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GREATER SAGE-GROUSE SURVIVAL, BREEDING ECOLOGY, RESOURCE SELECTION, AND WEST NILE VIRUS PREVALENCE ON THE EASTERN FRINGE OF THEIR RANGE

BY

LINDSEY ANNE PARSONS

A dissertation submitted in partial fulfillment of the requirements for the

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2019

GREATER SAGE-GROUSE SURVIVAL, BREEDING ECOLOGY, RESOURCE SELECTION, AND WEST NILE VIRUS PREVALENCE ON THE EASTERN FRINGE OF THEIR RANGE

LINDSEY ANNE PARSONS

This dissertation is approved as a credible and independent investigation by a candidate for the Doctorate of Philosophy in Wildlife and Fisheries Sciences degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the Department of Natural Resource Management.

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ABSTRACT

GREATER SAGE-GROUSE SURVIVAL, BREEDING ECOLOGY, RESOURCE SELECTION, AND WEST NILE VIRUS PREVAENCE ON THE EASTERN FRINGE OF THEIR RANGE

LINDSEY ANNE PARSONS

2019

The greater sage-grouse (*Centrocercus urophasianus*) is a sagebrush (*Artemisia* spp.) obligate species that has experienced population declines over the past several decades. Sage-grouse are a species of conservation concern throughout the Intermountain West and are considered a species of greatest conservation need in South Dakota. Numerous studies have documented drivers of demographic performance at the core of their distribution; however, relatively few studies have examined sage-grouse inhabiting the eastern extent of their range, in South Dakota. We sought to examine sage-grouse space use in multiple seasons, estimate survival, and determine factors affecting nest success in South Dakota during 2016 and 2017. Additionally, we quantified resource selection during spring/summer, winter, at nest-sites, and at brood-sites. Lastly, sage-grouse are highly susceptible to West Nile virus (WNV); thus, we evaluated the impact of WNV to this population of sage-grouse while simultaneously estimating infection rates in the primary arthropod vector, *Culex tarsalis.* We found that at a landscape scale, sage-grouse consistently exhibit positive selection responses to sagebrush and leks, and negative responses to forest, roads, and rugged terrain. At a local scale, when selecting nest-sites and brood-sites, sage-grouse consistently select for shrub cover and taller grass, while avoiding areas with greater percent grass cover. Estimated nest success was 29% (95% CI=20–42%). Distance to forest, distance to lek, road density, and percent undisturbed (unplowed) land had the greatest influenced on nest survival. Using remotely triggered cameras, we identified the American badger (*Taxidea taxus*) as the primary nest predator of sage-grouse. Adult female sage-grouse survival during the reproductive season (1 April−15 September) was estimated to be 68% (95% CI=56–78%). Survival varied temporally with lower survival during the nesting season compared to other periods during the reproductive season. We observed limited resistance to WNV (<2%), but WNV was not a significant source of sage-grouse mortality in South Dakota during this study (5% of total mortalities). We observed low levels of WNV in *Culex tarsalis* (minimum infection rate=1.6–3.3/1,000 mosquitoes tested). We did not observe a severe WNV outbreak during our study, but these data do serve as a baseline for enzootic levels of the virus in this landscape. Lastly, with our data we were able to develop a priority sage-grouse area in South Dakota, which encompasses known utilization as well as predicted use. Overall, this research has provided data from a population with limited prior information, as well as provided information that can enhance landscape management for the species.

CHAPTER 1: INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a sagebrush (*Artemisia* spp.) obligate species (Wallestad and Eng 1975), which has experienced population declines over the past several decades (Connelly et al. 2004, WAFWA 2015). Sagebrush (*Artemisia* spp.) vegetation encompasses over 29 million hectares across North America (Miller et al. 2011), and over 350 sagebrush associated plants and animals are considered species of conservation concern (Wisdom et al. 2005). Sage-grouse are considered sagebrush obligates because adult sage-grouse primarily consume sagebrush year-round, with supplementary forbs and arthropods (Wallestad and Eng 1975). In addition, sage-grouse typically select nest-sites that are under sagebrush canopy (Wallestad and Pyrah 1974), and non-sagebrush nests are less successful than sagebrush nests (Connelly et al. 1991). Moreover, sage-grouse association with sagebrush has led them to be considered an “umbrella species” for sagebrush-steppe conservation, and for other sagebrush obligate species conservation (Rowland et al. 2006, Hanser and Knick 2011).

Currently, sage-grouse occupy about 56% of the estimated pre-settlement sage-grouse distribution (Shroeder et al. 2004). This decreasing range is thought to be caused by the cumulative effect of habitat loss, fragmentation, and degradation of sage-grouse habitat via alterations to the sagebrush-steppe including but not limited to; conversion to cropland, conversion to grassland, pesticides, herbicides, urban development, altered fire regimes, invasion of non-native species, coniferous tree encroachment, increasing road infrastructure, and overgrazing (Braun et al. 1977, Shroeder et al. 2004, Crawford et al. 2004, Johnson et al. 2011, Naugle 2011, LeBeau 2014). Species declines also have resulted from predation (Gregg et al. 1994, Shroeder and Baydack 2001, Coates and Delehanty 2010, Hagen 2011), disease (Walker et al. 2007, Swanson 2009), and potentially population isolation (Knick and Hanser 2011, Schulwitz 2014, Davis et al. 2015).

Sage-grouse in South Dakota occupy the eastern edge of the current sage-grouse and sagebrush distribution (Johnson 1979, Schroeder et al. 2004, Lewis 2004). Historically, sage-grouse existed in at least five counties in South Dakota (Smith et al. 2004). As of 2016, the only documented sage-grouse in South Dakota exist in Butte and Harding counties (South Dakota Game, Fish and Parks 2014). The Dakotas have always been at the eastern edge of the sage-grouse distribution (Shroeder et al. 2004, Smith et al. 2004), as this is a natural transition zone between sagebrush species and grassland species (Cook and Irwin 1992, Smith et al. 2004, Johnson and Larson 2007). South Dakota is unique in that the sagebrush communities are shorter and have a lower percent canopy cover than found elsewhere throughout sage-grouse range (Connelly et al. 2000, Kaczor et al. 2011).

Despite shorter sagebrush and less canopy cover, sage-grouse nest success in South Dakota was 48% in a 2006–2007 study (Kaczor 2008). It is possible that sage-grouse in South Dakota are compensating for a lack of sagebrush cover with grass and other herbaceous cover to maintain adequate levels of survival and nest success (Kaczor 2008, Stiver et al. 2015). Overwintering habitat has been found to be sufficient in mild winters, with winter survival >90% (Swanson 2009, Swanson et al. 2013). Because they are at the fringe of the species distribution, sage-grouse in South Dakota face unique challenges such as increased vulnerability to isolation (Shroeder et al. 1999, Aldridge et al. 2008) and extirpation (Caughley et al. 1988, Lande 1993). The South Dakota sage-grouse range is moderately similar to the currently extirpated range, indicating this population may be at risk for extirpation based on habitat characteristics as well (Wisdom et al. 2011).

Previous sage-grouse research occurred in North Dakota (2005 and 2006) and South Dakota (2006 and 2007; Herman-Brunson et al. 2009, Swanson 2009, Kaczor et al. 2011a & b). Research in North Dakota was focused in Bowman County. In South Dakota, research was focused in Butte County. Between these two focus areas, lies Harding County, South Dakota; thus, little was known about sage-grouse space use and vital rates in Harding County.

A recent sage-grouse spring population peak of 608 total males was observed in 2006 followed by a decline of over 80% resulting in a total male count of 109 in 2014 (SD GFP). Additionally, during previous sage-grouse research in the Dakotas, West Nile virus (WNV) was documented as a source of mortality for sage-grouse (Kaczor 2008, Swanson 2009). However, lag time in carcass recovery for sage-grouse mortalities resulted in; possible WNV caused mortalities that could not be tested, or sage-grouse carcasses that falsely tested negative for WNV due to degradation of viral RNA.

Growing concern about the declining fringe sage-grouse population, and the need to better understand WNV in the sagebrush steppe, led to the current sage-grouse research being proposed. There was a need to identify factors influencing the breeding ecology of sage-grouse, and further investigate impacts of WNV on sage-grouse in South Dakota. Specific objectives addressed in this dissertation are:

1. Estimate prevalence of WNV in suspected primary greater sage-grouse vector, *Culex tarsalis*.
2. Identify specific surface water sources (stock dams, stock ponds, natural wetlands, ephemeral water, and other sources) selected as egg deposition sites for *Culex tarsalis*.
3. Test for WNV resistance (antibodies) in sage-grouse.
4. Estimate breeding season survival of female sage-grouse and determine cause-specific mortality.
5. Create resource selection functions to accurately identify sage-grouse habitat selection in multiple seasons.
6. Estimate resource selection of female sage-grouse with broods.
7. Estimate nest success, nesting rates, nest dispersal, nest-site selection, and cause-specific nest failure of sage-grouse.

STUDY AREA

This study was focused in Harding and Butte counties in northwest South Dakota, U.S.A. (Figure 1). The total area of both counties is 12,805 km^2. The land use in the study area is dominated by pastureland (>85%), followed by cropland (10−12%; USDA 2012). Over 84% of the study area has never been plowed (Bauman 2018). A majority of the land in the study area is privately owned (~75–80%; USGS GAP 2016). Annual average temperatures range from -1.7°C–10.6°C with an average of 39 cm of precipitation annually (NOAA 2019). The primary geologic formations in the study area include the Hell Creek formation, the Pierre Shale formation, the Ludlow formation, and the Fox Hills Sandstone formation (USGS Mineral Resources Program, 2005). The study area is transected by the Little Missouri River and Moreau River, as well as scattered with artificial ponds (stock dams and stock ponds), with few natural wetlands.

Common shrubs in the study area include: silver sagebrush (*Artemisia cana*), big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), broom snakeweed (*Gutierrezia sarothrae*), western snowberry (*Symphoricarpos occidentalis*), winterfat (*Krascheninnikovia lanata*), greasewood (*Sarcobatus vermaculatus*), and silver buffaloberry (*Shepherdia argentea*; Johnson and Larson 2007).

Common grasses in the study area include: crested wheatgrass (*Agropyron cristatum*), sideoats grama (*Bouteloua curtipendula*), blue grama (*Bouteloua gracilis*), smooth bromegrass (*Bromus inermis*), japanese brome (*Bromus japonicas*), downy brome (*Bromus tectorum*), buffalograss (*Buchloe dactyloides*), prairie sandreed (*Calamovilfa longifolia*), inland saltgrass (*Distichlis spicata*), thickspike wheatgrass (*Elymus lanceolatus*), slender wheatgrass (*Elymus trachycaulus*), intermediate wheatgrass (*Elytrigia intermedia*), foxtail barley (*Hordeum jubatum*), junegrass (*Koeleria macrantha*), false buffalograss (*Munroa squarrosa*), western wheatgrass (*Agropyron smithii*), Kentucky bluegrass (*Poa pretensis*), sandburg bluegrass (*Poa secunda*), russian wildrye (*Psathyrostachys juncea*), little bluestem (*Schizachyrium scoparium*), needleandthread (*Stipa comata*), and green needlegrass (*Stipa viridula*; Johnson and Larson 2007).

Common forbs in the study area include: yucca (*Yucca glauca*), desert biscuitroot (*Lomatium foeniculaceum*), wild parsley (*Musineon divaricatum*), common yarrow (*Achillea millefolium*), western ragweed (*Ambrosia psilostachya*), small leaf pussytoes

(*Antennaria parvifolia*), western sagewort (*Artemisia campestris*), fringed sagewort (*Artemisia frigida*), hairy goldaster (*Chrysopsis villosa*), horseweed (*Conyza canadensis*), fetid marigold (*Dyssodia papposa*), purple coneflower (*Echinacea angustifolia*), blanket flower (*Gaillardia aristata*), curlycup gumweed (*Gindelia squarrosa*), prairie coneflower (*Ratibida columnifera*), common dandilion (*Taraxacum officinale*), goatsbeard (*Tragopogon dubius*), cocklebur (*Xanthium strumarium*), western wallflower (*Erysimum asperum*), field pennycress (*Thlaspi arvense*), kochia (*Kochia scoparia*), two grooved poisonvetch (*Astragalus bisulcatus*), alfalfa (*Medicago falcate*), yellow sweetclover (*Melilotus officinalis*), silverleaf scurfpea (*Pediomelum argophyllum*), breadroot scurfpea (*Pediomelum esculentum*), american vetch (*Vicia americana*), indian wheat (*Plantago patagonica*), hoods phlox (*Phlox hoodii*), white milkwort (*Polygala alba*), prairie smoke (*Geum triflorum*), and common mullein (*Verbascum Thapsus*; Johnson and Larson 2007).

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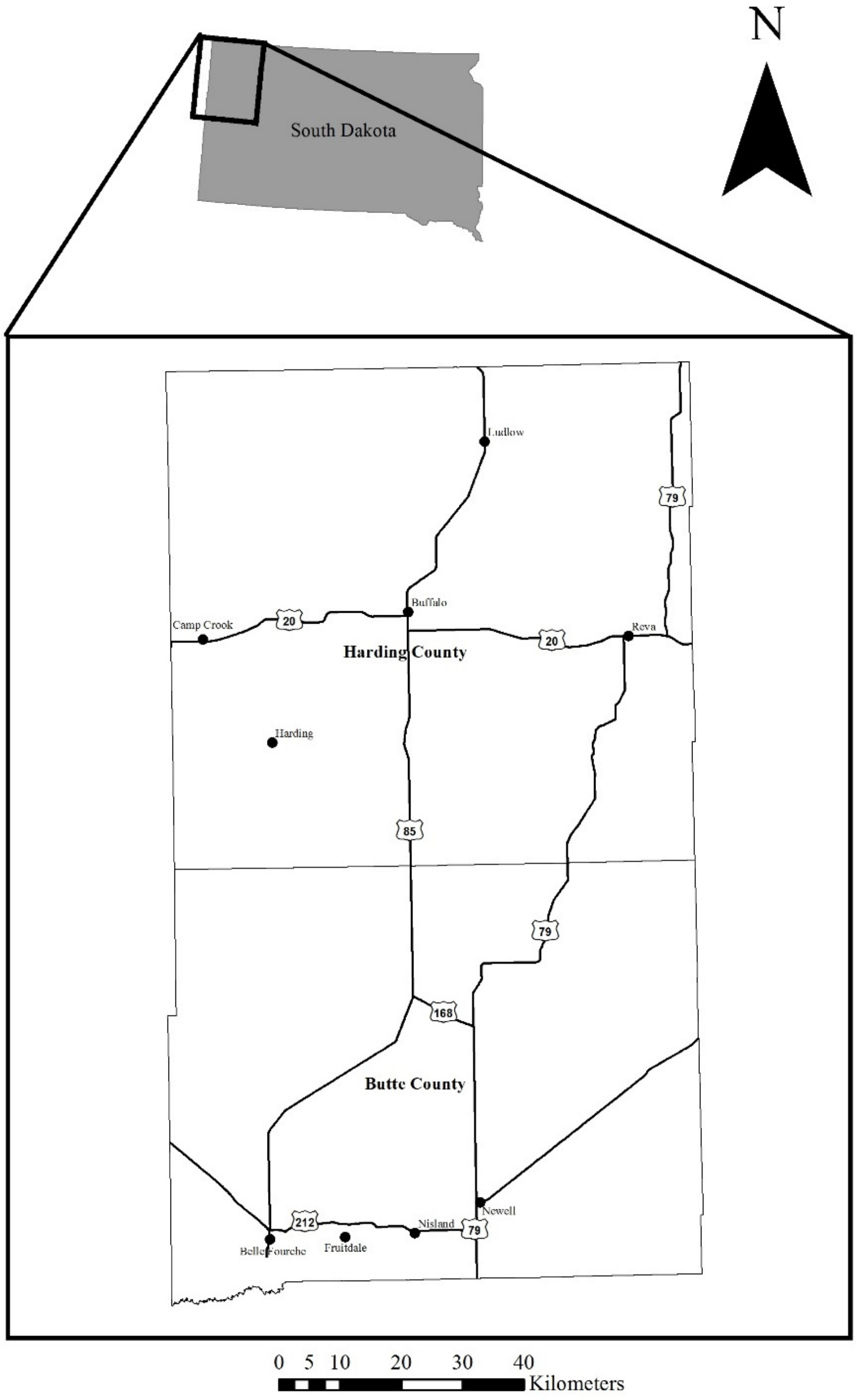

Figure 1. Greater sage-grouse study area in northwestern South Dakota, USA. Study took place during 2016 and 2017.

CHAPTER 2: WEST NILE VIRUS PREVALENCE IN SYMPATRIC POPULATIONS OF GREATER SAGE-GROUSE AND *CULEX TARSALIS* ON THE EASTERN FRINGE OF THE SAGEBRUSH STEPPE

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) are a species of conservation concern and are highly susceptible to mortality from West Nile virus (WNV). *Culex tarsalis* is suspected as the primary vector for transmitting WNV to sage-grouse. To determine WNV prevalence in sage-grouse in South Dakota, we collected blood from 158 individuals in 2016 and 2017 and tested blood-serum for WNV antibody titers. We also captured and fitted female sage-grouse with VHF radio-transmitters and monitored their survival daily during peak WNV season (15 June−15 September). Deceased birds were tested for WNV. We trapped mosquitoes with CO_2 baited traps four nights per week (542 trap nights) to estimate WNV minimum infection rate (MIR). We sampled river habitats, wetlands, stock ponds, culverts, ephemeral water, and stock tanks within the study site for mosquito larvae (n=449) to determine oviposition-site selection of *Cx. tarsalis*. One male (1.2%; 95% CI = 0.1−7.5%) and two female (2.6%; 95%CI= 0.5−10.0%) sage-grouse contained antibodies; three sage-grouse (1.9%; 95% CI=0.5−5.9%) contained antibodies. Eight total mortalities occurred during the WNV seasons of 2016 and 2017; five had recoverable tissue and were tested, one of five tested positive for WNV infection. We captured 12,472 mosquitoes of which 3,933 (32%) were *Cx. tarsalis*. Estimated WNV minimum infection rate (MIR) per 1,000 *Cx. tarsalis* during 2016 and 2017 was 3.3/1,000 and 1.6/1,000, respectively, resulting in a WNV prevalence rate in *Cx. tarsalis* of 0.2−7.8%. We found *Cx. tarsalis* larvae in all water body types with the exception of stock tanks. Our results suggest sage-grouse in South Dakota have

limited resistance to WNV, but WNV was not a significant source of sage-grouse mortality in South Dakota during 2016 and 2017. Given the epizootic nature of WNV, the potential impacts could be devastating to this particular fringe population of sage-grouse during an outbreak year.

INTRODUCTION

Epizootic diseases pose threats to wildlife populations worldwide (Daszak et al. 2000). Because of the complex nature of relationships between vectors, hosts, and the environment, zoonotic diseases cycle (Muul 1970, Daszak et al. 2000, Burri et al. 2011). Cumulative effects of disease with other environmental stressors can significantly increase threats to wildlife populations (Daszak et al. 2003, Pounds et al. 2006, Mills 2012, Taylor et al. 2013). With the expansion of the human population and anthropogenic effects on landscapes, infectious diseases also have expanded (Daszak et al. 2000, Morse 2001).

West Nile virus (WNV) is a zoonotic disease that is relatively new to North America; it was first detected in New York City, in the summer of 1999 (Lanciotti et al. 1999). The virus persists in a mosquito–bird–mosquito cycle and has been detected in > 300 avian species in the United States (CDC 2015). Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is one avian species that is particularly susceptible to mortality from WNV (Clark et al. 2006). Sage-grouse infected with WNV exhibit behaviors such as: oral/nasal discharge, isolation from group, immobility, drooped wings, labored breathing, and incapability of coordinated locomotion (Clark et al. 2006). These results suggest that WNV infected sage-grouse might not be able to detect or flea from approaching predators; thus, mortality due to predation may be higher for a WNV infected sage-grouse.

The first documented sage-grouse mortalities due to WNV occurred in 2003 (Naugle 2004, Moynahan et al. 2006), shortly thereafter, the first documented sage-grouse to survive a WNV infection were found in the Powder River Basin of Montana and Wyoming in 2005 (Walker et al. 2007). Less than 5% of sage-grouse test positive for WNV neutralizing antibodies (Walker et al. 2007, Dusek et al. 2014) and it is unknown if WNV antibodies can be passed to sage-grouse chicks from their mothers during egg production via passive vertical transmission (Walker et al. 2007), as observed in other avian species (Stout et al. 2005, Hahn et al. 2006, Nemeth and Bowen 2007).

Culex tarsalis is a mosquito species shown to be the most efficient vector of WNV due to its high rates of infection and transmission compared to 10 other mosquito species (Goddard et al. 2002). *Cx. tarsalis* primarily obtains blood meals from bird species (Tempelis et al. 1965) and has also been identified as the primary vector of WNV transmission to sage-grouse (Naugle 2004). One way to manage mosquito-borne disease is by manipulating the environments in which mosquitoes breed (Small 2005, Hemingway 2005); thus, identification of *Cx. tarsalis* oviposition-sites in the sagebrush-steppe could have important management implications for sage-grouse.

Factors affecting *Cx. tarsalis* oviposition-sites or *Cx. tarsalis* larval abundance include; chemical factors associated with presence of other *Cx. tarsalis* individuals (Hudson and McLintock 1967), number of inlets to a water source (Irwin 2010), abundance of Coleopteran larvae, pond age (Walton et al. 1990), vegetation coverage, surface water hectares, and perimeter distance of water source (Watchorn 2015).

In the Northern Great Plains, and South Dakota specifically, *Cx. tarsalis* is the second most common mosquito, (Gerhardt 1966, Easton 1987, Vincent 2018) and the primary vector of WNV (Bell et al. 2005, Johnson et al. 2010, Vincent 2018). Also, South Dakota is on the eastern fringe of the current sage-grouse distribution (Shroeder et al. 2004), and WNV has been documented as a source of sage-grouse mortality in the state (Kaczor 2008, Swanson 2009). In 2006, a recent sage-grouse spring population peak of 608 total males was observed, followed by a 44% decline by spring of 2008 (SD GFP). During this time, WNV was documented as a source of mortality for sage-grouse (Kaczor 2008, Swanson 2009), and it is thought that WNV could have caused this population decline. Elsewhere, WNV contributed to a 25% decline in survival across four sage-grouse populations during the initial outbreak in 2003 (Naugle et al. 2004). Therefore, WNV has the potential to cause extreme population-level impacts to sage-grouse.

Sage-grouse in South Dakota face unique challenges in that they are a fringe population. Generally speaking, species at the edge of their range are more vulnerable to extinction than those located in the main portion of the range (Caughley et al. 1988, Lande 1993). Due to characteristics associated with peripheral populations in general, the South Dakota population has an increased risk of becoming disjunct from core sage-grouse populations and has a higher risk of extirpation (Shroeder et al. 1999, Aldridge et al. 2008).

