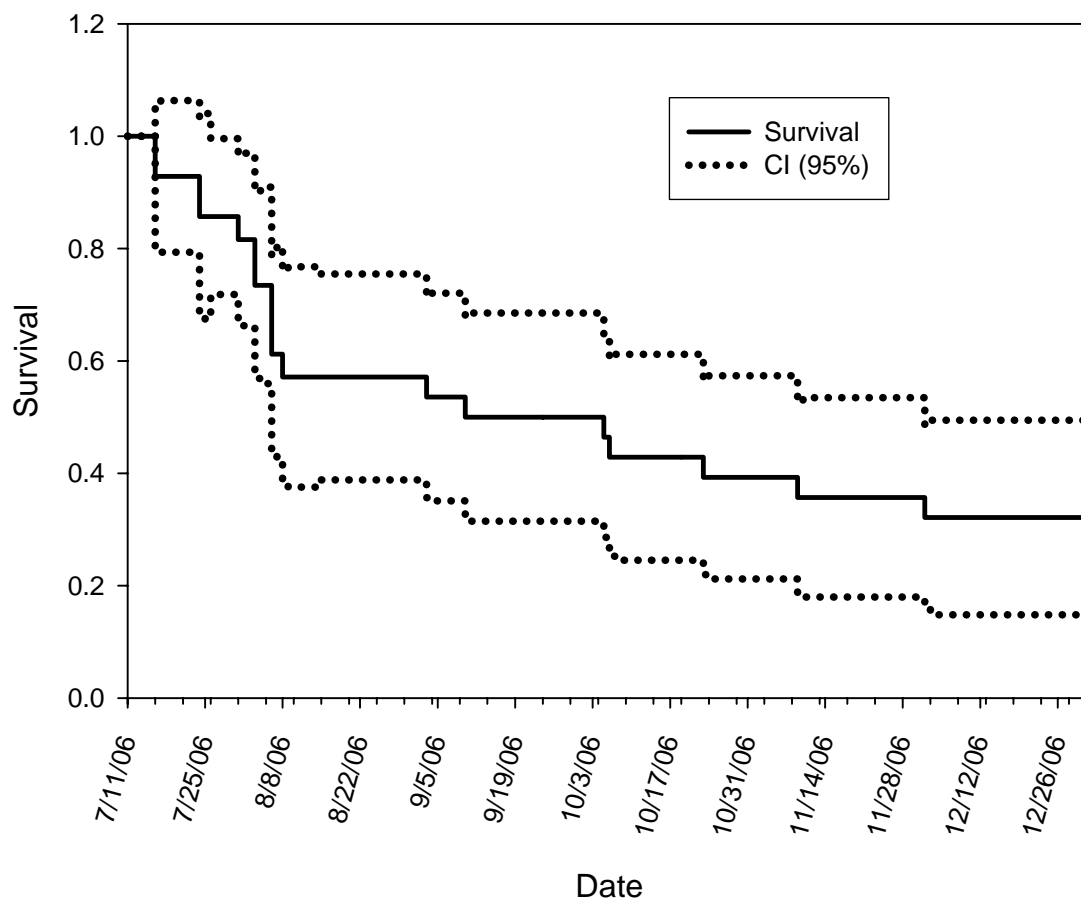


Figure 9. Greater sage-grouse chick survival rate and 95% confidence intervals (dashed lines) of chicks captured at 5-6 weeks of age that recruited into the population as of January 1 2007 in southwestern North Dakota, USA (Kaplan and Meier 1958, Pollock et al. 1989).