Combined risks of WNV along with other environmental stressors, such as oil and gas development, have been shown to have a more severe additive effect on sage-grouse populations than any factor alone (Taylor et al. 2013). The vulnerability of the South Dakota sage-grouse population to extirpation can be further exacerbated due to the disease risk associated with additive mortality from WNV.

Our overall goal was to assess the interactions between sage-grouse, *Cx. tarsalis,* and WNV in South Dakota. Our specific objectives were to; 1) document relative abundance of mosquito species; 2) estimate WNV prevalence rates in *Cx. tarsalis*; 3) identify oviposition-sites of female *Cx. tarsalis*; 4) document seroprevalence rates of WNV neutralizing antibodies in sage-grouse; and 5) estimate influence of WNV on sage-grouse survival.

METHODS

STUDY AREA

This study primarily occurred in Harding and Butte counties of northwest South Dakota. The total area of both counties combined is 12,805 km^2. The land use of the study area is dominated by pastureland (>85%), followed by cropland (10–12%; USDA 2012). The majority of the land in the study area is privately owned (~75−80%; USGS GAP 2016). Annual average temperature ranges from -1.7–10.6°C with an average of 39 cm of precipitation annually (NOAA 2019). The study area contains numerous man-made water sources (stock ponds and stock dams), as well as some natural wetlands. Additionally, the Little Missouri and Moreau Rivers transect the study area.

Our study area represents the eastern edge of the sagebrush distribution where an ecotone between sagebrush steppe and grassland ecosystems occurs (Johnson 1979, Cook and Irwin 1992, Lewis 2004). Sagebrush communities found in South Dakota are shorter and have a lower percent canopy cover than found elsewhere in the sagebrush steppe (Kantrud and Kolgiski 1983, Connelly et al. 2000, Kaczor et al. 2011). Common shrubs in the study area include silver sagebrush (*Artemisia cana*) and big sagebrush (*Artemisia tridentata*; Johnson and Larson 2007).

WNV AND VECTORS ON THE LANDSCAPE

Adult mosquitoes were trapped 1 June–15 September using standard miniature light traps with photocell controlled CO_2 release (John W. Hock Company; Model 1012.CO2) 4 nights per week. CO_2 traps were set to deliver 0.5L CO_2/min (Vincent 2018). In South Dakota, it is estimated that 97% of sage-grouse nests are within 7 km of an active lek (Kaczor et al. 2011, Parsons 2019; Chapter 6). *Cx. tarsalis* have been shown to move > 25 km to fulfill life cycle requirements (Bailey et al. 1965); however, most commonly, movements are between 1−12.6 km (Milby et al. 1983, Riesen et al. 1992). To study overlapping populations of *Cx. tarsalis* and sage-grouse throughout the WNV season, we trapped mosquitoes near active lek sites (within 1.3–1.8 km of leks; Figure 1).

Captured mosquitoes were frozen and sorted to species. Female mosquitoes contribute to the transmission of WNV due to their requirement to consume blood meals prior to oviposition (Hubert et al. 1954) and although there are examples of male mosquitoes infected with WNV (Anderson et al. 2006a, Unlu et al. 2010), they are typically not of interest when researching WNV (US EPA 2017). Therefore, we identified female mosquitoes and sorted each to species based on morphological characteristics using a dichotomous identification key (Darsie and Ward 2005). If individual mosquitoes could not be identified due to poor condition, or lacking body parts, we placed them in an “unknown” category.

Several mosquito species known to be found in South Dakota are considered competent vectors of WNV (Woodring et al. 1996, Goddard et al. 2002). However, other than *Cx. tarsalis*, all of them primarily feed on mammalian hosts (Tempelis and Washino 1967, Gunstream et al. 1971, Tempelis 1975, Nasci 1984, Anderson and Gallaway 1987, Goudarz and Andreadis 2006) and are less efficient at transmitting WNV than *Cx. tarsalis*. Therefore, the other species are likely not a primary vector of WNV to sage-grouse in South Dakota and we opted to test only *Cx. tarsalis* mosquitoes for WNV.

Female *Cx. tarsalis* were placed in vials of up to 50 individuals and couriered to the South Dakota Department of Health for WNV testing. Samples of *Cx. tarsalis* were homogenized and tested for WNV using a TaqMan Reverse Transcriptase-PCR Assay, as described in Lanciotti et al. (2000) with slight modifications. Minimum infection rate (MIR) was calculated by counting the number of vials that tested positive divided by total number of mosquitoes tested; MIR is reported as minimum number of WNV positive mosquitoes/1,000 mosquitoes tested. This method assumes the minimum number (one mosquito) is WNV positive in each vial.

To assess the oviposition-site selection of *Cx tarsalis*, water bodies within the study area were sampled for mosquito larvae using a 350 ml mosquito larvae dipper with extendable handle (BioQuip; model #1132BQC/1132H). Approximately 500 ml of surface water was collected at each sampling site. To track changing mosquito population dynamics through the season, 9 pre-determined sites were sampled weekly from 1 June–15 September. Other samples were collected opportunistically to increase sample coverage. We categorized the type of water body as ephemeral, stock pond/stock dam, stock tank, culvert/irrigation ditch, natural wetland, or river. Water samples were placed into mosquito larval rearing traps (BioQuip; model #1425). Within two days, each larval rearing trap was examined for the presence of mosquito eggs and larvae. If either were present, the samples were stored at ambient temperature and fed ~ 1 alfalfa pellet/5 days until emergence. Once larvae emerged as adult mosquitoes, they were frozen and identified to species.

WEST NILE VIRUS INFECTION IN SAGE-GROUSE

We annually captured breeding-age male and female sage-grouse near active leks March–May, as well as at high sage-grouse use areas in August and September using nocturnal spotlighting and a long-handled net (Giesen et al. 1982, Wakkinen et al. 1992). We aged and sexed captured sage-grouse based on plumage and morphological characteristics (Crunden 1963, Beck et al. 1975, Bihrle 1993). We fit female sage-grouse with a 21.6 g necklace-type Very High Frequency (VHF) radio transmitter (model A4060, Advanced Telemetry Systems, Isanti, MN, USA) as well as a uniquely numbered aluminum butt-end leg band (National Band & Tag Company). We weighed all birds at the time of capture to ensure that radio-transmitters were less than 3% of body weight (Kenward 2001).

To detect WNV antibody titers in sage-grouse, we used a 22-gauge needle to collect 1 ml of blood from the brachial vein (Gregg et al. 2006). Whole blood was placed in a 2 ml Vacuette® blood tube with Z Serum Clot Activator, then centrifuged within 12 hours of collection. Serum was decanted, placed into a sterile 2 ml Cryovial®, and frozen until testing (Walker et al. 2007). Serum samples were tested for WNV antibodies using a Plaque-reduction neutralization assay at Cornell University's Animal Health Diagnostic Center (Naugle et al. 2004, 2005, Walker et al. 2007). Samples were considered negative for WNV antibodies if titers were not detected at the minimum serum dilution (1:10). Radio-collared sage-grouse were recaptured at the conclusion of the study. Blood samples were collected and tested for WNV antibodies again; radio-collars were removed. This allowed us to document any radio-collared sage-grouse that had become infected with WNV, developed antibodies, and survived the duration of the study. All animal handling procedures were approved by the Institutional Animal Care and Use Committee at South Dakota State University (IACUC approval # 15-074A).

We tracked survival by monitoring VHF signals of all radio-collared females twice weekly from 15 April–14 June and daily from 15 June−15 September. Daily monitoring reduced bias associated with lag-time in recovery of corpses in determining true cause-specific mortality (Bumann and Stauffer 2002, Stevens et al. 2011). If a sage-grouse radio-collar signal was detected on mortality mode, the sage-grouse and VHF radio-collar were recovered immediately, and cause of death was investigated. If the mortality occurred during WNV season (1 June–15 September), any available tissues (intestines, proventriculus, liver, kidney, lung, heart and brain) were recovered and frozen until tested for presence of WNV using a Reverse Transcriptase-PCR Assay at Cornell University's Animal Health Diagnostic Center (Porter 1993, Shi 2001).

RESULTS

ASSESSING WEST NILE VIRUS AND VECTORS ON THE LANDSCAPE

A total of 12 mosquito species were identified, but *Cx. tarsalis, Aedes vexans, Ochlerotatus dorsalis* and *Culeseta inornata* accounted for over 94% of the total number sampled (Figure 2). We collected a total of 12,472 mosquitoes, 32% of which were *Cx. tarsalis* (Table 1). In 2016, six WNV detections occurred at four of five CO_2 mosquito trap sites. In 2017, there were three WNV detections, occurring at two CO_2 mosquito trap sites. When standardized by trap night, both total mosquitoes and *Cx. tarsalis* captured per trap night were greater for 2016 (26.1 and 7.6, respectively) than 2017 (20.3 and 7.0, respectively). Estimated WNV minimum infection rate (MIR) per 1,000 *Cx. tarsalis* ranged from 3.3−1.6/1,000 (Table 1). Estimated WNV prevalence in *Cx. tarsalis* during our study ranged from 0.2–7.8% (Table 1). In 2016 and 2017, 3.3% and 1.5%, respectively, of mosquito pools (vials) tested positive for WNV.

A total of 449 water samples were examined for the presence of mosquito larvae (Table 3). Stock ponds/stock dams and natural river habitats were sampled most frequently. Culverts/irrigation ditches contained the highest frequency of *Cx. tarsalis* larvae (33% of culvert/irrigation water samples), however, few water samples came from culverts/irrigation ditches (Table 3). Mosquito larvae were detected in all types of water sampled with the exception of stock tanks (Table 3).

WEST NILE VIRUS INFECTION IN SAGE-GROUSE

We tested 158 individual sage-grouse (76 females and 82 males) for WNV neutralizing antibodies. Two females (2.6%; 95% CI=0.3%–9.1%) and one male (1.2%; 95% CI=0.03%–6.6%) tested positive for WNV neutralizing antibodies. In total, three sage-grouse (1.9%; 95% CI=0.4%–5.5%) contained WNV neutralizing antibodies. We re-captured 17 radio-collared female sage-grouse at the conclusion of the study (44% of remaining radio-collared sage-grouse) to remove collars and collect blood samples. There were no sage-grouse that had developed WNV antibodies since their original capture; however, one individual positive for WNV antibodies at initial capture still contained detectable levels of WNV antibody titers upon re-capture (199 days between captures; ≥ one year post WNV infection).

In 2016 and 2017, we monitored 29 and 47 female sage-grouse, respectively. We observed 10 mortality events each year from 1 April–15 September. Across both years, mammalian predation was the leading cause of mortality (40%), followed by unknown sources of mortality (25%), avian predation (15%), unknown predation (15%), and lastly, WNV (5%; Figure 3). Predation was the leading cause of mortality of sage-grouse in South Dakota, accounting for ≥70% of breeding season (1 April–15 September) mortality in 2016 and 2017.

In 2016, five of 10 mortalities occurred during WNV season, three of which had sufficient recoverable tissue to be tested for WNV; none tested positive for WNV. During 2017, three of 10 mortalities occurred during the WNV season, two of which had recoverable tissue tested for WNV; one tested positive, indicating WNV infection. Overall, our tissue recovery rate and testing of those mortalities was 63% (5 of 8).

DISCUSSION

We found low prevalence of WNV in *Cx. tarsalis* during this study (0.2–7.8%). The true prevalence rate was likely at the low end of this range because mosquitoes were tested in vials of up to 50 mosquitoes. Each positive result could be; 1 in 50 mosquitoes was positive for WNV, or 50 of 50 mosquitoes were positive for WNV. However, a majority of the vials contained no WNV positive mosquitoes; therefore, we suspect that 50 of 50 (or other very high rates) mosquitoes testing positive for WNV is unlikely. Our MIR per 1,000 mosquitoes was 3.3 in 2016 and 1.6 in 2017. The MIR documented in the sagebrush steppe in Wyoming during an outbreak year was 7.16/1,000 *Cx. tarsalis*, this outbreak is suspected of causing a 25% decline in that study's sage-grouse population (Naugle et al. 2004). Similarly, in the sagebrush steppe in Alberta, mosquitoes were sampled during a WNV outbreak year, and a non-outbreak year. During the outbreak year, 12.2% of mosquito vials tested positive, while the non-outbreak year had <1% of mosquito vials test positive (Naugle et al. 2005). During our study, 3.3% and 1.5% of vials tested positive for WNV in 2016 and 2017, respectively. It appears that the prevalence documented during our study was lower than documented elsewhere during WNV outbreak years, while slightly higher than the non-outbreak years.

We found *Cx. tarsalis* larvae in each category of water we sampled with the exception of stock tanks. Typically, gravid *Cx. tarsalis* females select oviposition-sites that are in inundated vegetation (Bohart and Washino 1978) with high amounts of detritus and microbial activity (Reiter 1986). It is possible that stock tanks do not contain enough organic matter to be attractive to gravid female *Cx. tarsalis* when selecting oviposition-sites. All other types of water bodies sampled can have the attractive qualities sought after by gravid female *Cx. tarsalis*. It is possible that irrigation ditches and culverts have high quantities of flooded vegetation, detritus, and microbial activity, which is why we frequently found *Cx. tarsalis* in these water body types; however, sample sizes for water samples from culverts/irrigation ditches were relatively low, so interpretation of these results is cautioned. Overall, there was a low occurrence of *Cx. tarsalis* larvae relative to the number of bodies of water sampled.

Our observed overall low occurrence of sage-grouse with WNV neutralizing antibodies is consistent with previous research (Walker et al. 2007, Dusek et al. 2014), and indicates that it is at least possible for sage-grouse in South Dakota to survive WNV infection. The low occurrence of antibodies suggests three non-mutually exclusive possibilities: 1) that the majority of sage-grouse have not been exposed to WNV and therefore, have had no opportunity to develop antibodies, 2) that WNV is lethal to the majority of the population and that there are a limited number of birds with the ability to survive infection and develop antibodies, or 3) that sage-grouse are mounting an immune response other than via producing WNV specific antibodies and thus, we cannot detect infection by evaluating WNV neutralizing antibodies. This last possibility was observed in a budgerigar (*Melopsittacus undulates*) that was indeed harboring WNV infection within the heart tissue but showed low viremia levels (only detected day 1 post inoculation) and did not develop WNV antibodies over the course of the study (14 days; Komar et al. 2003). We observed one mortality attributed to WNV during both breeding seasons; nearly all other mortalities were due to predation. Therefore, WNV was not suspected as a population-level influence during our study.

We documented detectable WNV neutralizing antibodies in sage-grouse ≥ 12 months post-infection, which is longer than previously documented (< 6 months) for sage-grouse (Walker et al. 2007). Although it is possible that this individual became re-infected with WNV between sampling periods, this is unlikely based on the low levels of WNV detected on the landscape during this time. WNV neutralizing antibodies have been shown to last ≥ 12 months in other avian species (Langevin et al. 2001, Gibbs et al. 2005).

The observed low levels of WNV found in *Cx. tarsalis* mirror the low prevalence of WNV in sage-grouse. This relationship suggests WNV transmission was frequency dependent, whereby the transmission rates were reflective of the number of vector encounters, as well as proportion of infected vectors (Thrall et al. 1993 & 1995). We estimated prevalence rates of WNV in *Cx. tarsalis* were low. We do not have a relative index of *Cx. tarsalis* abundance for the study area over time to determine whether numbers observed were above, below, or average for the area. However, the average number of *Cx. tarsalis* captured per trap night was < 8, indicating that if we assume sage-grouse have the same attractiveness as our CO_2 traps, few vector encounters between *Cx. tarsalis* and sage-grouse may have occurred. Thus, in a year with environmental conditions favorable for *Cx. tarsalis*, we would expect higher numbers of *Cx. tarsalis* and higher numbers of vector encounters. Also, in a year with favorable conditions, all components of frequency dependent transmission are increased and thus, we would expect a WNV epizootic event.

This leads us to examine the conditions favorable for WNV on the landscape. There is considerable annual fluctuation in the prevalence of WNV, but even in low WNV incidence years, the virus persists at a baseline or endemic level, on the landscape (Lindsey et al. 2010). Local climate can be responsible for the annual variation in prevalence (Hubálek and Halouzka 1999, Epstein 2001, Ruiz et al. 2010), as ambient temperature is important to both *Cx. tarsalis* development (Hagstrom and Workman 1971), abundance (Chuang et al. 2011, Danforth 2015), as well as the time it takes WNV to; infect, replicate and be transmitted from an arthropod host such as *Cx. tarsalis* (Reisen 2006). Therefore, it is believed that WNV transmission can be regulated via environmental temperature (Hagstrom and Workman 1971, Reisen et al. 2006, Chuang et al. 2011, Danforth 2015).

In previous research in South Dakota, WNV outbreaks occurred and WNV was identified as a factor impacting survival (Kaczor 2008, Swanson 2009). We did not detect an outbreak during our study, and therefore we wanted to examine climatic and weather trends that may have contributed to WNV outbreak and non-outbreak years within our study system. We compared monthly weather data from June–September during 2006 and 2007, and 2016 and 2017. We examined the Palmer Drought Severity Index, maximum temperature, minimum temperature, average temperature, and precipitation. We did not detect any clear trends differentiating the outbreak years (2006 and 2007) from the non-outbreak years (2016 and 2017). It is possible that specific timing of weather events within each month were significant (and not detected at a monthly scale), or a combination of factors contributed to creating conditions suitable for WNV outbreak years in 2006 and 2007.

These baseline results suggest that sage-grouse in South Dakota have limited immune response to WNV, but also had a limited WNV infection potential during this time, as WNV was not a significant source of sage-grouse mortality in South Dakota during 2016 and 2017. Our results support the conclusion that given the epizootic nature of WNV and sage-grouse susceptibility to WNV, the potential impacts of WNV could be devastating to this particular fringe population of sage-grouse during an outbreak year.

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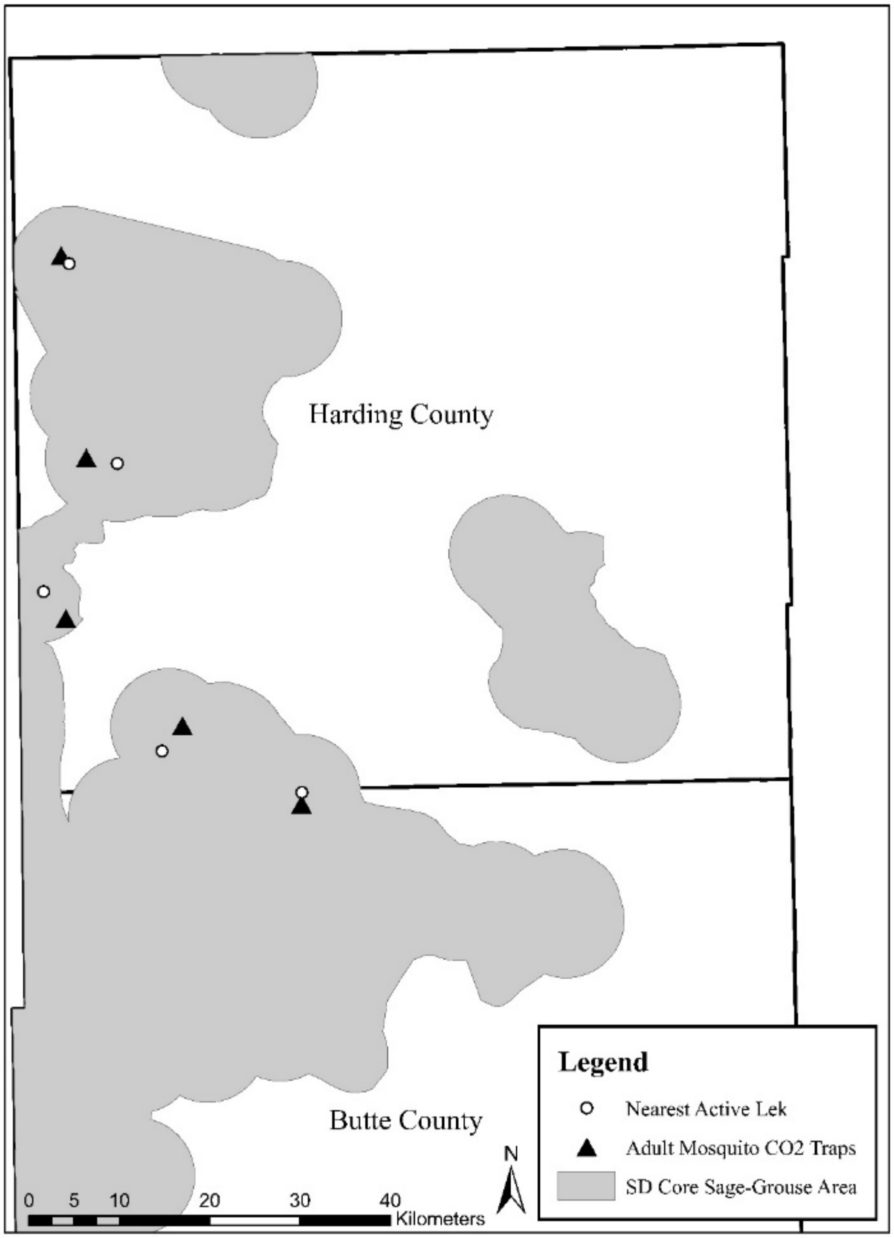

Figure 1. CO_2 baited mosquito trap locations and nearest active sage-grouse lek to each mosquito trap. Distance from trap to nearest active lek ranged from 1.3–3.8 km.

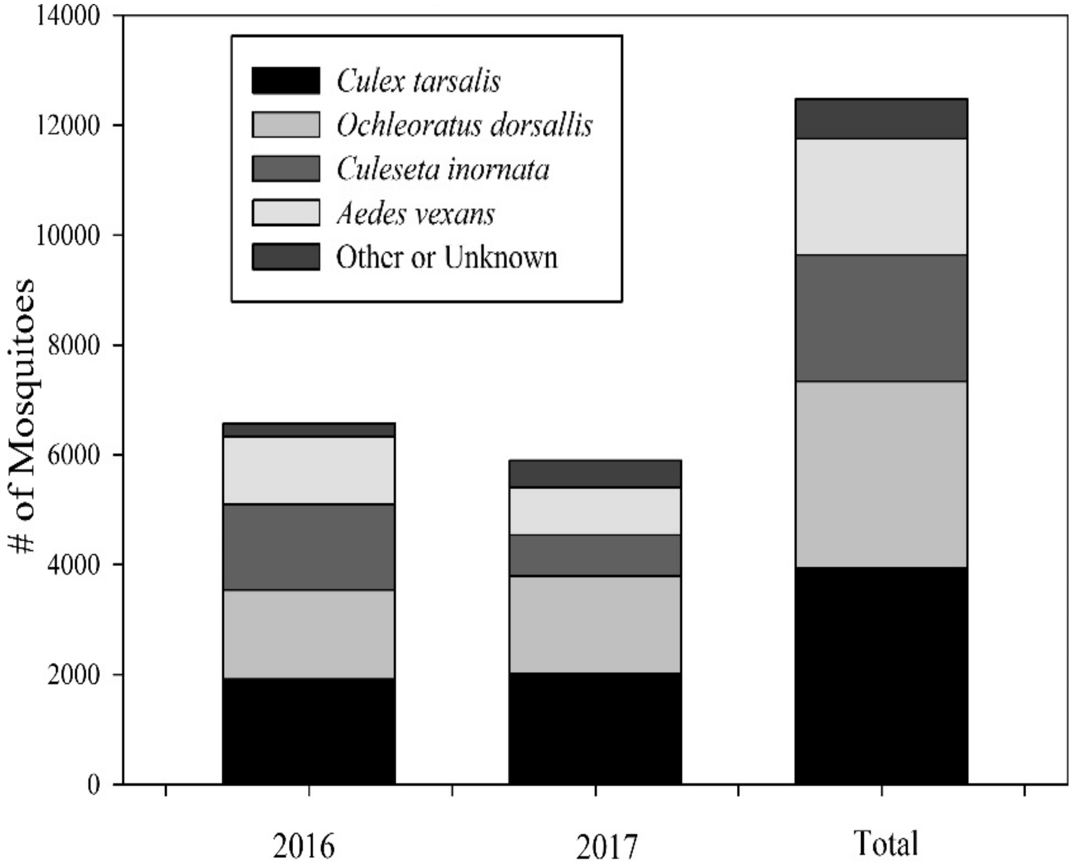

Figure 2. Composition of mosquito species collected 1 June–15 September 2016 and 2017 using five CO_2 traps in Butte and Harding counties, South Dakota. Other species included; *Culex pipiens*, *Anopheles walkeri*, *Coquillettidia perturbans*, *Culex salinarius*, *Ochlerotatus fitchii*, *Ochlerotatus triseriatus*, *Ochlerotatus trivittatus*, *Ochlerotatus sollicitans*.

Table 1. Total numbers of mosquitoes collected 1 June–15 September 2016 and 2017 using five CO_2 traps in Butte and Harding counties, South Dakota. West Nile Virus (WNV) detections occurred from; 20 July 2016–4 September 2016 and 27 July–23 August 2017.

	2016	2017	Total
Trap Nights	252	290	542
WNV Minimum Infection Rate/1,000	3.3	1.6	1.6–3.3
Estimated WNV Prevalence	0.3–7.8	0.2–4.9	0.2–7.8
Culex tarsalis	1915	2018	3933
Ochlerotatus dorsalis	1627	1776	3403
Aedes vexans	1241	871	2112
Culeseta inornata	1557	747	2304
Other or Unknown	233	487	720
Total	6573	5899	12472

Table 2. Mosquito larval samples taken opportunistically and at nine established locations sampled weekly from 1 June−15 September. Detections indicate presence of *Culex tarsalis* larvae.

	Weekly		Opportunistically		Total	
Year	# positive larval detection (n)	%	# positive larval detection (n)	%	# positive larval detection (n)	%
2016	4 (144)	2.8	3 (55)	5.5	7 (199)	3.5
2017	5 (144)	3.4	2 (106)	1.9	7 (250)	2.8

Table 3. Types and frequencies of water bodies sampled for and found containing *Culex tarsalis* larvae from 1 June–15 September 2016 and 2017 in Butte and Harding counties, South Dakota.

Water Type	% of water samples (n=449)	% of water type samples containing *Culex tarsalis* larvae
Natural river habitats	33	3
Natural wetlands	4	6
Stock ponds/stock dams	49	2
Culverts/irrigation ditches	2	33
Ephemeral water	7	3
Stock tanks	6	0

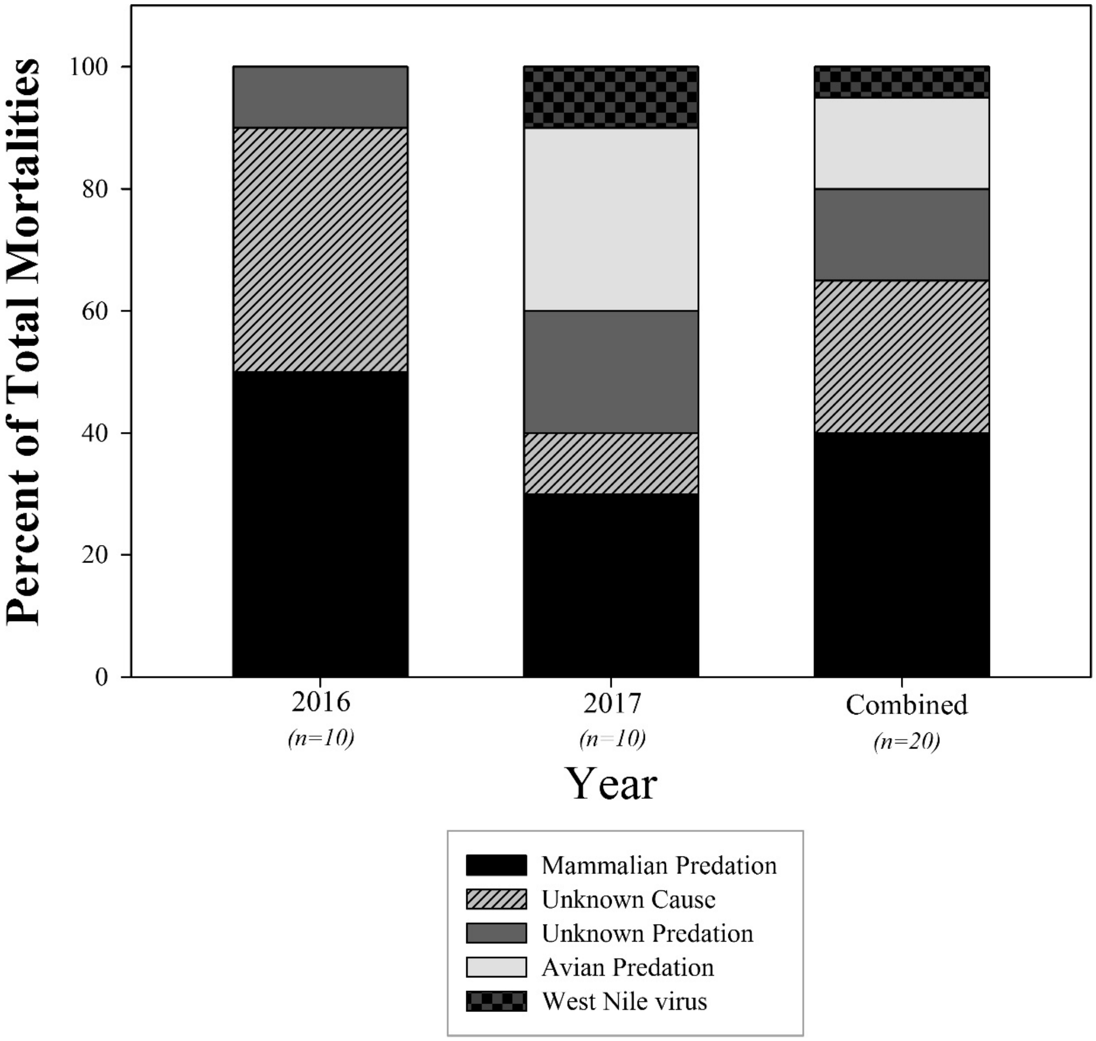

Figure 3. Cause-specific mortality rates in female sage-grouse for 2016 and 2017.

CHAPTER 3: GREATER SAGE-GROUSE SURVIVAL AND CAUSES OF MORTALITY DURING THE REPRODUCTIVE SEASON

ABSTRACT

We modeled adult female greater sage-grouse (*Centrocercus urophasianus*; n=74) survival during the reproductive seasons of 2016 and 2017 using known fate survival models in Program MARK. Our survival estimates indicated that survival during the reproductive season (1 April−15 September) was 0.68 (95% CI= 0.56–0.78). Survival varied temporally with lower survival during the nesting season compared to other periods during the reproductive season. Other covariates considered included female age and year; however, neither was informative. Cause-specific mortality was difficult to verify due to the possibility of post-mortem scavenging. However, mammalian predators were the leading suspected cause of mortality (40%), followed by unknown (25%), avian predation (15%) and unknown predation (15%), and West Nile virus (5%). Our findings are similar to previous sage-grouse survival and cause-specific mortality conclusions for South Dakota.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus;* hereafter sage-grouse) are relatively long-lived and put less effort into annual reproduction than other upland game birds (Bergerud and Gratson 1988, Shroeder et al. 1999, Connelly et al. 2011). To increase fitness, long-lived species reduce annual reproductive effort during unfavorable conditions in favor of increasing survival and the prospect of future reproduction (MacArthur and Wilson 1967). Most upland gamebird species' populations rely heavily on production and survival of offspring (Peterson and Silvy 1996, Wisdom et al. 2000, Clark et al. 2008). However, adult female survival has been shown to be a primary population driver for sage-grouse (Johnson and Braun 1999, Sedinger 2007, Dahlgren 2009, Taylor et al. 2012), and other Galliformes as well (Sandercock et al. 2005, McNew et al. 2012). Using a range-wide assessment of multiple vital rates, Taylor et al. (2012) found that female survival, chick survival, and nest success were, respectively, the most important vital rates for sage-grouse population growth.

Female sage-grouse annual survival rates vary from 16–77% range wide (Wallestad 1975, Wik 2002, Zablan et al. 2003, Hausleitner 2003, Holloran 2005, Swanson 2009, Sedinger et al. 2011, Blomberg 2013b). Previous research indicates yearling sage-grouse have higher annual survival than adults (Wallestad 1975, Zablan et al. 2003, Hausleitner 2003, Holloran 2005, Taylor et al. 2012); however, others have noted no difference or mixed findings when assessing age-specific survival (Swanson 2009, Blomberg 2013b).

Survival varies by season. Generally, over winter survival is high (Schroeder et al. 1999, Wik 2002, Hausleitner 2005, Swanson 2009, Blomberg et al. 2013b) except in instances of extreme weather events causing high mortality (Moynahan et al. 2006, Anthony and Willis 2009). Nesting and brood rearing occur during the spring and summer; during this time, survival can be lower compared to other seasons (Connelly et al. 2000a, Moynahan et al. 2006). Alternatively, some research has documented sage-grouse experience the lowest seasonal survival during late brood rearing/fall, followed by the nesting season (Wik 2002, Swanson 2009, Blomberg et al. 2013b, Davis et al. 2014). In these cases, West Nile virus (WNV; Swanson 2009), and sage-grouse harvest (Wik 2002) were impacting sage-grouse survival. Additionally, females that successfully raise a brood are more susceptible to mortality after a lag-time, and therefore, mortality associated with successfully reproducing may not occur until late brood rearing/fall (Blomberg et al. 2013b, Davis et al. 2014). Blomberg et al. (2013b) suggested this phenomenon may be caused by; decreased body condition (Hanssen et al. 2005), delayed molt (Dawson et al. 2000), use of risky habitats (Connelly et al. 2011b, Hagen 2011) or risky behavior (Schroeder 1999).

Predation has been identified as the primary cause of mortality for most gallinaceous birds (Bergerud and Gratson 1988), including sage-grouse (Schroeder et al. 1999, Connelly et al. 2000a, Blomberg et al. 2013a, Davis et al. 2014). Previous research in South Dakota support predation as the primary cause of adult sage-grouse mortality (Swanson 2009) and have documented annual survival of female sage-grouse in the Dakotas to vary between 0.41–0.78 (Swanson 2009). However, in 2006 and 2007, lower than average adult sage-grouse survival (0.44 and 0.46 respectively) occurred between July–October and coincided with suspected WNV outbreaks in those years (Swanson 2009). This suggests that WNV may have an additive effect to sage-grouse mortality during outbreak years (Taylor et al. 2013), which could place South Dakota sage-grouse populations at increased risk of extirpation.

Our study had two primary objectives. First, we characterized and assessed individual sources of sage-grouse mortality including contributions of predation and WNV. Second, we estimated female sage-grouse survival during the reproductive season and characterized variation in survival among biologically relevant time periods during the reproductive seasons of 2016 and 2017.

METHODS

STUDY AREA

Our study took place in Harding and Butte counties of northwest South Dakota. The total area of both counties combined is 12,805 km^2. Land use in the study area is dominated by pastureland (>85%), followed by cropland (10−12%; USDA 2012). Over 84% of Butte and Harding counties has never been plowed (Bauman 2018). The majority of the land in the study area is privately owned (~75–80%; USGS GAP 2016). Annual average temperatures range from -1.7°C–10.6°C with an average of 39 cm of precipitation annually (NOAA, 2019).

Our study area represents the eastern edge of the sagebrush distribution where an ecotone between sagebrush steppe and grassland ecosystems occurs (Johnson 1979, Cook and Irwin 1992, Lewis 2004). Sagebrush communities found in South Dakota are shorter and have a lower percent canopy cover than found elsewhere in the sagebrush steppe (Kantrud and Kolgiski 1983, Connelly et al. 2000b, Kaczor et al. 2011). Common shrubs in the study area include silver sagebrush (*Artemisia cana*) and big sagebrush (*Artemisia tridentata*; Johnson and Larson 2007).

FIELD METHODS

We captured breeding-age female sage-grouse near active leks March−May, and at high sage-grouse use areas in August and September using nocturnal spotlighting and a long-handled net (Giesen et al. 1982, Wakkinen et al. 1992). We aged and sexed captured sage-grouse based on morphological characteristics and plumage (Crunden 1963, Beck et al. 1975, Bihrle 1993). We fit each captured female sage-grouse with a 21.6 g necklace-type Very High Frequency (VHF) radio-transmitter (model A4060, Advanced Telemetry Systems, Isanti, MN, USA) and a uniquely numbered aluminum butt-end leg band (National Band & Tag Company). Radio-transmitters were equipped with an eight-hour mortality switch. We weighed all birds at the time of capture to ensure that radio-transmitters were less than 3% of body mass (Kenward 2001). All animal handling procedures were approved by the Institutional Animal Care and Use Committee at South Dakota State University (IACUC approval # 15-074A).

We used telemetry data to obtain known fate estimates of breeding season survival and mortality. We located female sage-grouse ≥ 2 times per week by homing throughout the breeding season from 15 April–15 September (Samuel and Fuller 1996, Fuller and Fuller 2012). Locations were fixed using either a hand-held 3-element Yagi antenna or via a fixed-wing aircraft equipped with a 2 element, “H” type, antenna on each wing. During peak WNV season (15 June−15 September), VHF signals were monitored daily to detect mortality signals.

If a sage-grouse radio-transmitter signal was detected on mortality mode, the sage-grouse was recovered immediately, and cause of death was investigated. We assumed predation occurred if portions of the carcass were consumed. Also, we assumed predation occurred if no carcass could be found, but the collar was removed with evidence of a struggle nearby such as blood on collar and numerous feathers. We differentiated mammalian predation from avian predation based on characteristics found at mortality site. If bite or chew marks were present on bones or collar, or if the carcass was buried, we assumed mammalian predation. If feathers were plucked, head was severed, and/or bones and collar did not display chew/bite marks, we assumed avian predation. Daily monitoring of sage-grouse reduced bias associated with lag-time in recovery of corpses in determining true cause of mortality (Bumann and Stauffer 2002, Stevens et al. 2011). If the mortality occurred during the WNV season, any tissues available (intestines, proventriculus, liver, kidney, lung, heart and brain) were recovered and frozen until being sent to Cornell University Animal Health Diagnostic Center where they were tested for presence of WNV using a Reverse Transcriptase-PCR Assay (Shi 2001).

SURVIVAL ANALYSIS

We used known-fate models in Program MARK (White and Burnham 1999) with the logit-link function and staggered entry design (Pollock et al. 1989) to estimate survival. Individuals were considered to have equal survival probabilities regardless of interval in which they entered the study. Models were evaluated using Akaike's Information Criterion corrected for sample size (AIC_c; Burnham and Anderson 2002). Models within 2 ΔAIC_c units from the top model were considered candidate models. We included an intercept only model in both model sets to evaluate relative model fit and explanatory power. An intercept only model represents constant survival over all time intervals, and no effect of additional covariates. Models that did not outcompete the intercept only model were not considered competitive models.

Due to the nature of our data and time intervals, all models were inherently nested. Although time intervals were combined with one another, or allowed to fluctuate with time, survival was estimated for each time interval in all models. We examined our candidate model set for uninformative parameters by calculating 85% confidence intervals around β parameter estimates; if 85% confidence intervals overlapped 0, the variable was deemed uninformative (Arnold 2010) and model candidacy was re-evaluated. If model-selection uncertainty existed, all models within 2 ΔAIC_c units of the top model were averaged to generate full model averaged estimates and standard errors (Burnham and Anderson 2002). We did not conduct a Goodness of Fit test because with known-fate data, the saturated model axiomatically fits the data perfectly; and thus, there are no methods to estimate deviance of the saturated model (Cooch and White 2016).

To facilitate comparison with previous survival analyses in South Dakota, we used biologically relevant time periods established by Swanson (2009) with slight modifications. The seasons used in our analysis included; pre-nesting (1 Apr–21 April), 2), nesting (22 April–9 June), early brood-rearing (10 June–28 July), and late brood-rearing (29 July–15 September). Over 75% of incubation during our study occurred during the specified nesting time period. Of all female sage-grouse included in analysis, 19% had broods at some point during early brood-rearing. We stopped monitoring broods at seven weeks old; for most this occurred before 29 July. Therefore, we could not estimate how many female sage-grouse had broods during the late brood-rearing season. We separated the brood-rearing period into two seasons, early and late due to differences in food requirements and behavior during these periods (Peterson 1970, Berry and Eng 1985, Drut et al. 1994, Hannon and Martin 2006). We evaluated a model considering nesting and non-nesting seasons being distinct from one another; non-nesting season included pre-nesting, early brood-rearing, and late brood-rearing. Individual covariates included in model set 2 were: age (adult or yearling), and year (2016 or 2017).

We constructed 2 sets of candidate models: model set 1 quantified temporal differences in survival among and within specified time periods (pre-nesting, nesting, early and late brood-rearing). We tested constant survival within each time period (.), time dependent survival within each time period (t), and we also tested combined time periods ($\geq$2 time periods equal to one another). Model set 2 quantified the influence of individual covariates on sage-grouse survival. We used the best approximating model from model set 1 (model with lowest AIC_c score) as the underlying structure for all models in model set 2 to account for maximum variation in the data (Burnham and Anderson 2002, Hill et al. 2003, Grovenburg et al. 2012).

RESULTS

We included 74 individuals (47 adults and 27 yearlings) in our survival analysis (2016=28, 2017=46) over a total of 24, seven-day intervals. We right-censored individuals that left the study area and were never relocated (n=6), or if the radio-transmitter failed (n=1).

In the 2016 reproductive season (1 April–15 September), we monitored a total of 29 radio-collared females. Two of the radio-collared females were right-censored due to leaving the study area (n=1), and radio-collar failure (n=1). Eleven mortality events occurred, however, one occurred within seven days of capture and therefore, was censored from survival analysis (White and Garrott 1990, Kenward 2001). The remaining 10 mortalities were the result of; mammalian predation (50%), unknown predation (10%), and unknown causes (40%; Figure 1).

During the 2017 reproductive season (1 April–15 September), we monitored a total of 47 radio-collared females. Five radio-collared females left the study area and were right-censored. Eleven mortality events occurred, one of which was classified as capture related and thus, was censored from survival analyses (Kenward 2001, White and Garrott 1990). The remaining 10 mortalities were attributed to; mammalian predation (30%), avian predation (30%), unknown predation (20%), West Nile virus (10%), and unknown causes (10%; Figure 1).

Combining both reproductive seasons, mammalian predation was the leading cause of mortality during this time (40%), followed by unknown sources of mortality (25%), avian predation (15%), unknown predation (15%), and lastly West Nile virus (5%; Figure 1).

SURVIVAL

We observed model uncertainty within our first model set (Table 1). However, we used the top model as the underlying structure for model set 2. Neither of the additional covariates from model set 2 (age or year) significantly contributed to explaining additional variation. Therefore, we solely used model set 1 to calculate survival estimates. We considered four models as competing models (<2 ΔAIC_c units from 0; Table 1). All four candidate models contained informative parameters (all parameters had 85% CI's that did not overlap 0). Also, all four candidate models indicated constant survival within each time interval, however, the combinations of time intervals differed. All four models indicated highest survival during pre-nesting.

Using model averaged estimates of each time period's real function parameter estimates, we estimated survival at 0.68 (95% CI= 0.56–0.78) for the period from 1 April–15 September. To directly compare survival during each time interval, we calculated weekly survival estimates. Weekly survival during estimates were; pre-nesting=1.0 (95% CI= 0.99–1.0), nesting 0.98 (95% CI=0.96–0.99), early brood rearing = 0.98 (95% CI= 0.97–0.99), and late brood rearing 0.98 (95% CI= 0.97–0.99). We estimated survival for each time interval by extrapolating weekly survival estimates to the length of each time interval. Estimated survival during the three-week pre-nesting time interval was 0.99 (95% CI= 0.97–1.00; three weeks). We observed no mortality events during the three-week pre-nesting season; which could result in inflated error estimates. The remaining time intervals were seven weeks long; estimated survival during nesting was 0.85 (95% CI=0.74–0.92), early brood rearing was 0.90 (95% CI= 0.81–0.95), and late brood rearing was 0.89 (95% CI=0.80–0.94; Figure 2).

DISCUSSION

Our overall estimate of a female surviving the reproductive season (1 April–15 September) was 68%. If we assume high overwinter survival, which has been documented in the Dakotas previously (Swanson 2009), or survival rates similar to what was observed during our reproductive season throughout the other seasons, then our annual survival estimates would be within the range of estimates documented across the sage-grouse distribution (16−77%; Wallestad 1975, Wik 2002, Hausleitner 2003, Zablan et al. 2003, Holloran 2005, Swanson 2009, Sedinger et al. 2011, Blomberg 2013b). More specifically, our annual estimates would also be within the range of survival documented in previous studies in the Dakotas during 2005–2007 (41–78%; Swanson 2009).

We found that survival was lowest during nesting, when a majority of nest incubation was occurring. This finding is similar to other studies where female sage-grouse incur higher mortality than other times of the year (Connelly et al. 2000a, Moynahan et al. 2006). During nesting, female sage-grouse are contending with multiple stressors, both internal (nutritional demands) and external (predation). Although less than 1% of female sage-grouse die on the nest (Bergerud and Gratson 1988), hesitation to flush from nest, less mobility during egg laying and incubation, highly active feeding while on incubation breaks, and risky behavior such as distraction displays can cause increased mortality during this time period (Svedarsky 1988, Bergerud and Gratson 1988). Plasma protein and albumin levels have been documented to be lowest 17 May–22 June (Dyer et al. 2009), indicating a nutritional deficit during nesting. Additionally, immediately upon hatching, gallinaceous females and broods have increased detection by predators due to increased movement, sound, and scent (Svedarsky 1988) and the habitats required by young broods may lead to less concealment of the brooding female (Christenson 1970, Maxson 1977, Begerud and Gratson 1988).