Kaplan-Meier ($n = 39$)
5-6 Week Survival-Recruitment

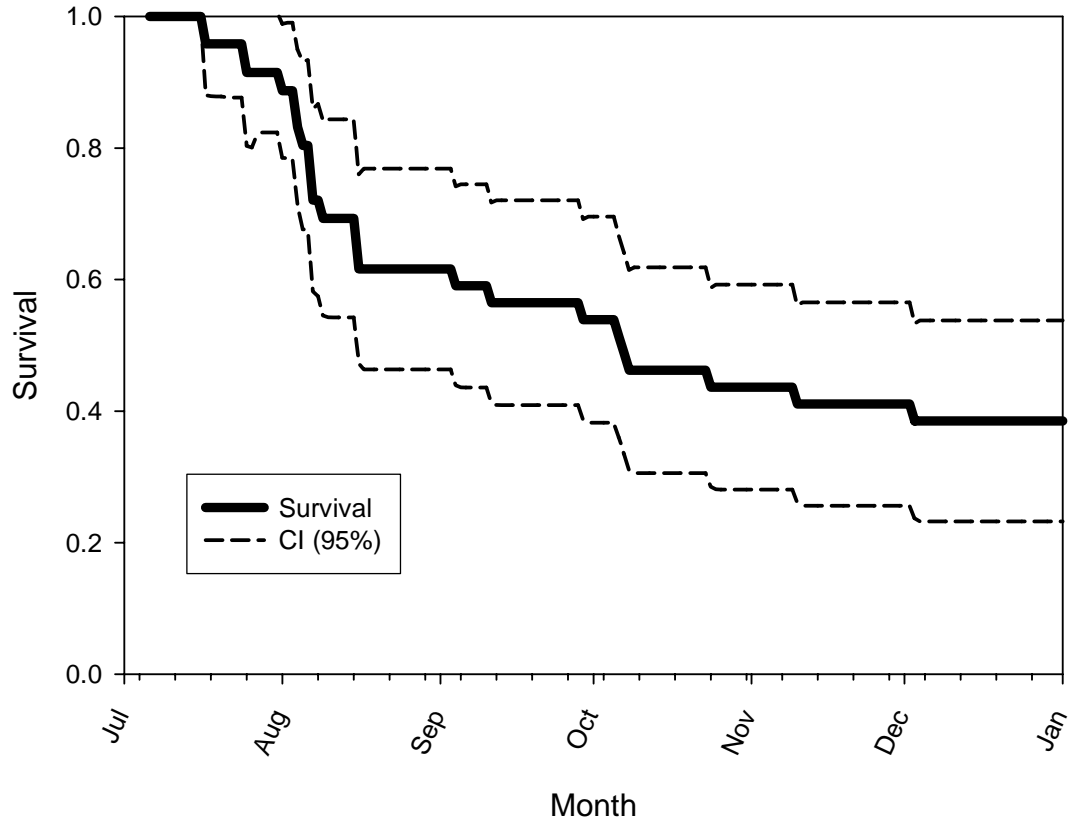


Figure 10. Overall chick survival rate and 95% confidence intervals (dashed lines) of chicks captured at 5-6 weeks of age that recruited into the population as of January 1 for 2005 and 2006 in southwestern North Dakota, USA (Kaplan and Meier 1958, Pollock et al. 1989).

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Appendix D. Four-digit code, common name and scientific name of plant species identified at brood sites and random sites in southwestern North Dakota, USA, 2005-2006.

Variable	Name	Scientific Name
acmi	Western yarrow	<i>Achillea millefolium</i>
aggl	false dandelion	<i>Hypochoeris radicata</i>
agst	Redtop	<i>Agrostis gigantea</i>
alfa	Alfalfa	<i>Medicago spp.</i>
arca	silver sage	<i>Artemisia cana</i>
arfi	fringed sagewort	<i>Artemisia frigida</i>
arlu	cudweed sagewort	<i>Artemisia ludoviciana</i>
artr	big sagebrush	<i>Artemisia tridentata wyomingensis</i>
atri	<i>Atriplex spp.</i>	<i>Atriplex spp.</i>
bear	beards tongue	<i>Penstemon spp.</i>
bell	bluebells	<i>Mertensia spp.</i>
bogr	blue grama	<i>Bouteloua gracilis</i>
brin	Smooth brome	<i>Bromus inermis</i>
brja	japanese brome	<i>Bromus japonicus</i>
bkbr	buckbrush	<i>Symphoricarpus occidentalis</i>
blue	little bluestem	<i>Vulpia octoflora</i>
buda	buffalo grass	<i>Buchloe dactyloides</i>
cafi	threadleaf sedge	<i>Carex filifolia</i>
calo	prairie sandreed	<i>Calamovilfa longifolia</i>
carr	wild carrot	<i>Daucus carota</i>
cele	wild celery	<i>Apium graveolens</i>
chea	cheatgrass	<i>Bromus tectorum</i>
cone	purple coneflower	<i>Echinacea Moench</i>
crew	Crested wheatgrass	<i>Agropyron cristatum</i>
curd	curly doc	<i>Rumex crispus</i>
disp	inland saltgrass	<i>Distichlis spicata</i>
dwarf	dwarf alyssum	<i>Alyssum cuneifolium</i>
ercs	Eastern red cedar	<i>Juniperus virginiana</i>
fiel	field bindweed	<i>Convolvulus arvensis</i>
gayf	gayfeather	<i>Liatris spicata</i>
gold	goldenrod	<i>Solidago spp.</i>
gotb	goatsbeard	<i>Tragopogon dubius</i>
gpea	golden pea	<i>Thermopsis rhombifolia</i>
grra	grayragwort	<i>Senecio incanus</i>
gumb	gumbo lily	<i>Oenothera caespitosa</i>
gumw	curlycup gumweed	<i>Grindelia squarrosa</i>
gusa	broom snakeweed	<i>Gutierrezia sarothrae</i>
hoju	foxtail barley	<i>Hordeum jubatum</i>