Our finding of lowest survival during nesting contradicts research documenting lowest survival during late brood rearing (Wik 2002, Swanson 2009, Blomberg 2013b, Davis 2014). However, we did not detect severe impacts of WNV. Parsons (2019; Chapter 2), quantified the prevalence of WNV in mosquitoes within our study system during this time (minimum infection rate of 1.6–3.3/1,000 mosquitoes), and documented WNV levels were not high enough to cause an epizootic event in sage-grouse during this study. Additionally, although South Dakota had a limited sage-grouse harvest in 2016, the dates of the season were outside of our survival intervals. Therefore, we could not quantify the impacts of harvest on survival. However, all harvested sage-grouse were required to be reported and checked by officials, and none of the radio-collared females were harvested.

Predation was the leading cause of mortality for sage-grouse in Butte and Harding counties, South Dakota. Up to 70% of female mortalities (11% of all monitored sage-grouse included in analysis) in 2016 and 2017 were attributed to predation. Similarly, predation was the leading cause of adult sage-grouse mortality in the main sage-grouse range in Idaho and Nevada (Connelly et al. 2000a, Blomberg et al. 2013a). It seems that sage-grouse on the eastern fringe of the range are experiencing the same primary cause of mortality (predation) found in the main range.

Although predation impacts to breeding age female sage-grouse could be detrimental to populations in certain scenarios, it has not been considered a limiting factor to sage-grouse populations elsewhere (Connelly and Braun 1997, Flake et al. 2010, Hagen 2011). Effects of predation and habitat are undeniably intertwined (Braun 1998) and managing for quality habitat can mitigate predation on prairie grouse (Hamerstrom et al. 1957). Often times management recommendations include improving habitat to reduce the effect of predation (Braun 1998, Schroeder and Baydack 2001).

For sage-grouse in particular, adult survival has been declared as a fairly unmanageable vital rate (Schroeder and Baydack 2001). Sage-grouse life history favors survival in any given year over reproduction and thus, adult survival is likely to have a high elasticity (Heppel et al. 2000, Sæther and Bakke 2000, Taylor et al. 2012). Typically, vital rates with high sensitivities and elasticities are buffered against variability

(Gaillard et al. 1998, Mills 2012). This combination of factors makes it difficult to manage adult female survival for sage-grouse. Nevertheless, adult female survival is an important vital rate for this species and thus, it should be monitored and documented whenever possible. These baseline data can help gauge future impacts to fringe populations including; habitat alterations, oil and gas development, and disease outbreaks.

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Table 1. Survival models of greater sage-grouse in northwestern South Dakota and USA, 2016–2017, from model set 1.

Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	K[e]	Deviance
{Pre(.),Nest(.)=EBR(.)=LBR(.)}	203.64	0.00	0.27	2	199.63
{Pre(.), Nest(.), EBR(.)=LBR(.)}	204.10	0.45	0.21	3	198.08
{Nest(.), Non-Nest(.)}	205.35	1.70	0.11	2	201.34
{Pre(.),Nest(.), EBR(.), LBR(.)}	205.48	1.84	0.11	4	197.45
{Pre(.),Nest(.)=EBR(.),LBR(.)}	205.65	2.01	0.10	3	199.63
{S(.)}	205.91	2.27	0.09	1	203.91
{Pre(.)=Nest(.),EBR(.)=LBR(.)}	207.49	3.85	0.04	2	203.48
{Pre(.)=Nest(.)=EBR(.), LBR(.)}	207.84	4.19	0.03	2	203.83
{Pre(.)=Nest(.), EBR(.), LBR(.)}	208.87	5.23	0.02	3	202.85
{Pre(t),Nest(.),EBR(.),LBR(.)}	209.51	5.87	0.01	6	197.45
{Pre(.),Nest(.),EBR(.), LBR(t)}	210.21	6.57	0.01	10	190.03
{Pre(.)=Nest(.)=EBR(.), LBR(t)}	212.53	8.89	0.00	8	196.41
{Pre(.),Nest(t),EBR(.),LBR(.)}	212.98	9.34	0.00	10	192.80
{Pre(.),Nest(.),EBR(t),LBR(.)}	213.19	9.55	0.00	10	193.01
{S(t)}	229.96	26.32	0.00	24	180.95

[a] Pre = Pre nesting season (1 April–21 April), Nest = nesting season (22 April–9 June), EBR = early brood rearing season (10 June–28 July), LBR = late brood rearing season (29 Jul–15 Sept), Non-Nest= Pre-nesting, early brood rearing and late brood rearing, (.) = constant survival, and (t) = time-dependent survival in weekly intervals, "=" time intervals were set equal to one another

[b] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[c] Difference in AIC_c relative to minimum AIC_c.

[d] Akaike weight (Burnham and Anderson 2002).

[e] Number of parameters.

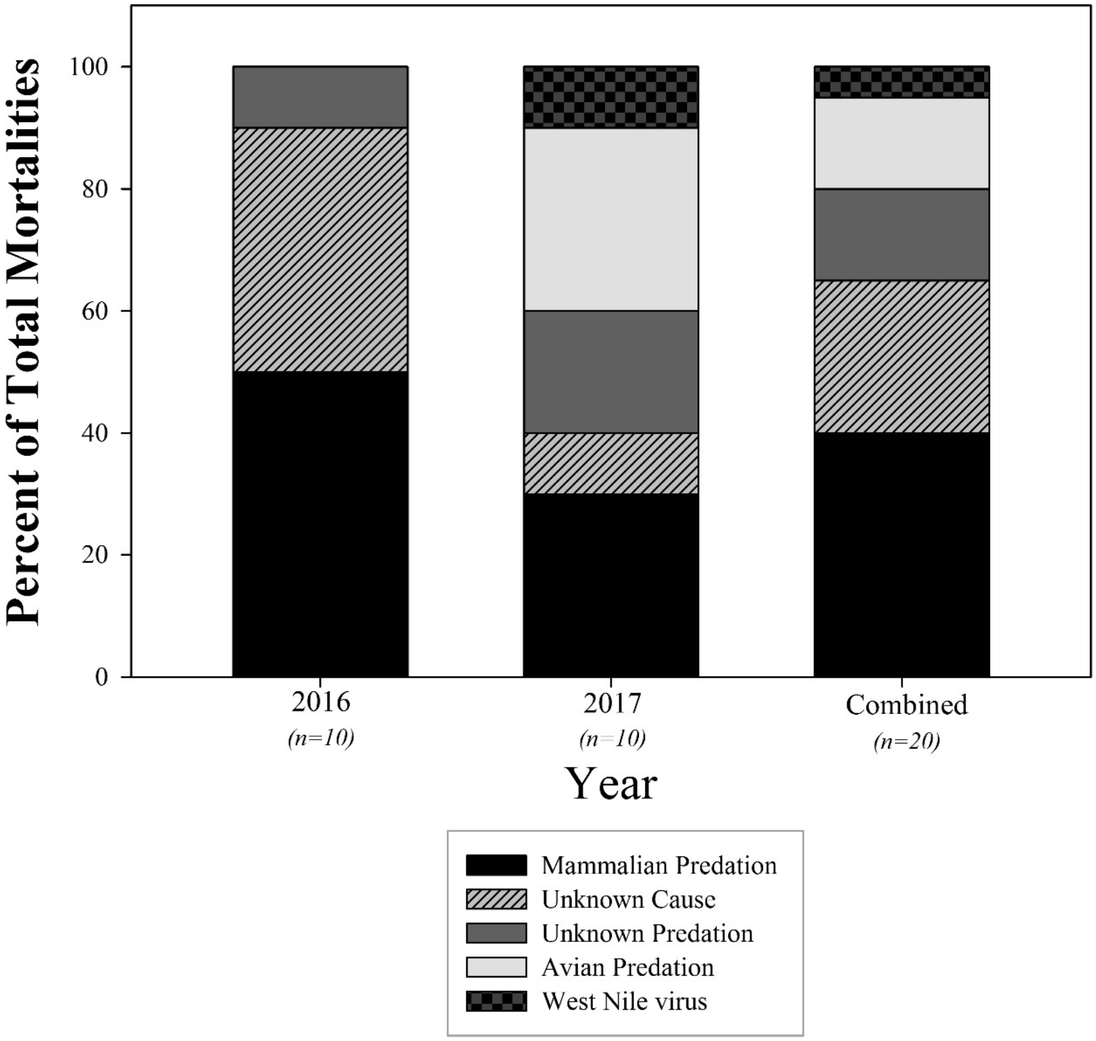

Figure 1. Cause-specific mortality rates in female sage-grouse for 2016 and 2017.

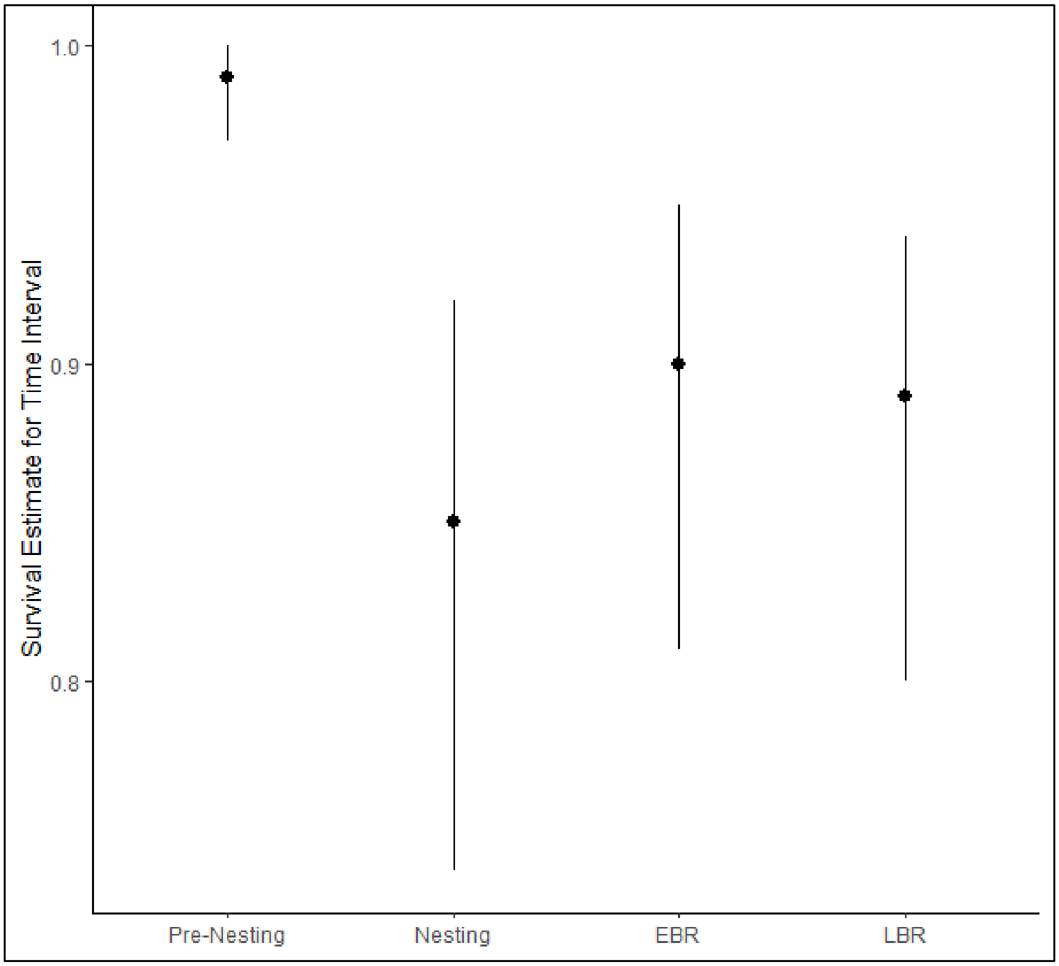

Figure 2. Model averaged survival estimates for each time period within the reproductive season. Pre-nesting (1 April–21 April; three weeks), Nesting (22 April–9 June; seven weeks), Early brood rearing (10 June–28 July; seven weeks), Late brood rearing (29 July–15 September; seven weeks).

CHAPTER 4: COMPARING SIMPLE AND COMPLEX METHODS USED TO DEFINE PRIORITY MANAGEMENT AREAS FOR GREATER SAGE-GROUSE IN SOUTH DAKOTA

ABSTRACT

Wildlife managers delineate priority areas for species to define critical habitat and to prioritize management effort. Each method used to identify priority habitat involves data that can be unavailable or expensive to obtain. Therefore, it is of interest to determine how efficient simple methods are compared to more complex methods in terms of defining areas that encompass areas used by the species of interest. South Dakota is at the periphery of the distribution for greater sage-grouse (*Centrocercus urophasianus*), and sage-grouse are listed as a species of greatest conservation need in the state. South Dakota Department of Game, Fish and Parks delineated a Core Sage-Grouse Area within the state using: 6.4 km buffers around active leks, high use areas, connectivity corridors and expert opinion. The designated core area encompasses 3,977 km^2, 95% of known nest locations, 92% of breeding season locations, and 99% of winter locations in South Dakota. We created priority areas for sage-grouse in South Dakota using two alternative methods: 1) combined seasonal utilization distribution models, and 2) combined seasonal resource selection function (RSF) models. We compared these methods and priority areas generated from them to the current designated Core Sage-Grouse Area in South Dakota. Using combined utilization distributions from spring/summer (1 April–15 September), winter (1 November–28 February), and a lek buffer encompassing 90% of known nest-sites (n=150), we developed a priority area encompassing 5,410 km^2. This area includes 100% of known spring/summer and winter locations, as well as 100% of known nests. Seasonal RSF models (spring/summer, winter, and nest-site) allowed us to predict areas

of high use during each season. We generated a map identifying areas predicted to be used ≥ 90% in all three seasons; it encompasses 1,143 km^2. All three methods overlapped in terms of defined priority areas (21%–100%). Specifically, the area of predicted use (≥ 90%) in all three seasons was 100% within and 96% within the combined seasonal Utilization Distribution and current South Dakota Core Area, respectively. Also, the current Core Sage-Grouse Area for South Dakota and combined seasonal utilization distribution core areas overlapped 70% and 96%. We recommend updating South Dakota's Core Sage-Grouse Area to the core area we created using combined seasonal utilization distributions, which encompasses 100% of the areas of predicted to be used (≥ 90%) in all three seasons (identified using RSFs). Our more complex methods created a more encompassing core area for sage-grouse in South Dakota, but it is crucial to note that the simpler methods currently used by South Dakota Game, Fish and Parks, sufficiently encompassed sage-grouse nests and multi-season use. In data poor systems, the simpler methods used to define priority areas seem adequate but conservative. Our newly recommended core area created using combined seasonal utilization distributions may be more socially and politically acceptable due to the fact that it is purely data driven. Wildlife managers should consider the constraints of their data before selecting a method to use for prioritizing habitat. When data are limited, lek buffers, expert opinion, and connectivity corridors suffice to encompass >90% of known use. However, if adequate location and habitat data are available, estimates of known use and modeled resource selection can be used to develop data driven estimates of areas predicted to be selected for and used by sage-grouse.

INTRODUCTION

Limited resources and an increasing need for conservation has created a push towards defining and prioritizing areas of high conservation value (Groves et al. 2002). Particularly when taking a species-centric approach to conservation, areas where a particular species can persist long-term are sought out to be identified and prioritized (Margules and Pressey 2000). Various methods have been used to define priority areas, which vary depending on scale being assessed (Poiani et al. 2000).

One common method that can be implemented with minimal data is the use of conservation buffers placed around known areas of importance (Burke and Gibbons 1995, Jorgensen et al. 2000, Qui 2010, Manier et al. 2014). Another commonly used method is modeling resource selection and prioritizing areas based on high levels of predicted use/selection (Johnson et al. 2004, Rachlow and Svancara 2006, Fedy et al. 2014). Although less common, priority areas also can be estimated directly from location data via utilization distributions (UDs; Sawyer et al. 2009).

One species that has warranted great efforts to define priority habitats is the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse). The sage-grouse is a sagebrush (*Artemisia* spp.) obligate species (Wallestad and Eng 1975), which has experienced population declines over the past several decades (Connelly et al. 2004, WAFWA 2015). Currently, the sage-grouse distribution is 56% of the estimated pre-settlement distribution (Shroeder et al. 2004).

Defining priority areas has become increasingly important for this species and has been completed at multiple scales. On a continent–wide scale, the Sage-Grouse

Conservation Area was defined using the historical distribution of sage-grouse and including a 50 km buffer; this area was used in a range-wide conservation assessment (Connelly et al. 2004, Shroeder et al. 2004).

At smaller scales, when information is limited, using breeding season location data to generate core areas suffices to encompass a high percentage of summer and winter locations as well as breeding season use (Fedy et al. 2012). Fedy et al. (2012) recommended modeling seasonally explicit habitat selection within the sage-grouse distribution. There are multiple methods for identifying seasonally explicit habitat selection. Occurrence models along with risk models have been used to identify highly selected sage-grouse habitats (Aldridge and Boyce 2007, Dzialak et al. 2011). Landcover type within an Ecological Niche Factor Analysis has been used to identify and map suitable sage-grouse brood rearing habitat (Atamian et al. 2010). Modeling resource selection using resource selection functions (RSFs; Manly et al. 2002) has become a common method for identifying priority areas for sage-grouse (Doherty et al. 2008, Carpenter et al. 2010, Fedy et al. 2014).

For example, in Wyoming, lek locations and lek attendance data were used to map core sage-grouse breeding areas using kernel density functions (Doherty et al. 2010a and 2011). These kernel density functions, along with the most likely dispersal routes (connectivity corridors) and winter concentration areas modeled using RSF models were used to delineate core areas (State of Wyoming 2015). A North Dakota core sage-grouse area was defined by examining breeding densities (Doherty et al. 2010a) and placing an 8.5 km buffer around all active leks (Robinson 2014).

Similarly, Montana defined a core sage-grouse area by calculating male density using two methods; 1) using a 6,440 m moving window analysis with highest male counts; and 2) using a fixed kernel density estimator on the average highest male counts at leks. Once sage-grouse density was determined, areas were constrained to a 10 km buffer around active leks with few exceptions. Then, suitable and unsuitable habitats were identified by modeling (Montana Natural Heritage Program) and areas were included or excluded as necessary. Expert opinion, telemetry data, and re-location data indicating connectivity corridors (Smith et al. 2013) further refined Montana's Sage-Grouse Conservation Area (MT FWP 2014).

Sage-grouse in South Dakota are on the eastern fringe of the current sage-grouse distribution (Shroeder et al. 2004). Adjacent to South Dakota's sage-grouse distribution, are sage-grouse populations in North Dakota, Montana, and Wyoming. Currently, the South Dakota population is genetically contiguous with the population in southeast Montana and southwest North Dakota (Cross et al. 2016), but data indicate that immigration and emigration are low (Swanson 2009).

South Dakota Game, Fish and Parks delineated a core sage-grouse area for the state of South Dakota, which was created using; a buffer of 6.4 km around all active leks, known high use areas, known or expected sage-grouse movement corridors, and expert opinion (SD GFP 2014). This core area is thought to encompass >90% of sage-grouse nests in South Dakota (Kaczor 2008, SD GFP 2014).

Using conservation buffers around leks is a common method for defining priority areas (SD GFP 2014, MT FWP 2014, Robinson 2014, State of Wyoming 2015).

However, adequate buffer distances are highly variable. In western Wyoming, Idaho, and South Dakota, >90% of nests were within 8.5 km, 3 km, and 6.4 km, respectively, of an active lek (Wakkinen et al. 1992a, Holloran and Anderson 2005, Kaczor 2008, SD GFP 2014). Aldridge and Boyce (2007) suggested that >90% of source habitats occur within ~10 km of lek sites and therefore, buffers that are <10 km may not be sufficient for encompassing brood rearing and nesting habitats.

Several assumptions must be met for conservation buffers to create an adequate priority area for sage-grouse. The first assumption is that by encompassing leks and a majority of nests, other important seasonal and life stage requirements also are included within the buffered area. Secondly, lek detection must be high, and third, nest-lek distances are stable. In South Dakota the relatively low number of sage-grouse leks and recent efforts to detect new or shifted leks using aerial surveys with and without forward looking infrared cameras suggest that lek detection is likely high (Travis Runia, SD GFP, *personal communication*).

Ultimately, the data available to wildlife managers determines the methods that may be used to identify priority areas. Although additional data may allow for creation of more accurate and precise conservation areas, it may be expensive or unfeasible to obtain. Therefore, we compared conservation areas created using all possible data (data rich) as well as limited data (data poor) methods to determine if simpler methods used to derive conservation buffers in data poor systems can result in efficient conservation areas. More specifically, we compared the simpler methods currently used to define priority areas for sage-grouse in South Dakota to two more complex methods of defining priority areas for sage-grouse conservation in South Dakota. Assessment included total area identified within conservation area, number of known nests included, and number of known locations included.

METHODS

STUDY AREA

This study was focused in Harding and Butte counties in northwest South Dakota. The total area of both counties is 12,805 km^2. Land use in the study area is dominated by pastureland (>85%), followed by cropland (10−12%; USDA 2012). Over 84% of Butte and Harding counties has never been plowed (Bauman 2018). A majority of the land in the study area is privately owned (~75–80%; USGS GAP 2016). Annual average temperatures range from -1.7°C–0.6°C with an average of 39 cm of precipitation annually (NOAA, 2019).

Our study area represents the eastern edge of the sagebrush distribution where an ecotone between the sagebrush steppe and grassland ecosystems occurs (Johnson 1979, Kantrud and Kologiski 1983, Cook and Irwin 1992, Lewis 2004, Smith et al. 2004, Johnson and Larson 2007). Sagebrush found in South Dakota are shorter and have a lower percent canopy cover than those found elsewhere in the sagebrush steppe (Kantrud and Kolgiski 1983, Connelly et al. 2000, Kaczor et al. 2011). Common sagebrush species in the study area include silver sagebrush (*Artemisia cana*) and big sagebrush (*Artemisia tridentata*; Johnson and Larson 2007).

FIELD METHODS

We captured breeding-age female sage-grouse near active leks March–May, as well as at high sage-grouse use areas in August and September 2016–2017 using nocturnal spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992b). We aged and sexed captured sage-grouse based on morphological characteristics and plumage (Crunden 1963, Beck et al. 1975, Bihrle 1993). We fit each captured female sage-grouse with a 21.6 g necklace-type Very High Frequency (VHF) radio transmitter (model A4060, Advanced Telemetry Systems, Isanti, MN, USA) as well as a uniquely numbered aluminum butt-end leg band (National Band & Tag Company). We weighed all birds at the time of capture to ensure that radio-transmitters were less than 3% of body weight (Kenward 2001). All animal handling procedures were approved by the Institutional Animal Care and Use Committee at South Dakota State University (IACUC approval # 15-074A). Additionally, we used sage-grouse location data from 2006 and 2007 collected using similar methods (Swanson 2009, Kaczor et al. 2011), which included breeding age male and female locations as well as juvenile locations.

Sage-grouse were located ≥1 times per week from 15 April–15 September using the homing method (Samuel and Fuller 1996, Fuller and Fuller 2012) with a hand-held 3-element Yagi antenna or via fixed-wing aircraft equipped with a 2 element, “H” type, antenna on each wing.

CURRENT METHODS USED BY SOUTH DAKOTA GAME, FISH AND PARKS

Techniques utilized by South Dakota Game, Fish and Parks to create the South Dakota Core Sage-Grouse Area in 2014 (SD GFP 2014) included; creating a 6.4 km buffer around all active leks in South Dakota (SD GFP 2014) and using expert opinion to include connectivity corridors and delineate known high use areas. In South Dakota's Core Sage-Grouse Area, active leks were considered those with ≥ two males in at least one of the previous five years.

QUANTIFYING KNOWN UTILIZATION

Commonly used for estimating home ranges, UDs were first defined by Van Winkle (1975) as the probability of re-locating an animal in a given place at any time. UDs can be developed by creating a bivariate normal fixed kernel estimate of a probability density around known animal locations (Worton 1989). Home range estimates are a contour surrounding a given percentage (e.g., 95% or 50%) of the underlying probability density distribution.

To use UDs to generate priority areas two assumptions must be met. First is the assumption that radio-collared individuals are a representative sample of the population's space use. This is particularly important for sage-grouse that are highly associated with lek locations; in order to have space use around a lek represented, it must have individuals captured and radio-collared from it or have individuals that are already radio-collared move to it. Second, individuals should be located at relatively equal time intervals and in relatively equal frequencies to one another. Equal time intervals for tracking allow for an unbiased estimate in terms of changes in movement within a season. UDs are created on an individual basis; however, if certain individuals are not tracked as frequently as others due to; access, land cover, land use, or another factor, bias could be introduced when individual UDs are summed.

We prioritized areas of known use by sage-grouse by generating lek buffers to encompass nests, and calculated UDs for individuals during two seasons; spring/summer (1 April–15 September) and winter (1 November–28 February). We used the fixed-kernel method implemented via Home Range Tools 2.0 (Rodgers et al. 2015) for ArcGIS with sage-grouse tracking data to calculate probability density maps. UDs were calculated for each individual by creating a bivariate normal fixed kernel estimate of the probability density around each location. To be included in UD analysis, individuals were required to have $\geq$ 20 locations from 1 April–15 September to be included in spring/summer analysis, and $\geq$ 10 locations from 1 November–28 February to be included in winter analysis. If applicable, nest locations were only included once in the location data even if multiple locations were obtained while the female was incubating. Each individual was only included one year even if the individual was present during multiple years of data collection. In addition, each individual was limited to two locations per seven-day time interval.

To avoid over-smoothing, which would result in a positive bias in the probability density estimates, we used a rule based *ad hoc* smoothing parameter ($h_{ad\ hoc}$) by choosing the smallest increment of the reference bandwidth (h_{ref}) that resulted in a contiguous 95% kernel home range (Worton 1989, Kie 2013). The reference bandwidth (h_{ref}) was decreased by increments of 10% of (h_{ref}), until the most efficient smoothing parameter could be determined (i.e., $h_{ad\ hoc} = 0.90 \times h_{ref}$, $0.80 \times h_{ref}$, $0.70 \times h_{ref}$ etc.; Klaver et al. 2008, Grovenburg et al. 2012, Kie 2013). However, since ($h_{ad\ hoc}$) is not allowed to be larger than (h_{ref}; Kie 2013), if the 95% home range was fragmented at (h_{ref}), then (h_{ref}) was accepted as the smoothing parameter.

Each individual's UD was generated at its full extent, which sometimes included areas of estimated utilization in Montana and North Dakota. Subsequently, each individual's UD was clipped to the South Dakota state boundary after creation. Individual UDs were merged across the study area using the Raster Calculator Tool in ArcGIS to generate a single figure representing cumulative utilization of the landscape during each season. To delineate priority areas within each season, we created an isopleth including 90% and 99.9% of the estimated utilization using the Contour Tool within the Spatial Analyst package in ArcGIS for both seasons. After isopleth creation, we merged the spring/summer 99.9% isopleth polygon to the winter 99.9% isopleth.

The maps created from summed individual UDs and contoured at 99.9% may overestimate the area being "utilized". If certain individuals have a dispersed UD, with large distances between locations, there are small probabilities of relocation within each pixel between locations. Thus, when contoured at such a high percentage, those areas are included. Alternatively, summed UDs that are contoured at 90% could be biased due to individuals with dispersed UDs being excluded because only more extreme values are outlined. For example, an individual with a UD encompassed within a small area would have higher pixel values within that area; whereas an individual with a dispersed UD would have more pixels, but all would have lower values. The individual with a dispersed UD might not have any pixels in the top 90% of values contoured. Therefore, to minimize bias against certain individuals, we used the 99.9% contour, which represents all individuals included in UD analyses.

Because we created UD estimates for used locations during spring/summer and winter seasons, we also wanted to include known nest-sites. Therefore, we calculated the distance from active leks that encompassed 90% of nest locations. We calculated distance to lek using leks known to be active in the year the nest was documented and buffered the lek locations such that ≥ 90% of nests were contained within the buffered region. We combined the nest-lek buffer layer with the combined 99.9% UD isopleths to generate a final priority area based on known utilization estimates.

MODELING LANDSCAPE USE-RESOURCE SELECTION FUNCTIONS

If RSF models and relative predicted probability of use maps are used to create priority habitat delineations, several assumptions set forth by Manly et al. (2002) must be met. First, uniquely identified individuals are random, and a representative sample of the population. Second, relocations of individuals are independent in time. Third, individuals and their selection of resources are independent of each other. Fourth, habitat availability is constant over the study area and is known. Fifth, accuracy of location data is within the range of model co-variates. Sixth, important variables to selection are selected and distribution of variables remains constant. Lastly, remote sensed data accurately represent variables on the landscape.

We prioritized areas using RSFs for nest-site, spring/summer (1 April–15 September), and winter (1 November–28 February) selection. We sought to create RSF models that assessed 3rd order selection; selection of points within the home range (Johnson 1980). We implemented the use/available design, design II (nest-site selection), and design III (spring/summer and winter selection models) defined by Manly (2002). In design II, resources used are assessed at an individual level, but availability of resources is quantified at a population level whereas in design III, both used and available resources are quantified at an individual level (Manly 2002).

VARIABLES AND VARIABLE SELECTION

We developed landscape variables that were biologically relevant to sage-grouse habitat selection using the Spatial Analyst package in ArcGIS. Variables of interest included; lek locations, sagebrush, forest, water, roads, ruggedness, and undisturbed (unplowed) land (Table 1).

Although not specifically a habitat variable, we considered that sage-grouse may select resources based on the locations of leks, specifically during the breeding season and when selecting a nest-site. The hotspot hypothesis of lek evolution states that quality nesting habitat is located in closer proximity to leks than expected at random (Schroeder and White 1993, Gibson 1996, Aldridge and Boyce 2007, Doherty et al. 2010b); also, leks seem to establish within or adjacent to nesting habitat (Connelly et al. 2000). Therefore, we used lek locations as a proxy for quality habitat.

Lek count data was acquired from South Dakota Game, Fish and Parks. Active leks were defined for each of four years during which data were collected (2006, 2007, 2016, and 2017). Leks were considered active if ≥ 1 male was observed displaying. We assigned lek data to each individual sage-grouse based on leks that were active in the year they were monitored. In final prediction maps, all leks that were considered active from 2006–2018 were used.

A data layer representing roads included both paved and gravel (SD DOT 2018, MT State Library 2019, Wyoming DOT 2019). Ruggedness of the landscape was quantified by using the Benthic Terrain Modeler Toolbox (Wright et al. 2005) in ArcGIS with the National Elevation Dataset (Gesch et al. 2002).

We used the Native Lands Data Layer (Bauman et al. 2018), which discriminates between land that has been plowed and land that has not. We considered unplowed land to be “undisturbed” and plowed land to be “disturbed”. Wyoming big sagebrush (*Artemisia tridentata wyomingensis)* communities take ≥ 30 years to re-establish after disturbance such as burning (Harniss and Murray 1973, Wambolt et al. 2001, Lesica et al. 2007). However, it has been shown that plowed sagebrush can re-establish rather quickly (within 15 years) due to an available seed source and elimination of competition (Wambolt and Payne 1986). This data layer alone, does not distinguish between land that has been plowed and remains as non-sagebrush, and areas that were once plowed and contain regenerated sagebrush. Additionally, these data represent land that was plowed, and does not take into account other methods of sagebrush removal that might have occurred (e.g., spraying, burning, chaining). Thus, to explore the response of sage-grouse to historically and currently plowed lands, we included the Native Lands Data Layer as a variable.

We included land cover attributes extracted from the 2011 National Land Cover Database (NLCD; Homer et al. 2015) including sagebrush (NLCD Shrubland Products; USGS 2017), water, and forest (NLCD 2011). The NLCD Shrubland Products, percent sagebrush data layer (NLCD Shrubland Products; USGS 2017) has been shown to accurately represent the presence of sagebrush in South Dakota, but is inaccurate at predicting sagebrush canopy coverage (Parsons et al. *In Review*). Therefore, the percent sagebrush layer was re-classified in ArcGIS to reflect presence or absence of sagebrush in each 30 m pixel. Water was identified by combining classes in the NLCD ("Open Water" + "Woody Wetlands" + "Emergent Herbaceous Wetlands"). Forest was identified by combining landcover classes from the NLCD ("Deciduous Forest" + "Evergreen Forest" + "Mixed Forest").

Although we assumed that each variable included in this analysis was influential to sage-grouse resource selection, we were uncertain of which form of the variable was most informative (i.e., distance to feature or density/percent of feature). Therefore, we created both distance metrics to each variable (with the exception of ruggedness) as well as mean values at multiple scales (Carpenter et al. 2010, Fedy et al. 2014). All layers were initially generated at a 30 m grain size.

We followed the methods of Fedy et al. (2014) and generated variables of interest at five scales (0.006 km^2, 1 km^2, 7.07 km^2, 32.17 km^2, and 138.67 km^2), which have been shown to be biologically relevant to sage-grouse (Holloran and Anderson 2005, Aldridge and Boyce 2007, Walker et al. 2007, Holloran et al. 2010, Carpenter et al. 2010, Doherty et al. 2010b, Fedy et al. 2012). We used a moving window analysis to calculate mean values or percentages within each neighborhood using the Focal Statistics Tool in ArcGIS. Neighborhood was defined as a circular buffer with a search radius corresponding to each biologically relevant scale (0.006 km^2;0.045 km radius, 1 km^2;0.564 km radius, 7.07 km^2;1.5 km radius, 32.17 km^2;3.2 km radius, and 138.67 km^2;6.44 km radius; Fedy et al. 2014). Values were extracted to each point after moving window analysis was complete. Because many of the winter locations were obtained from a fixed-wing aircraft, the location error was assumed to be greater than locations obtained from the ground during spring/summer and at nests. Therefore, the smallest scale (0.0006 km^2) was excluded in the winter models.

We calculated percentages within each radius for: forest, sagebrush, water, and undisturbed layers. We calculated mean values of ruggedness within each radius. Lek Density was created using the Point Density Tool in ArcGIS. Road density was calculated within each scale using the Line Density Tool in ArcGIS. Lek and road density estimates were calculated at the five scales previously mentioned by changing the search radius to match each scale (Table 1).

Distances to features were calculated using the Euclidean Distance Tool in ArcGIS. We also created exponential decay as a function of Euclidean distance (Carpenter 2010, Fedy 2014). The decay function formula was as follows: $e^{(-d/\alpha)}$ where d is the Euclidean distance to feature, and α is the value corresponding with each scale's search radius (0.045 km, 0.564 km, 1.5 km, 3.2 km, and 6.44 km). Decay distance functions allow a non-linear response to distance from features, and values range from 1–0. Areas near to features have higher values and as distance to feature increases, values reach 0. Distances at which values decrease more rapidly (thresholds) are dependent upon the scale's search radius used in the decay equation. Euclidean distances represent linear responses of distances from features and values continue to increase until extent of the study area is reached. Distance decay values are closer to 1 when near to the feature, as distance increases, values reach 0. Euclidean distance values are low when near to the feature and increase as distance to features increase. Therefore, interpretation of distance decay coefficients is opposite Euclidean distance coefficients. Distance decay variables were generated using the Raster Calculator Tool in ArcGIS. Euclidean distance and decay function distances were calculated for the following variables: leks, water, forest, sagebrush, undisturbed, and roads (Table 1).

Prior to model development, we z-standardized all variables. To determine the form and scale that best represents sage-grouse resource selection, we ran univariate models. Each variable had a model set that included all forms and scales. We evaluated univariate models using Akaike's Information Criterion corrected for small sample size bias (AIC_c; Burnham and Anderson 2002). The selected form/scale combination with the lowest AIC_c score was used to represent that variable in the final model set (Gregory et al. 2011; Aldridge et al. 2012, Fedy et al. 2014). This approach allows for a multi-scale model that can contribute to better model performance compared to single scale models (Graf et al. 2005). We ran all possible combinations of variables in final model sets.

We tested for correlations between all variables using a Pearson Product Moment correlation test. Variables were considered significantly correlated if ($r > |0.7|$). We tested for multicollinearity among variables in the final model set using variance inflation factors (VIF). We specified a null model to compare relativistic fit of subsequent models.

SPRING/SUMMER AND WINTER RESOURCE SELECTION METHODS

To model seasonal resource selection, we used generalized linear mixed-effect models (GLMMs) of the binomial family (Gillies et al. 2006, Koper and Manseau 2009) within the R package, lme4 (Bates et al. 2018). Using this method, individual sage-grouse are treated as random effects (random intercepts), and our variables of interest as fixed effects. By treating each individual sage-grouse as a random intercept, individual responses to variables can vary in magnitude (Gillies et al. 2006). Models were evaluated using Akaike's Information Criterion corrected for small sample size bias (AIC_c; Burnham and Anderson 2002).

For our spring/summer RSF models, we used data from breeding-age female sage-grouse. Sage-grouse form flocks during the winter (Eng and Schladweiler 1972, Beck 1977); although sexual segregation can occur, most large flocks consist of both sexes (Beck 1977; Carpenter et al. 2010). During winter, female and male sage-grouse are consuming the same primary diet, which is sagebrush (Patterson 1952, Dalke et al. 1963, Wallestad et al. 1975, Remington and Braun 1985). Therefore, to increase our sample size, we used male sage-grouse locations in addition to our breeding-age female locations in our winter RSF models. We also included juvenile sage-grouse locations because during fall/winter, juveniles become independent from their mother (Swanson 2009), their diet shifts to primarily sagebrush (Klebenow and Gray 1968, Peterson 1970), and flocks are intermixed across age (Swanson 2009).

We observed multiple sage-grouse migrating into Montana during the winter. Thus, we extended our area of assessment into Montana for winter models. We excluded the undisturbed layer for winter, because it did not extend outside of South Dakota. We also excluded leks and water, as we did not see biological relevance for including these variables during winter.

To determine available resources for spring/summer and winter RSF models, we used individual UDs as previously described. We created a 95% isopleth for each UD and considered this a 95% seasonal home range. The area within each 95% seasonal home range was considered available to the sage-grouse for which it was created. We systematically generated available points at 250 m intervals within each individual's 95% seasonal home range using the Create Fishnet Tool in ArcGIS. By systematically generating available locations, models may be approximated with fewer known locations compared to models with randomly generated availability (Warton and Shepherd 2010, Aarts et al. 2012). Consequently, the number of available points was not directly related to number of used points, rather the sampled area potentially available to each sage-grouse was proportional to the area of the 95% seasonal home range of each individual.

Models within the final model set were evaluated using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). We considered models within 2 ΔAIC_c units from the top model as candidate models. We examined our candidate model set for nested models including ≥ 1 additional parameter and essentially the same log likelihood (Burnham and Anderson 2002). Also, we tested for uninformative parameters by calculating 85% confidence intervals around parameter estimates; if 85% confidence intervals overlapped 0, the variable was deemed uninformative (Arnold 2010). If model uncertainty existed, all models within 2 ΔAIC_c units from the top model were averaged to generate full model averaged coefficient estimates and standard errors (Burnham and Anderson 2002).

We calculated and reported 95% confidence intervals around coefficient estimates using the profile likelihood method. To explore the amount of variation captured by our random effects (individual sage-grouse), we compared our top model to a simple logistic regression model that included the same data and variables but did not take into account individual effects. We did this by conducting a likelihood ratio test with an analysis of variance. We tested significance using a Chi-square test.

NEST-SITE RESOURCE SELECTION METHODS

To model nest-site selection, we used binary regressions, with the logit link in R. To avoid overfitting models resulting in a singular fit from comparing one nest-site to multiple random sites, we pooled nests and available locations. To meet independence assumptions, individuals only had one nest used in the analysis even if there were multiple nests occupied by one individual within a single year or across years (Holloran and Anderson 2005, Fedy et al. 2014). When multiple nests were documented for an individual, we randomly selected one nest to be used in analyses.

To determine availability for nest-site RSF models, we calculated the maximum distance observed from nest to lek and buffered all leks by that amount. The nest-lek distance was specific to the active leks during the year in which the nest was active. Following the methods of Fedy et al. (2014), we generated random points within the buffered area at a density of 1 point/km^2 with the minimum allowed distance between available points being 30 m. Available data points were removed from analyses if they fell outside of the extent of spatial variable data. If model uncertainty existed, all models within 2 ΔAIC_c units from the top model were averaged to generate full model averaged coefficients and standard errors (Burnham and Anderson 2002).

MAPPING RELATIVE PREDICTED PROBABILITY OF USE

We made seasonal maps in ArcGIS using all variables in the top model from each season’s model set. We applied standardized estimates to standardized variable layers. Using the logistic equation, we developed a map, which was bound by 0 and 1. However, no single pixel had the highest possible values for all variables, and therefore, our observed values were all < 1. We divided the map by the maximum pixel value observed so that each seasonal map was scaled 0–1. Although this is typically not necessary, it eases interpretation but more importantly, it allowed us to sum all three seasonal models and have each equally represented.

Additionally, we created categorical maps displaying areas in which 90% of seasonal use was predicted to occur. We calculated and identified this area using area adjusted frequencies. Specifically, we categorized the map into two “bins” based on raster values using the Re-classify Tool in ArcGIS. The utilization value is a function of the probability of use and includes the area within each bin (Johnson et al. 2006). We adjusted the cutoff RSF value between the two categories until 90% of utilization was estimated within a single bin.

To determine which areas were predicted to be used in multiple seasons, we summed the 90% predicted layers for spring/summer, winter, and nest-site. We added these layers using the Raster Calculator in ArcGIS.

MODEL VALIDATION

Many of the common methods used for evaluating logistic regression models (e.g., ROC, Hosmer Lemeshow goodness of fit, Kappa) are inappropriate for evaluating presence/available data (Boyce et al. 2002, Johnson et al. 2006). To validate our spring/summer and winter RSF models, we used out-of-sample validation techniques, which are suggested as an option for validation of use/available data (Boyce et al. 2002). Individuals were assigned to the out-of-sample dataset if they did not have the minimum number of locations required to generate a seasonal UD (≥20 or ≥10 locations for spring/summer and winter, respectively). To meet independence assumptions, none of the individuals were included in both training and out-of-sample datasets. In addition, locations from individuals used in the out-of-sample dataset only included one year, even if multiple years of location data were available.

Because our modeling approach using GLMM is conditional (individual based), we could have withheld a certain percentage of each individual's locations to validate our models (Koper and Manseau 2009). However, we elected to use new individuals in our out-of-sample dataset. By using this method, we were essentially testing whether our model created using selection preferences of individuals, could predict habitat selection of other individuals in the population. This approach indicates whether or not our model is robust in predicting habitat use at the population level using a conditional (individual based) approach. Although marginal (population level) estimates can be directly derived from conditional estimates, they can be biased (Agresti 2002). For validating our GLM nest-site models, we randomly withheld 29% of the nests from the training dataset for model validation (Huberty 1994, Fielding and Bell 1997).

We used model evaluation methods as described by Johnson et al. (2006). We used the quantile classification in ArcGIS to generate 5 ranked bins, each encompassing approximately the same amount of area (Koper and Manseau 2009). We calculated the utilization value for each bin as a function of the probability of use and the area within each bin. This value was multiplied by the number of locations in the out-of-sample dataset; this calculated value was number of observations expected per bin. Locations from the out-of-sample dataset were overlaid on the predicted probability of use map and the bin in which each was located was extracted using the Extract Values Tool in ArcGIS.

To compare observed vs. expected numbers of observations in each bin, we used linear regression, regressing observed and expected observations across five bins. We also used a Chi-square test comparing observed and expected numbers of observations (Johnson et al. 2006). We considered a model as valid if the following criteria were met: 1) slope of the regression line was significantly different than 0 and not significantly different from 1; 2) intercept was not significantly different from 0; 3) high r^2 value; and 4) non-significant Chi-square test. If these criteria were met, then the model was considered proportional to the probability of use (Johnson et al. 2006).

RESULTS

CURRENT METHODS USED BY SOUTH DAKOTA GAME, FISH AND PARKS

The current Sage-Grouse Core Area defined by South Dakota Game, Fish and Parks encompasses 3,977 km^2 (Figure 1; SD GFP 2014). Over 95% of known sage-grouse nests (n=150) are located within the boundaries of this core area. Approximately 93% of breeding-age female locations (n=2,475) during spring/summer were within the defined area. Of the winter sage-grouse locations in South Dakota, 99% (n=740) were within the current Sage-Grouse Core Area.

QUANTIFYING KNOWN UTILIZATION

We created spring/summer UDs for 73 female sage-grouse, characterizing 2,021 locations. The isopleth containing 99.9% of known utilization during spring/summer

(Figure 2) encompasses 4,084 km^2. Similarly, we created winter UDs for 45 individuals characterizing 529 locations. The isopleth encompassing 99.9% of estimated utilization (Figure 3) encompasses 3,737 km^2. To characterize areas of known nest-sites, we buffered active leks by a distance of 6 km. This buffer distance encompasses 90% of known nests (n=150; Figure 4). Total area encompassed by the lek buffer is 3,084 km^2.

To create a core area from known utilization estimates across seasons, we combined the 99.9% isopleths from the spring/summer and winter UDs, along with the 6 km lek buffer area (Figure 5), estimated to encompass 90% of known nest-sites. This combined utilized area encompasses 5,410 km^2. It also encompasses 100% of known nests (n=150), 100% of known breeding-age female spring/summer locations (n=2,475), and 100% of known winter locations (n=740). Approximately 70% of the combined known utilization core area overlaps with the current South Dakota Sage-Grouse Core Area.