Appendix D. Continued

hors	horseweed	<i>Conyza</i> spp.
hory	hairy fleabane	<i>Conyza bonariensis</i>
indw	indian wheat	<i>Plantago patagonica</i>
intw	intermediate wheatgrass	<i>Thinopyrum intermedium</i>
koma	junegrass	<i>Koeleria macrantha</i>
long	Longleaf wormweed	<i>Artemisa longifolia</i>
must	Mustard	<i>Cardaria</i> spp.
navi	green needle	<i>Nassella viridula</i>
nutv	nuttall's violet	<i>Viola nuttallii</i>
opun	Cactus	<i>Opuntia</i> spp.
pars	wild parsley	<i>Musineon</i> spp.
pasm	Western wheatgrass	<i>Pascopyrum smithii</i>
penn	pennycress	<i>Thlaspi arvense</i>
pepp	pepperweed	<i>Lepidium densiflorum</i>
phho	hood's phox	<i>Phlox hoodii</i>
plan	Slender plantain	<i>Plantago heterophylla</i>
prpr	prickly pear	<i>Opuntia</i> spp.
popr	kentucky bluegrass	<i>Poa pratensis</i>
povw	povertyweed	<i>Iva axillaris</i> Pursh
psut	pussytoes	<i>Antennaria</i> spp.
redg	red goosefoot	<i>Chenopodium rubrum</i>
redt	Redtop	<i>Agrostis stolonifera</i>
ripg	prairie cordgrass	<i>Spartina pectinata</i>
rose	wild rose	<i>Rosa woodsii</i>
rubb	rubber rabbitbrush	<i>Ericameria nauseosa</i>
sand	sandbergs bluegrass	<i>Poa secunda</i>
scgo	scarlet gaura	<i>Gaura coccinea</i>
scur	scurfpea	<i>Psoralea</i> spp.
side	sideoats grama	<i>Bouteloua curtipendula</i>
silv	silverbladder pod	<i>Lesquerella argyraea</i>
skel	skeletonplant	<i>Lygodesmia</i> spp.
spid	spiderwort	<i>Tradescantia ohiensis</i>
spco	scarlet globemallow	<i>Sphaeralcea coccinea</i>
stic	stickseed	<i>Hackelia</i> Opiz
stco	needle and thread	<i>Stipa comata</i>
sthy	Angelita daisy	<i>Hymenoxys acaulis</i>
sunf	sunflower	<i>Eriophyllum</i> spp.
swee	sweetclover	<i>Melilotus</i> spp.
taof	dandelion	<i>Taraxacum officinale</i>
toad	Bastard toadflax	<i>Commandra umbellate</i>
this	Thistle	<i>Cirsium</i> spp.
txon	textile onion	<i>Allium</i> spp.
vetc	<i>Astragalus</i> spp.	<i>Astragalus</i> spp.

Appendix D. Continued

vuoc	six weeks-fescue	<i>Vulpia octoflora</i>
wewa	Western wallflower	<i>Erysimum asperum</i>
wint	winter fat	<i>Krascheninnikovia</i> spp.
yucca	yucca	<i>Yucca glauca</i>

Appendix E. Definition of all acronyms used for vegetative sampling in southwestern North Dakota, USA, 2005-2006.

Acronym	Definition
TOCO	Percent total vegetative cover
TOFO	Percent total forb cover
TOSH	Percent total sagebrush cover
TOGR	Percent total grass cover
Litter	Percent total litter cover (ie. residual grasses, rocks, feces)
Bareground	Percent bareground
Effective Grass Hgt	Grass height beneath sagebrush from Robel pole (in)
Max Grass Hgt	Tallest reading of grass species surrounding Robel pole (in)
Sagebrush Hgt	Sagebrush height (cm)
Sagebrush Width	Sagebrush width (minor and major cords averaged) (cm)
Sagebrush density	Sagebrush density/hectare
Site-VOR	Visual obstruction reading for the site
10-m VOR	Average visual obstruction reading for 10-m around site
20-m VOR	Average visual obstruction reading for 20-m around site
30-m VOR	Average visual obstruction reading for 30-m around site
40-m VOR	Average visual obstruction reading for 40-m around site
50-m VOR	Average visual obstruction reading for 50-m around site