MODELED RESOURCE SELECTION RESULTS

SPRING/SUMMER AND WINTER RESOURCE SELECTION

Our spring/summer training dataset had 2,021 data points representing 73 female sage-grouse. Our final model set included six variables (Table 2). All variables in the final model set had correlation coefficients $r < |0.7|$ and all VIF among variables were < 2.0.

We observed little model uncertainty in the spring/summer RSF model set. The top model included 6 of the 7 variables and the global model was the only other model within 2 ΔAIC_c units of the top model (Table 2). We selected the true top model as the best fit because it was the most parsimonious, and the only other model within 2 ΔAIC_c units of it contained one additional uninformative parameter (percent undisturbed within 1.5 km). We deemed this variable uninformative, as its 85% confidence interval overlapped zero (Arnold 2010).

Coefficient estimates from the top model (Table 3) indicate the strongest driver of this model was percent forest within a 1.5 km radius. Sage-grouse were avoiding forested areas, roads, and rugged terrain during spring/summer (Table 3 and Figure 6). Sage-grouse were selecting for areas that were close to active leks, water, and sagebrush (Table 3 and Figure 6); the top forms of these variables are all distance decay variables indicating a non-linear response to the distance from each feature, or the likely presence of a threshold. The distance at which responses decayed differed between variables; sagebrush and water have a relatively local effect on selection (0.564 km radius), whereas leks have a larger radius of impact on selection (3.2 km radius).

Results of the likelihood ratio test using ANOVA indicate there was significant model improvement ($P < 0.05$) by including individuals as random effects within the mixed effect model compared to the simple logistic regression model. This indicates that by accounting for individual variation in selection and availability, we developed a better model as compared to methods that assumed all areas were available to all individuals at all times.

Our model validation included 454 out-of-sample locations from 53 individuals. Slope of the regression line was 1.06; which was significantly > 0 ($P < 0.05$) but not significantly different from 1 (95% confidence intervals overlap 1; 0.92–1.20). Our intercept was not statistically different from 0. Results from the Chi-square test were non-significant ($P > 0.05$). This indicates that our number of observed locations is each bin was not significantly different from our expected number of locations in each bin. Adjusted r^2 value of the linear regression model was 0.99. Our spring/summer RSF model met all of the requirements to be considered a model that was proportional to the probability of use (Johnson et al. 2006) and therefore, we consider our spring/summer RSF model to be predictive of relative probabilities of sage-grouse space use during this season.

We constructed two maps to visualize the relative predicted probability of selection during spring/summer within our study area. The first was a continuous map (Figure 7), the second was a categorical map displaying areas predicted to be used 90% of the time during spring/summer (Figure 8). To test our predicted 90% use map, we used out-of-sample data (n=454); 86% of test locations fell within the predicted area. Therefore, we considered our categorical map (Figure 8) to be accurate in spatially predicting sage-grouse use during spring/summer.

Our winter training dataset had 529 locations from 45 individuals. The final model set included four variables (Table 4). All variables in the final model set had correlation coefficients $r < |0.7|$ and VIF among variables were all < 2.0.

We observed little model uncertainty in the final winter RSF model set. The top model included three of the four variables and the global model was the only other model within 2 ΔAIC_c units of the top model (Table 4). We selected the true top model as being the best fit as it was the most parsimonious, and the only other model within 2 ΔAIC_c

units contained one additional uninformative parameter (percent forest within 6.4 km). We deemed this variable uninformative, as its 85% confidence intervals overlapped zero (Arnold 2010).

During winter, sage-grouse exhibited selection for areas near sagebrush and avoided areas with high road density and rugged terrain (Table 5; Figure 9). The strongest predictor among the three variables in the top model was mean ruggedness within a 0.564 km radius.

Results of the likelihood ratio test using ANOVA indicated there was significant model improvement ($P < 0.05$) by including individuals as random effects within the mixed effect model compared to the simple logistic regression model. These results indicate that by using mixed effects models and thus accounting for individual variation in selection and availability, we developed a better model as compared to assuming all areas were available to all individuals. This indicates that there is significant variation among individuals in terms of selection; this variation is better explained using mixed effect models.

To validate our model, we used out-of-sample test data, which included 296 locations from 47 individuals. Slope of the regression line was 0.94; this slope was significantly different from 0 ($P < 0.05$) and not significantly different from 1 (95% confidence intervals overlap 1: 0.81−1.06). Our intercept was not statistically different from 0. Results from the Chi-square test were non-significant ($P > 0.05$). Adjusted r^2 value of the linear regression model was 0.99. Our winter RSF model can be considered a model proportional to the probability of use (Johnson et al. 2006) and therefore, we consider our winter RSF model to be a model that can predict relative probabilities of sage-grouse space use during winter.

We constructed two maps to visualize the relative predicted probability of selection during winter within our study area. The first was a continuous map (Figure 10), the second was a categorical map displaying areas predicted to be used 90% of the time during winter (Figure 11). To test our predicted 90% use map, we used out-of-sample data and 89% of test locations (n=296) fell within the predicted area. Therefore, we considered our categorical map (Figure 11) to be accurate in spatially predicting sage-grouse use during winter.

NEST-SITE RESOURCE SELECTION

We had a total of 104 independent nests for modeling. We used 74 for training and 30 for validation. If an individual had more than one nest, the nest we included in analysis was selected randomly (across years or nesting attempts).

Upon examination of our top univariate model results for each variable's form and scales, we observed two that exhibited perfect separation (ruggedness at 0.564 km scale, and percent forest within 1.5 km). To avoid using inflated coefficient estimates and possibly creating an overfitted model, we used the second AIC_c ranked form for both variables (ruggedness at 1.5 km, and distance decay from forest 0.564 km). These two variables had a correlation coefficient $r \geq 0.7$ and $VIF > 2.0$; therefore, we chose the variable with the lower AIC score from univariate model comparison, which was decay distance from forest at the 0.564 km scale.

There were four nest-site models within 2 ΔAIC_c units from the top model indicating high model uncertainty (Table 6). Consequently, we model averaged the top four models. Collectively, these four models had a combined model weight $w_i = 0.67$. Our model averaged coefficient estimates indicate a positive selection response to leks and percent undisturbed lands within a 3.2 km radius. Sage-grouse appear to avoid forest, high road density, and high percent water when selecting nest-sites (Table 7).

To validate our model, we used 30 out-of-sample nests. Slope of our regression line for our expected vs. observed nests within 5 bins was 1.24, which was significantly different from 0 ($P < 0.05$). The slope of the line was not significantly different from 1 (95% confidence intervals overlap 1), however, it is important to note that our 95% confidence intervals were rather large (0.34 – 2.14). Results from the Chi-square test were non-significant ($P>0.05$). The intercept was also not statistically different from 0. Adjusted r^2 value of the linear regression model was 0.82. Although the nest-site selection model did not validate as well as the spring/summer and winter RSF models, it met the criteria for being a model that describes proportional probability of use (Johnson et al. 2006), which also suggests that it is a valid model. We considered this model to be accurate in predicting sage-grouse nest-sites, but our out-of-sample size was small; therefore, as a secondary measure of validation, we tested the nest RSF model on all observed nests.

This secondary validation included all known nests in South Dakota (n=150); it included nests that were used in model building, initial testing, and some that were not included in either analysis due to lack of independence (re-nest attempts, nests from same individual in different years). Slope of the regression line was 1.22, significantly different from 0 and not significantly different than 1. Chi-square test was non-significant and our adjusted r^2 value was 0.84. This model was validated again when tested against all nests; we consider it to be accurate in predicting sage-grouse nest-sites in South Dakota.

We made two maps to visualize the relative predicted probability of use for nesting within our study area. The first was a continuous map (Figure 12), the second was a categorical map displaying areas in which 90% of nest-sites were predicted to fall (using area adjusted frequencies; Figure 13). To test our predicted 90% of use map, we used our out-of-sample data and 90% of test locations fell within the predicted area (n=30). As a secondary measure, we also tested how many total known nests were within the predicted area; 91% (n=150) were within the predicted area. Therefore, we assume our models are accurately representing areas likely to be used for nesting.

MULTI-SEASON PREDICTED USE

Our multi-season predicted use map (Figure 14) combines areas that are predicted to be used 90% of the time in winter, spring/summer and for nest-sites. It is summarized as areas predicted to be used 90% of the time in; one season, two seasons, all three seasons, or predicted to be used <10% of the time in all three seasons. When we combined all known spring/summer and winter locations and compared them to the multi-season predicted use area, 70% were within areas predicted to be used 90% of the time in all three seasons, followed by 22% predicted to be used 90% of the time in two of the three seasons evaluated; 5% and 2% of locations were within the areas predicted to be used 90% of the time in one season, and none of the seasons, respectively (n=3,943). Approximately 96% of the areas predicted to be used 90% of the time in all three seasons are within the current South Dakota Core Sage-Grouse Area (Figure 15) and 100% of the areas predicted to be used 90% of the time in all three seasons are within the core area developed using known utilization (Figure 16).

DISCUSSION

We captured known and predicted landscape use by sage-grouse in South Dakota using our more complex methods for defining priority areas. All three methods used to define priority habitat for sage-grouse in South Dakota contained a high amount of the documented sage-grouse locations. The core area we developed by combining seasonal utilization estimates (Figure 5) is the largest area but also the most inclusive in terms of encompassing; nests, spring/summer locations, winter locations, and predicted use during all seasons (Figure 16). We propose the area delineated from known utilization (Figure 16) be used as the new priority area for sage-grouse in South Dakota for numerous reasons. First, biologically, it encompasses all areas known and predicted to be used by sage-grouse in the three critical seasons evaluated. Secondly, socially and politically, it may be better accepted due to the fact that it is entirely data driven and therefore, does not include “expert opinion”, which can cause bias.

It is crucial to note that the simpler method used from the data poor system that resulted in the current Sage-Grouse Core Area in South Dakota is sufficient in encompassing a large amount of sage-grouse nests and known locations, while being smaller in size than the newly proposed core area (created from known utilization). In the future when data within this system are limited, or in other data poor systems, this method seems efficient in identifying areas important to sage-grouse year-round.

CURRENT METHODS USED BY SOUTH DAKOTA GAME, FISH AND PARKS

The methods used for defining the current South Dakota Core Sage-Grouse Area suffice to meet the goals set forth in the South Dakota Sage-Grouse Management Plan (2014). The only stated goal of the core area is that it is targeted at productive landscapes in a fraction of the sage-grouse distribution (SD GFP 2014). Over 90% of seasonal use was included in South Dakota's current core sage-grouse area, and of the three methods evaluated it is the smallest area. However, some areas of predicted high multi-season use were not included in South Dakota's current core area, suggesting that the current South Dakota Core Sage-Grouse Area is not adequate (Figure 15). One caveat is that if the South Dakota core area were to be updated to include a buffer around recently discovered leks, a majority of crucial areas would be encompassed. Therefore, the methods currently used are sound, valid, and are an adequate approach to define management areas when more detailed location, movement, and landscape data are out of date and/or not available.

QUANTIFYING KNOWN UTILIZATION

One of the major benefits of the core area developed from the combination of seasonal estimated utilization is that it is purely data driven and has no influence of "expert opinion". The use of expert opinion in wildlife conservation applications has been shown to be sensitive to differing opinions (Johnson and Gillingham 2004), over or underestimating importance of certain features (Clevenger et al. 2002), or expert disagreement (Yamada et al. 2003). Use of expert opinion should be avoided unless data to build statistical models is lacking (Pearce et al. 2001). When the current South Dakota

Core Sage-Grouse Area was created, adequate data (location data from Harding County, and modeled habitat selection) were lacking; now that additional data are available, future core areas in South Dakota should be data driven until the location data and modeled estimates are no longer valid due to changing landscapes and/or changing sage-grouse population dynamics.

MODELING LANDSCAPE USE

Some generalizations can be made about sage-grouse resource selection in response to certain landscape characteristics. There was consistently a positive response to sagebrush, leks, and undisturbed lands, when included in top seasonal models. There were consistently negative responses to forest, ruggedness, and roads when included in the top seasonal models.

Sage-grouse selected areas in close proximity to sagebrush during spring/summer and winter. During spring/summer adult female diet includes forbs and arthropods along with sagebrush (Wallestad and Eng 1975). Therefore, although sagebrush is an important diet component year-round, sage-grouse likely seek out areas with abundant forbs and arthropods that are within close proximity to sagebrush during spring/summer. During winter, sage-grouse exclusively consume sagebrush (Wallestad and Eng 1975) and use sagebrush for roosting (Eng and Schladweiler 1972); thus, it is expected sagebrush is positively correlated with selection during this time. For nest-site selection, sage-grouse selected areas with a high percentage of sagebrush at a large scale (6.44 km). Sage grouse typically select nest-sites that are under a sagebrush (Wallestad and Pyrah 1974) and based on our results, they are typically selecting for higher amounts of sagebrush at a large scale (within 6.44 km).

Leks were positively associated with sage-grouse resource selection during spring/summer and nest-site selection. There are two plausible reasons for this association. First, sage-grouse select nest-sites near to leks because leks are the “hub” of year-round activity (Eng and Schladweiler 1972, Wallestad and Pyrah 1974, Wallestad and Schladweiler 1974, Braun et al. 1977). This hypothesis was rejected by Wakkinen et al. (1992a) who found that sage-grouse select nest-sites randomly with respect to lek locations. The second possible reason for the positive association between sage-grouse resource selection and leks, is that the same landscape features are driving sage-grouse resource selection during spring/summer, at nest-sites, and at lek-sites. The similarity in features being selected or avoided would result in positive associations between leks and spring/summer and nest-site resource selection.

We found that sage-grouse select nest-sites in areas with higher amounts of unplowed land within 3.2 km. Although we did not distinguish lands that were once plowed and had regenerated sagebrush vs. lands that were once plowed and are currently non-sagebrush, our results indicate that sites that have never been plowed are more likely to be selected for nest-sites by sage-grouse.

Sage-grouse avoided forested areas during spring/summer and when selecting nest-sites. This phenomenon is well documented, as forests have been shown to have negative impacts on sage-grouse demographics (Casazza et al. 2011, Baruch-Mordo et al. 2013) as well as avoidance in all seasons elsewhere (Doherty et al. 2008, Atamian et al.

2010, Doherty et al. 2010b). Sage-grouse in South Dakota also avoided rugged terrain (within 564 m) during spring/summer and winter; this finding is corroborated by research conducted elsewhere through multiple seasons and life stages (Doherty et al. 2008, Doherty et al. 2010b, Baruch-Mordo et al. 2013, Harju et al. 2013).

Lastly, sage-grouse exhibited a negative response to road density in all three seasons. In spring/summer and for selecting nest-sites, sage-grouse avoided roads within 3.2 km, whereas during winter, sage-grouse avoided high road density at a smaller scale (564 m). Reasons for sage-grouse avoiding roads may be attributed to: noise (Blickley et al. 2012), increased risk of vehicle collision (Trombulak and Frissell 2000), infrastructure associated with roads such as signs, reflectors, fences, and powerline poles used as raptor perches (Manier et al. 2014, DeGregorio et al. 2014), or roads serving as travel corridors for predators (Lariviére and Messier 2000, Ruiz-Capillas et al. 2013).

Water exhibited changing responses between seasonal models. Water was not included in the winter model but had a positive response during spring/summer and negative response during nesting. During brood rearing, sage-grouse will select for more mesic areas, particularly if they have broods (Klebenow 1969, Wallestad 1971, Connelly and Markham 1983, Gates 1983, Connelly et al. 1988). Our spring/summer top model indicated a positive response to water; specifically, sage-grouse selected areas in close *proximity* to water. We found that sage-grouse were avoiding selecting nest-sites in areas with a higher *percent* of water at a 6.4 km scale. This seems contradictory to sage-grouse selecting for water immediately after hatch when they have broods. When selecting a nest-site, sage-grouse generally select xeric sites in sagebrush (Patterson 1952, Wallestad and Pyrah 1974). Based on our results, sage-grouse are not selecting areas with large *quantities* of water within 6.4 km such as reservoirs, rivers, or stock ponds. However, this does not imply that sage-grouse are avoiding all water sources or water sources are not within close *proximity* to nest-sites.

Our predicted 90% use maps for spring/summer and winter both suggest the eastern side of the study area should be selected by sage-grouse (Figures 8 and 11). However, this area does not currently encompass any known sage-grouse use (leks or documented sage-grouse locations; Figure 15 and 16). There are numerous non-mutually exclusive explanations. First, the sagebrush data we used was re-classified to represent presence; then represented as percent sagebrush pixels or distance to sagebrush pixel. It is possible that although there is sagebrush located in the area, it does not meet the height or canopy cover requirements for sage-grouse. With the data available to us, we cannot differentiate sagebrush suitability based on height or canopy cover. Second, the habitat and resources in those identified areas are suitable and not occupied. Because South Dakota's sage-grouse are a fringe population that has experienced range and population constriction through time, the identified areas might have become extirpated and have not become re-populated (Hanski 1998). Third, it is possible that sage-grouse select habitats that are located in close proximity to critical habitat that is used in other seasons. This could explain why the majority of our known sage-grouse locations (~92%) are near or within habitat identified to be used in all three seasons or at minimum two seasons (Figure 14).

MANAGEMENT IMPLICATIONS

Using multiple methods, we captured known and predicted landscape use by sage-grouse in South Dakota. All three methods used to define priority habitat for sage-grouse in South Dakota contained a high amount of the documented sage-grouse locations. Therefore, wildlife managers should consider the constraints of their data before selecting a method to use for prioritizing habitat. When data are limited, lek buffers, expert opinion, and connectivity corridors suffice to encompass >90% of known use. However, if adequate location data are available, estimates of known use (UDs) and modeled resource selection (RSFs) can be used to develop data driven estimates of areas likely to be selected for and used by sage-grouse. Using UDs, we were able to develop a core area for South Dakota, which is biologically and socially/politically justified. Additionally, information pertaining to the scales of selection and important biological variables identified in our modeling efforts can be used to determine threshold distances for potential disturbances to sage-grouse resource selection in South Dakota. Lastly, it is not recommended that trees be planted, roads be constructed, or sagebrush be plowed within existing high-quality habitat due to the avoidance of these features by sage-grouse.

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Table 1. Variables considered for use in all RSF model types (nest-site, spring/summer, winter).

Variable	**Scales**[a]	**RSF Models**[b]	**Definition**
Ruggedness	*a, b, c, d, e*	n, s, w	Heterogeneity of slope and aspect from the National Elevation Dataset
Road Density	*a, b, c, d, e*	n, s, w	Line density of roads (paved or gravel)
Road Distance	Decays *a, b, c, d, e,* and Euclidean	n, s, w	Distance to roads (paved and gravel)
Lek Density	*a, b, c, d, e*	n, s	Point density of active leks; values coincide with year UD was generated
Lek Distance	Decays *a, b, c, d, e,* and Euclidean	n, s	Distance to active lek; values coincide with year which UD was generated
Forest Percent	*a, b, c, d, e*	n, s, w	Percent forest within given scale
Forest Distance	Decays *a, b, c, d, e,* and Euclidean	n, s, w	Distance to forest
Water Percent	*a, b, c, d, e*	n, s	Percent water within given scale
Water Distance	Decays *a, b, c, d, e,* and Euclidean	n, s	Distance to water
Sage Percent	*a, b, c, d, e*	n, s, w	Percent sage within given scale
Sage Distance	Decays *a, b, c, d, e,* and Euclidean	n, s, w	Distance to sagebrush
Undisturbed Percent	*a, b, c, d, e*	n, s	Percent undisturbed within given scale
Undisturbed Distance	Decays *a, b, c, d, e,* and Euclidean	n, s	Distance to undisturbed land

[a] Scales at which each variable was created, each corresponds to the moving window radii; *a*=0.045 km, *b*=0.564 km, *c*=1.5 km, *d*=3.2 km, and *e*=6.44 km.

[b] RSF models where variable was used; n=nest-site, s =spring/summer, w = winter

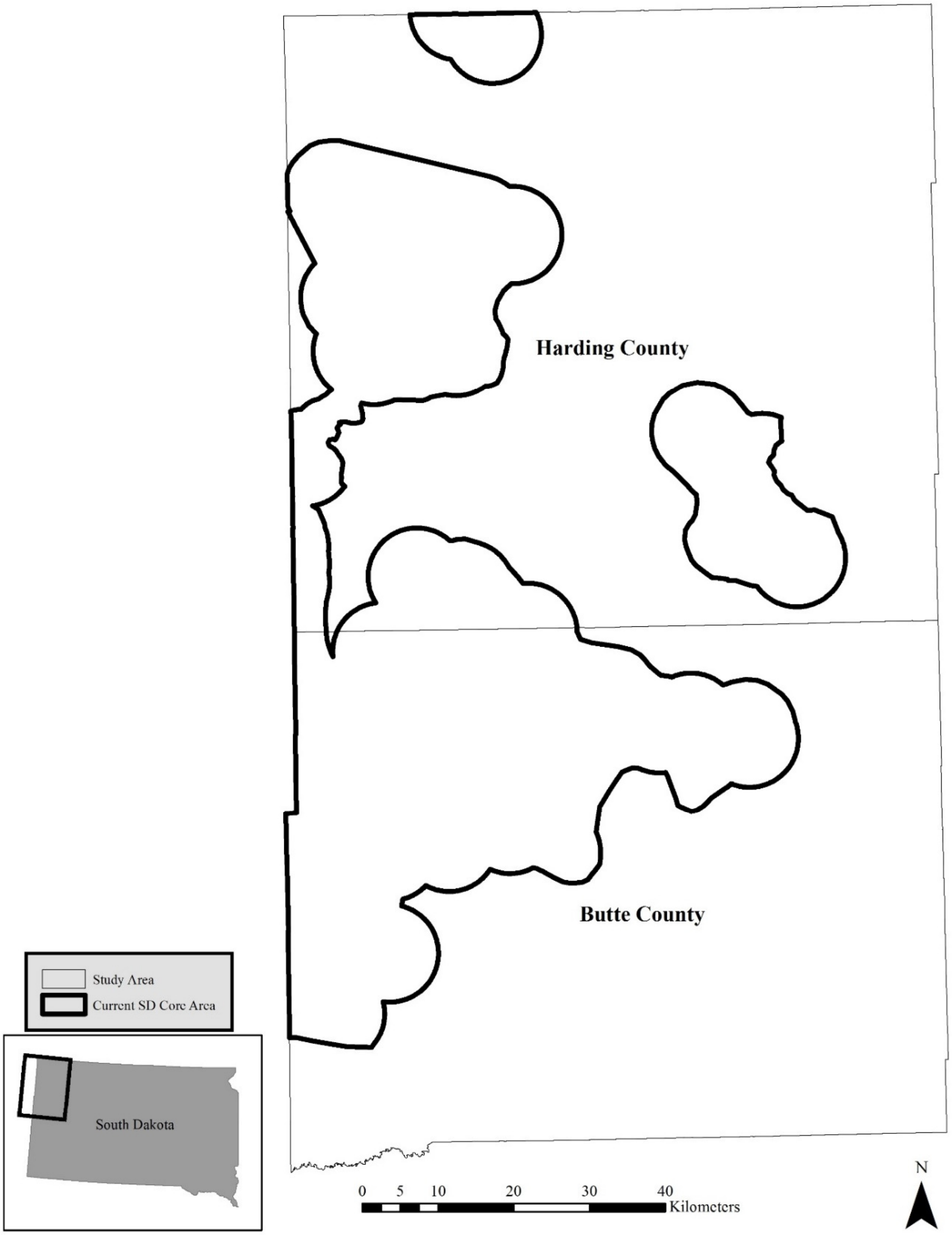


Figure 1. Current South Dakota Core Sage-Grouse Area. Defined by South Dakota Game, Fish and Parks, area encompasses 3,977 km^2 (SD GFP 2014).

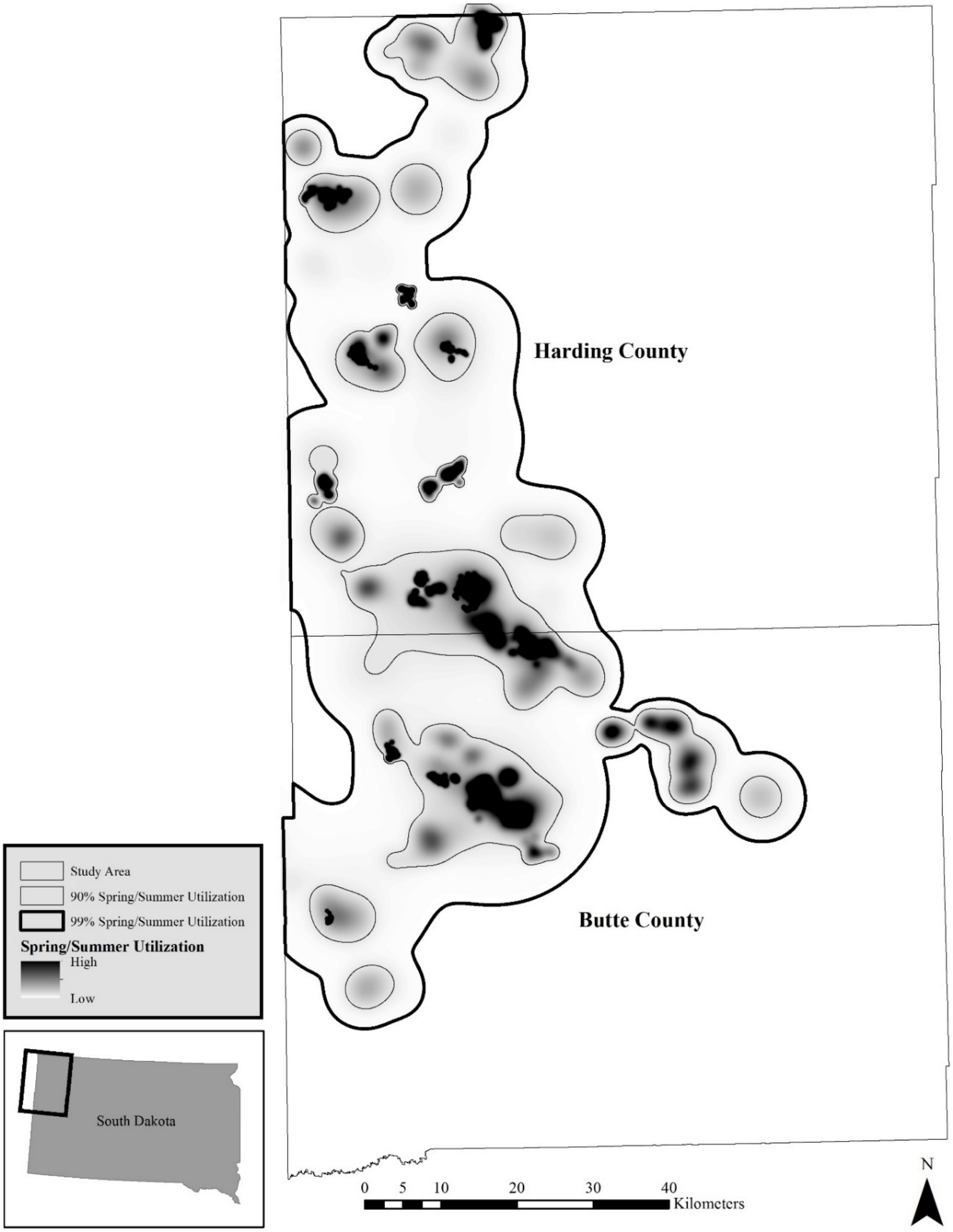


Figure 2. Spring/summer utilization distribution with 90% and 99.9% isopleths.

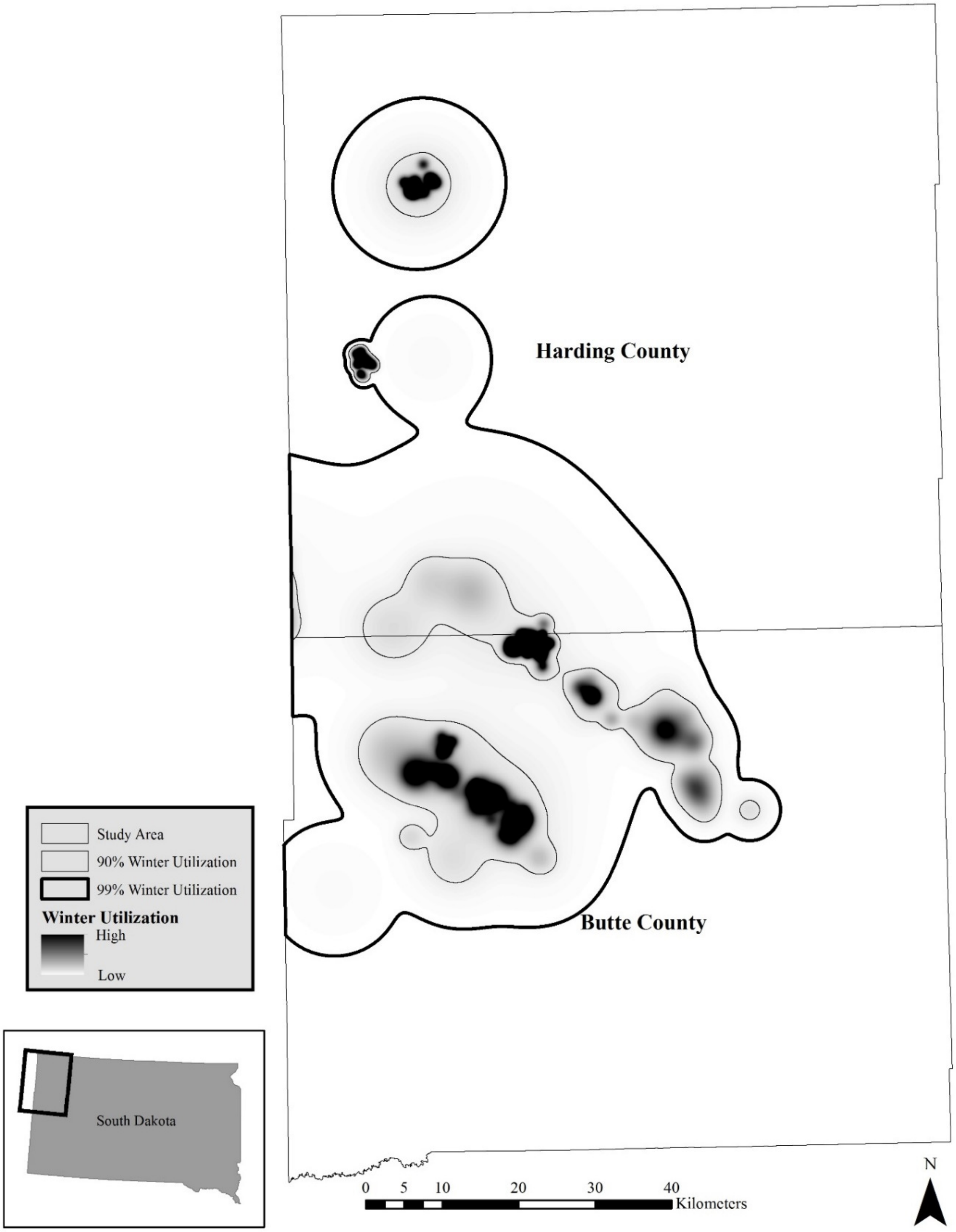


Figure 3. Winter utilization distribution with 90% and 99.9% isopleths.

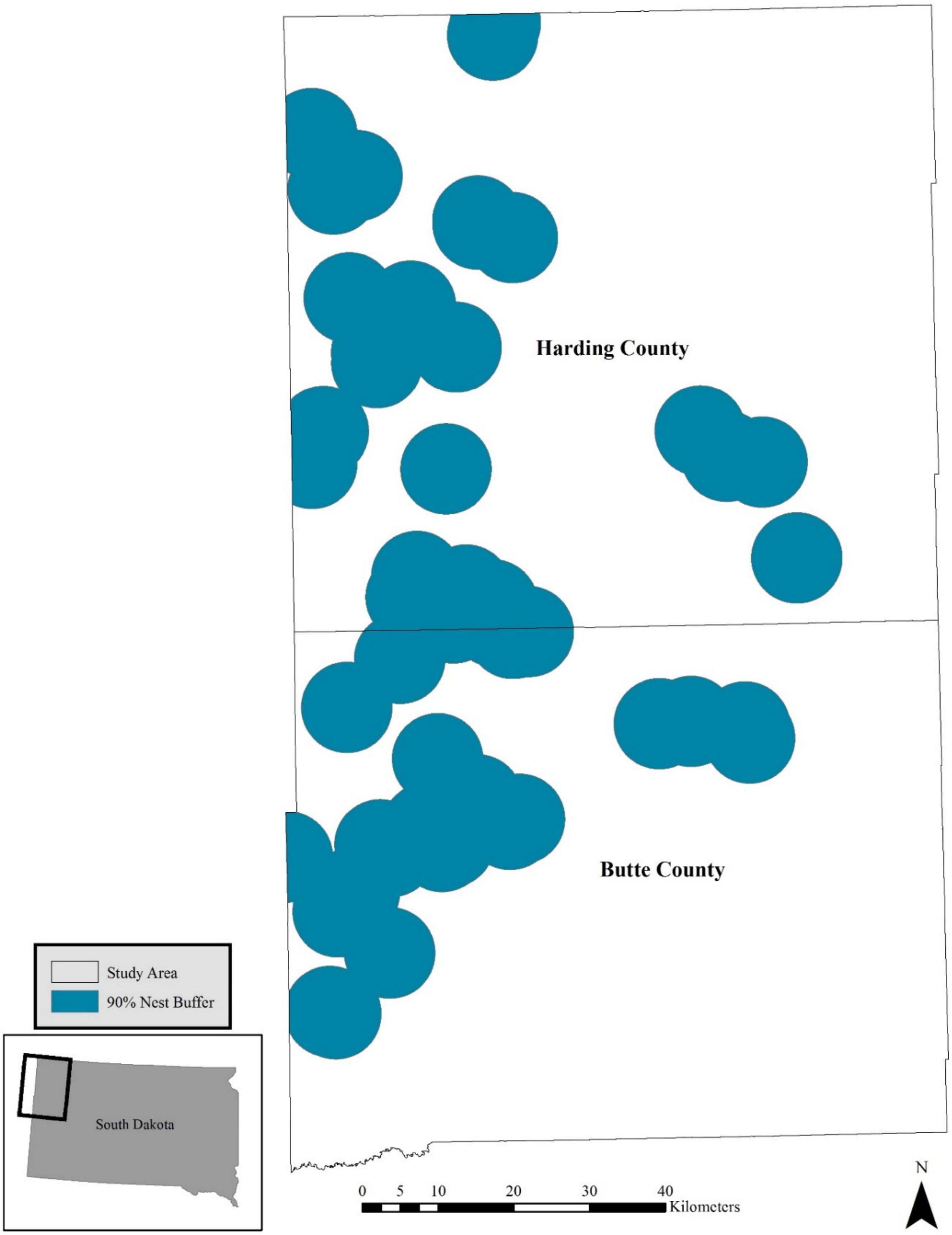


Figure 4. Lek buffer of 6 km. This area encompasses 90% of known nests in South Dakota (n=150).

Figure 5. Combined 99.9% isopleths from spring/summer and winter utilization distributions and 6 km lek buffer.

Table 2. Models for Spring/Summer RSF. Only top five models are presented, all possible combinations of seven variables were evaluated, as well as a null model (n=128).

Model[a]	***K***[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w_i***[e]	**−Log Likelihood**[f]
Lek_Dec3.2 + Sage_Dec0.564 + Water_Dec0.564 + %Forest1.5 + Road_Dens3.2 + Rug0.564	8	16,434	0	0.69	-8,208
Lek_Dec3.2 + Sage_Dec0.564 + Water_Dec0.564 + %Forest1.5 + Road_Dens3.2 + Rug0.564 + %Undisturbed1.5	9	16,435	1.6	0.31	-8,207
Lek_Dec3.2 + Sage_Dec0.564 + Water_Dec0.564 + Road_Dens3.2 + Rug0.564	7	16,457	23.0	0	-8,221
Lek_Dec3.2 + Sage_Dec0.564 + Water_Dec0.564 + %Undisturbed1.5 + Road_Dens3.2 + Rug0.564	8	16,458	24.5	0	-8,220
Lek_Dec3.2 + Sage_Dec0.564 + %Forest1.5 + Road_Dens3.2 + Rug0.564	7	16,483	48.9	0	-8,233

[a] Lek_Dec=Distance to lek with decay function, Sage_Dec= Distance to sagebrush with decay function, Water_Dec=Distance to water with decay function, %Forest=Percent forest, Road_Dens= Road density, Rug=Ruggedness, %Undisturbed= Percent. Numbers following variables represent moving window radii (km).

[b] Number of parameters

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC$_c$ relative to minimum AIC$_c$

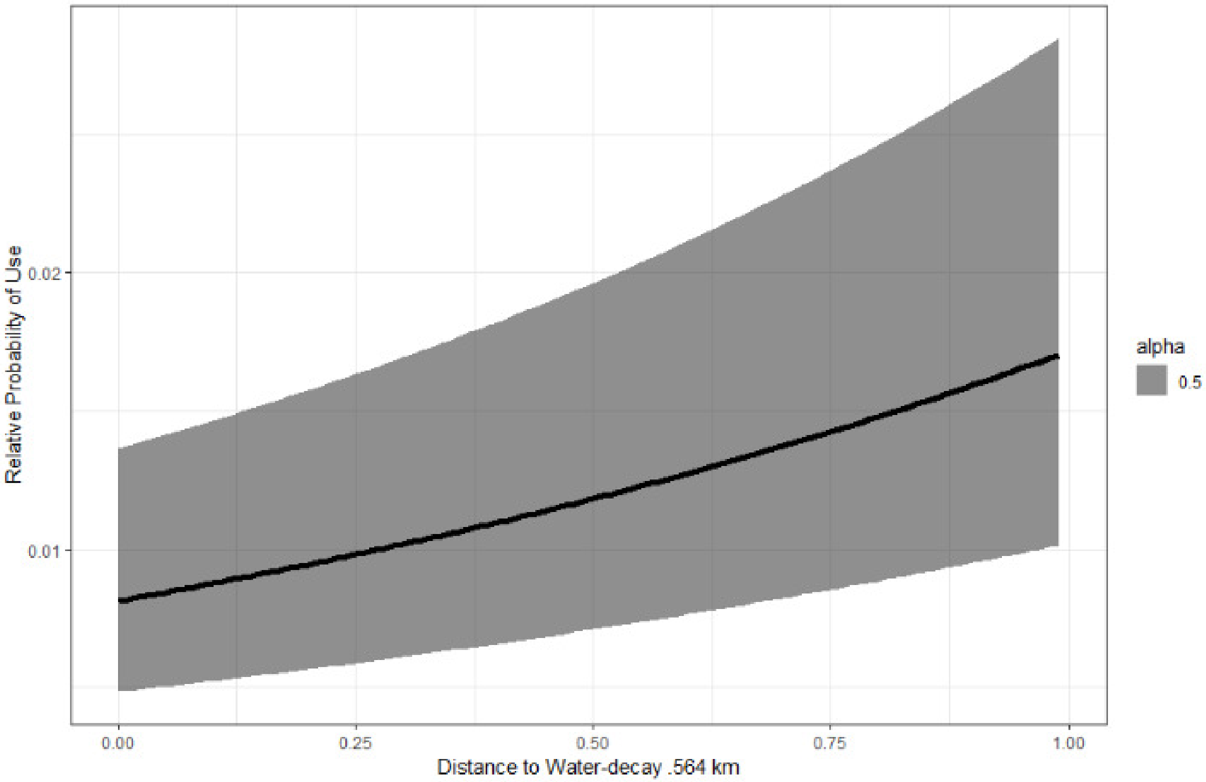
[e] Akaike weight (Burnham and Anderson 2002).

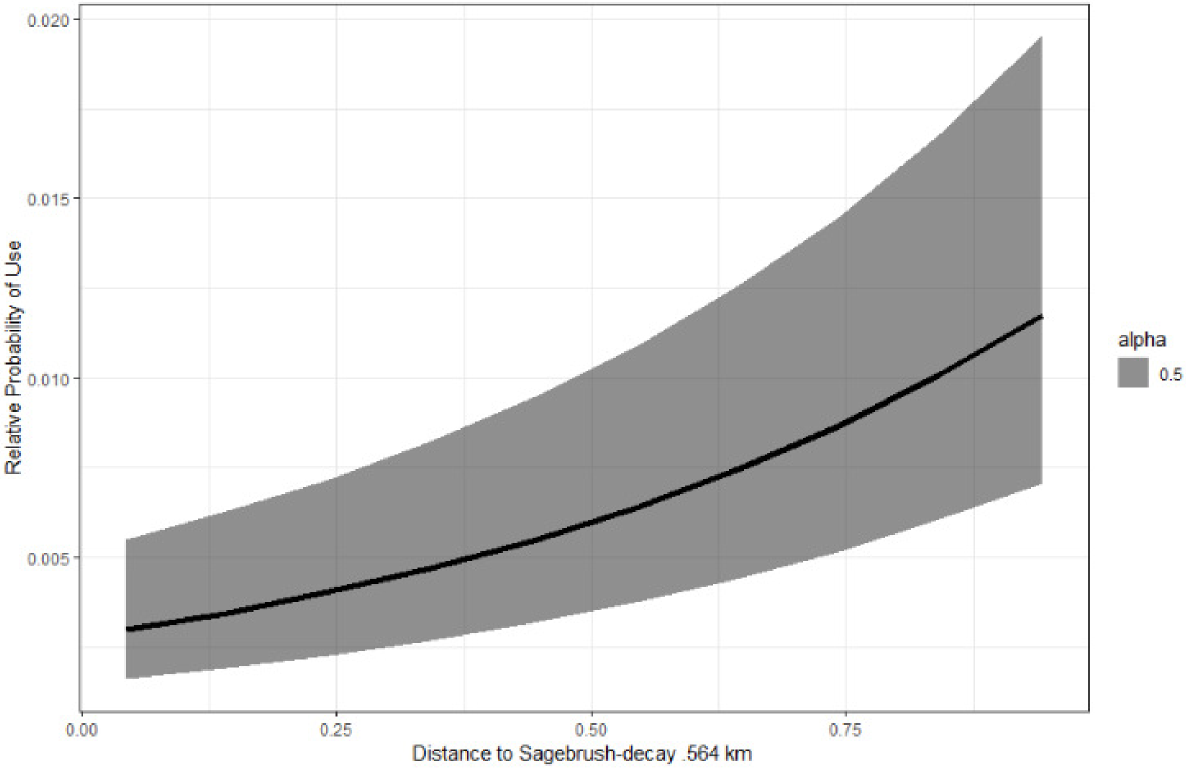
[f] Negative Log Likelihood

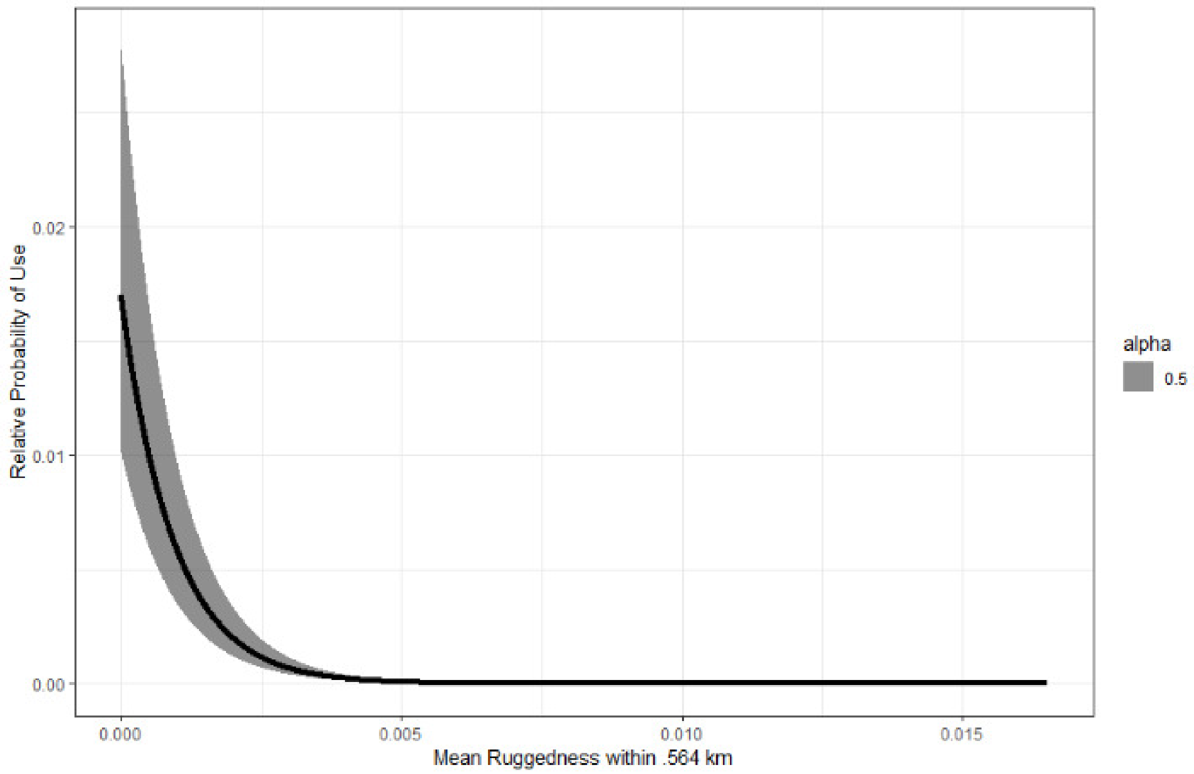
Table 3. Standardized coefficient estimates and profile likelihood 95% confidence intervals for top Spring/Summer RSF model.

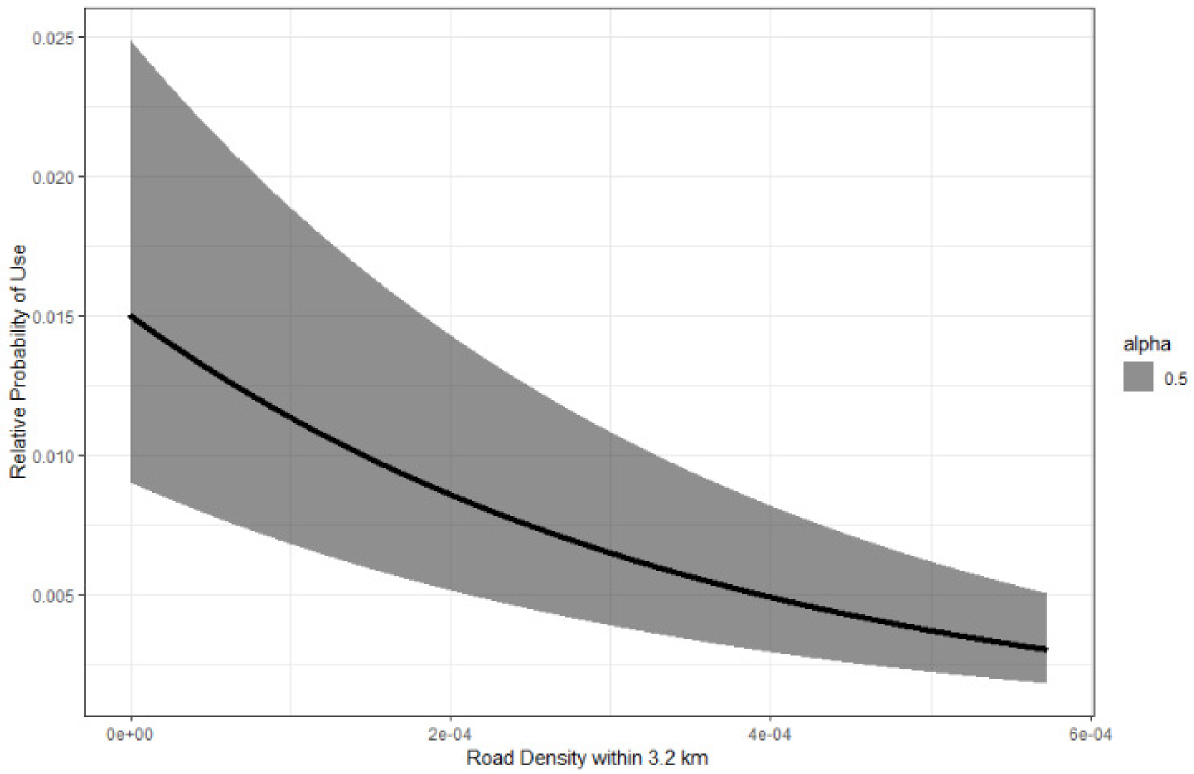
	Estimate	**SE**	**2.5%**	**97.5%**
Intercept	-4.581	0.268	-5.115	-4.072
Lek Distance Decay 3.2 km	0.305	0.025	0.256	0.355
Sage Distance Decay 0.564 km	0.282	0.038	0.208	0.357
Water Distance Decay 0.564 km	0.177	0.024	0.129	0.224
Percent Forest 1.5 km	-6.192	1.589	-9.458	-3.344
Road Density 3.2 km	-0.342	0.032	-0.407	-0.279
Ruggedness 0.564 km	-0.884	0.093	-1.071	-0.704

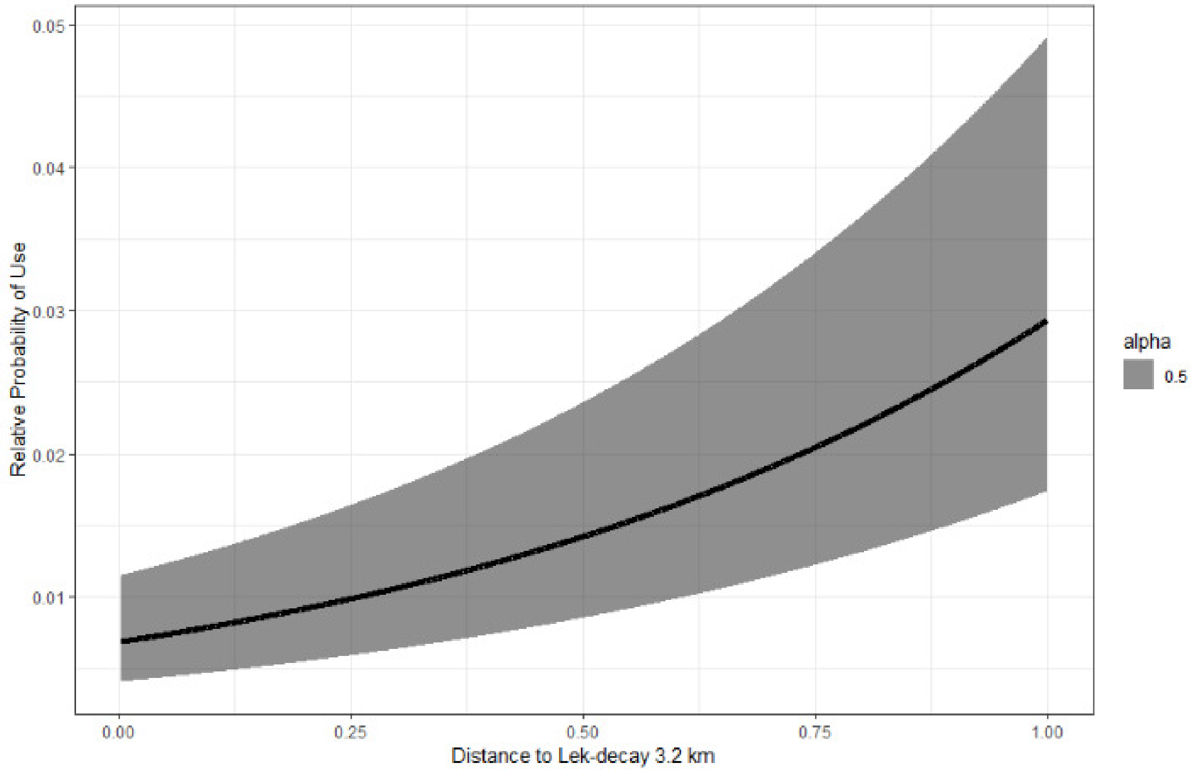
Figure 6. Spring/summer RSF coefficient prediction plots from variables included in the top model. Plots are truncated at maximum values observed at used/available sites. All other variables were held at their mean values for predictions.

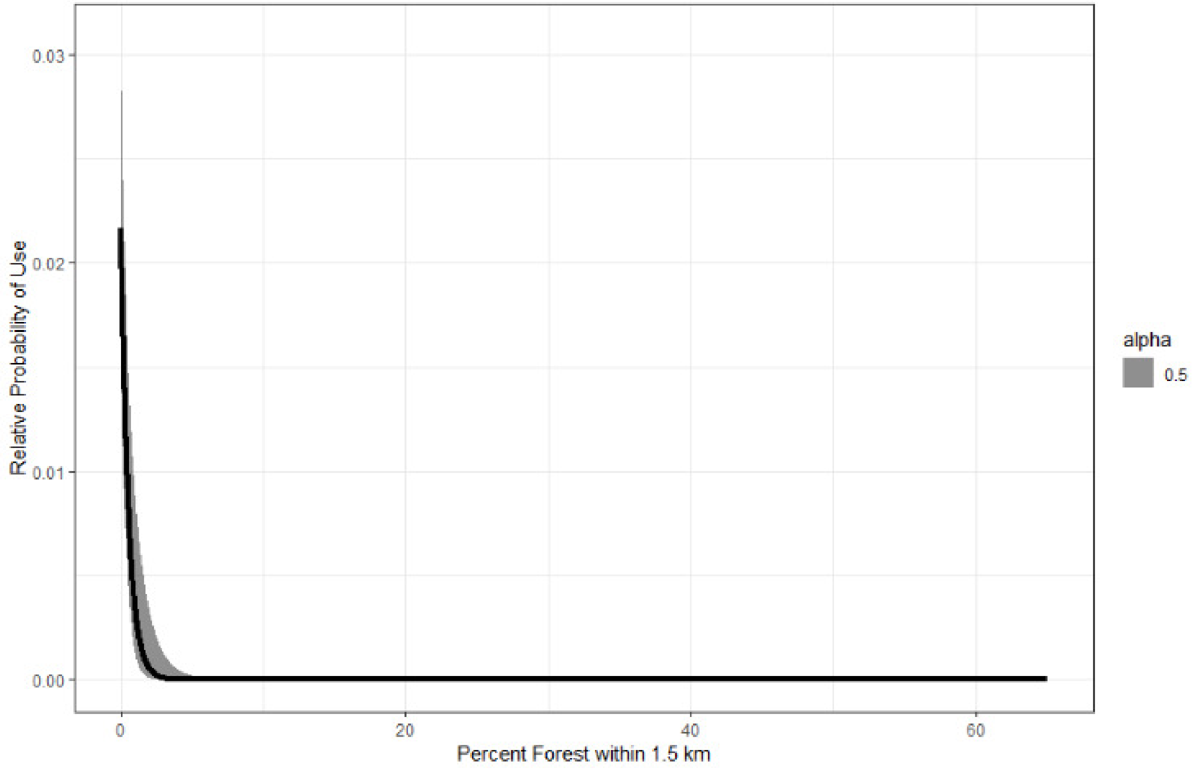





Relative Probability of Use
0.00
0.01
0.02
0.000
0.005
0.010
0.015
Mean Ruggedness within .564 km
alpha
0.5


Relative Probability of Use
0.005
0.010
0.015
0.020
0.025
0e+00
2e-04
4e-04
6e-04
Road Density within 3.2 km
alpha
0.5


0.05
0.04
0.03
0.02
0.01
Relative Probability of Use
0.00
0.25
0.50
0.75
1.00
Distance to Lek-decay 3.2 km
alpha
0.5


0.03
0.02
0.01
0.00
Relative Probability of Use
0
20
40
60
Percent Forest within 1.5 km
alpha
0.5

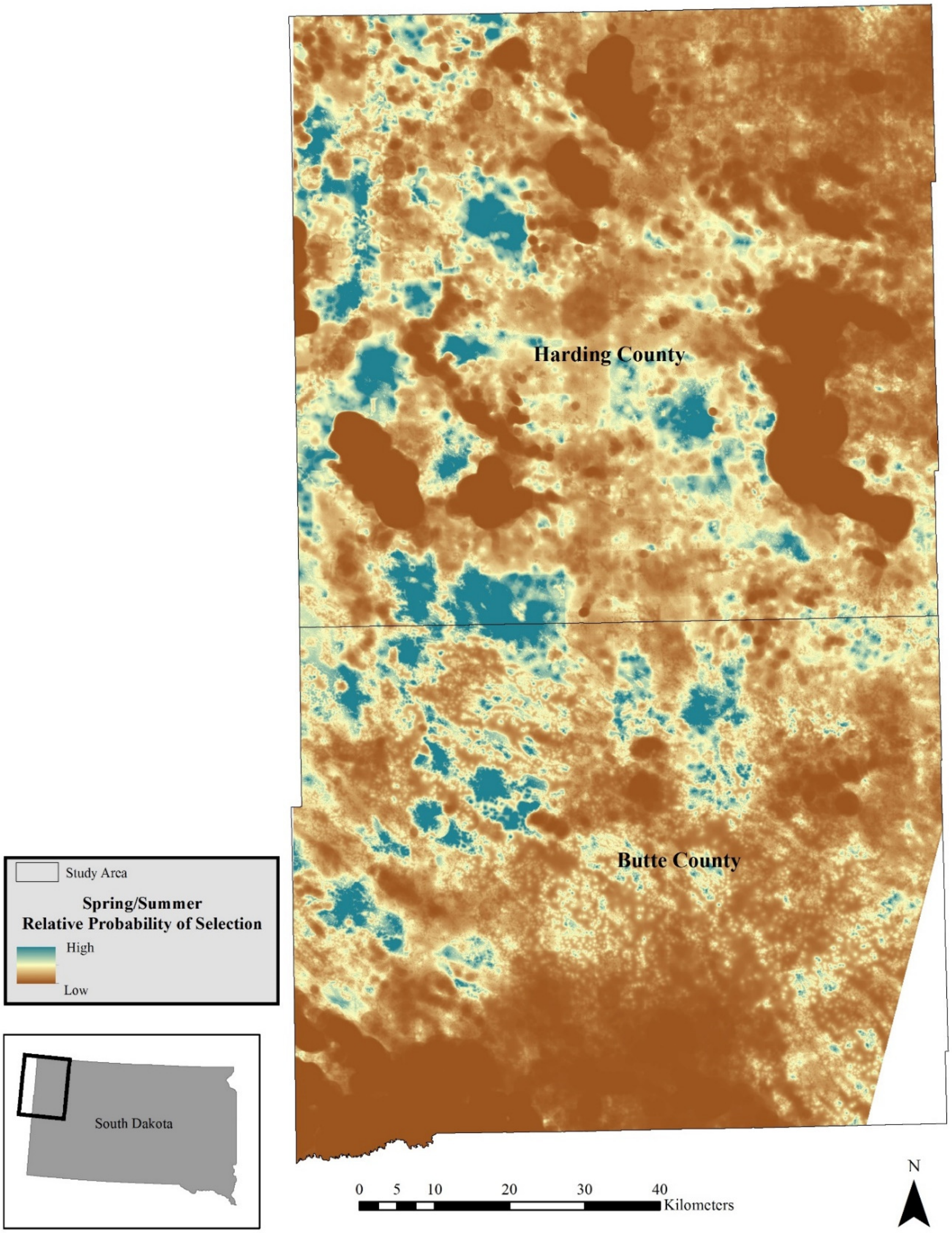


Figure 7. Relative predicted probability of use map for spring/summer. Map was generated from coefficient estimates included in the top resource selection function model for spring/summer.

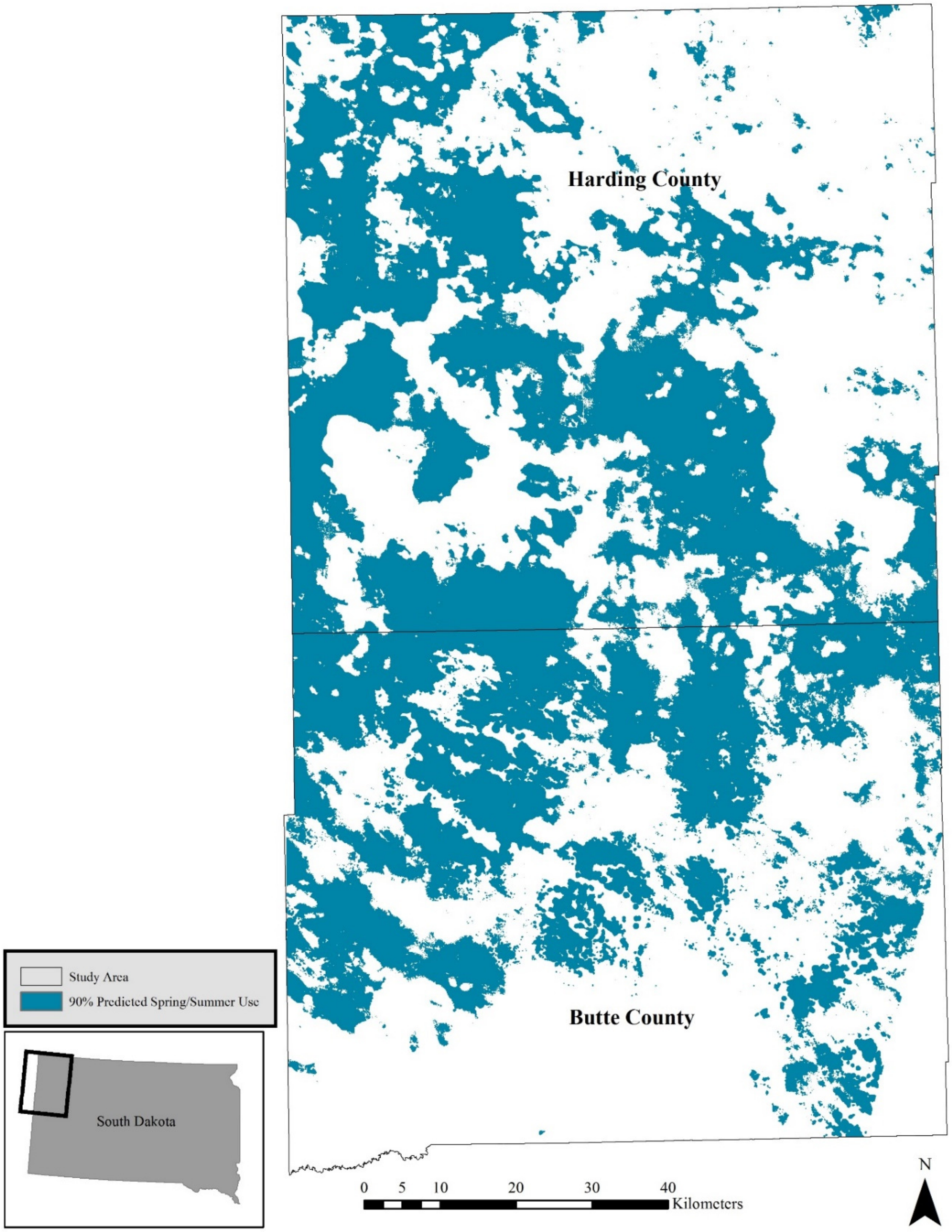


Figure 8. Darkened areas represent area in which 90% of spring/summer use is predicted to fall within.

Table 4. Models for winter RSF. Only top five models are presented, all possible combinations of 4 variables were evaluated, as well as a null model (n=16).

Model[a]	***K***[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w$_i$***[e]	**–Log Likelihood**[f]
EucDist_Sage + Road_Dens0.564 + Rug0.564	5	5,568.49	0	0.53	-2,778.48
EucDist_Sage + %Forest6.4 + Road_Dens0.564 + Rug0.564	6	5,568.77	0.28	0.46	-2,777.28
Road_Dens0.564 + Rug0.564	4	5,578.65	10.16	0	-2,784.83
%Forest6.4 + Road_Dens0.564+ Rug0.564	5	5,579.2	10.71	0	-2,783.83
EucDist_Sage + %Forest6.4 + Rug0.564	5	5,591.11	22.62	0	-2,789.79

[a] EucDist_Sage=Euclidean Distance to Sagebrush, Road_Dens= Road density, Rug=Ruggedness, %Forest=Percent forest, Numbers following variables represent moving window radii (km).

[b] Number of parameters

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC$_c$ relative to minimum AIC$_c$

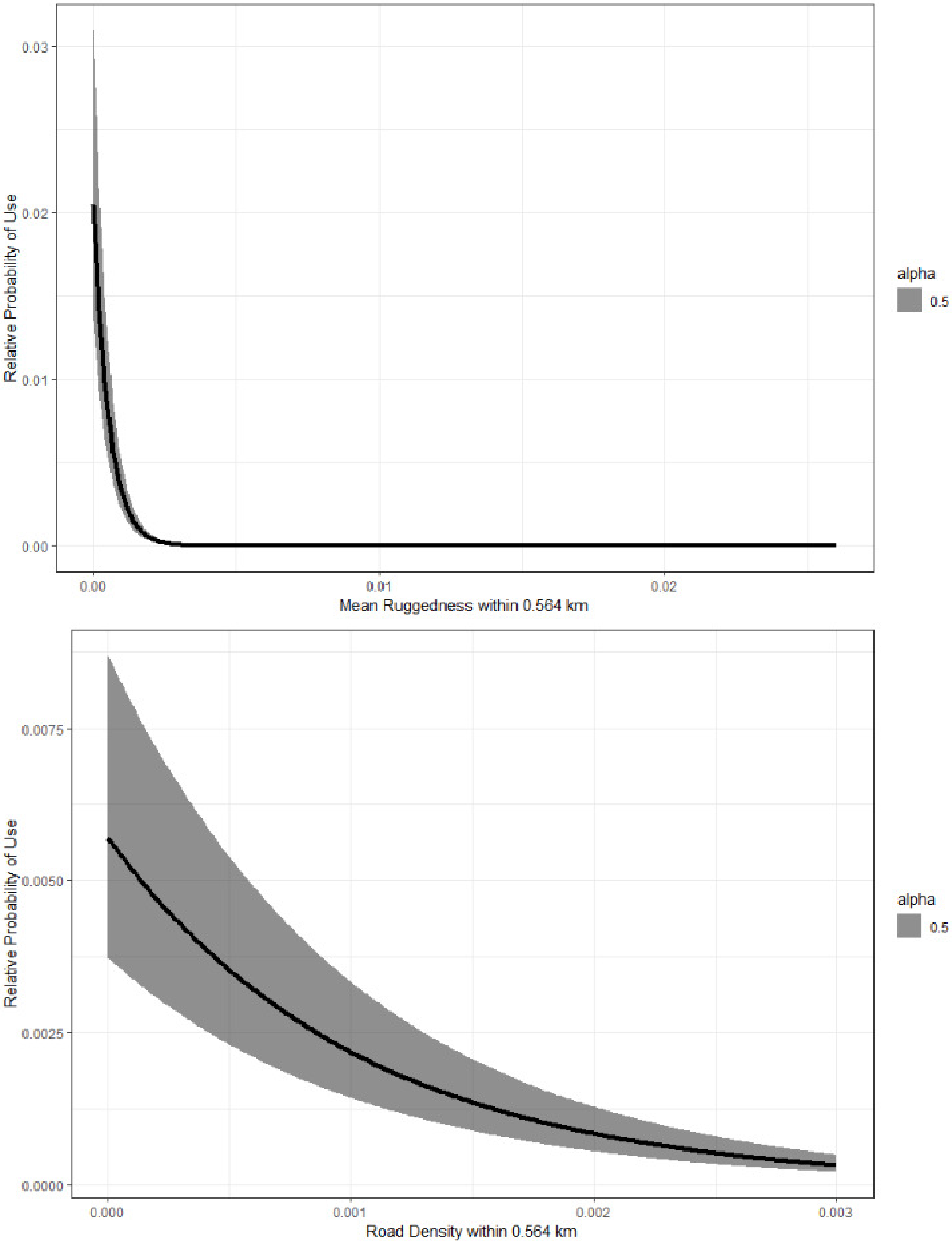
[e] Akaike weight (Burnham and Anderson 2002).

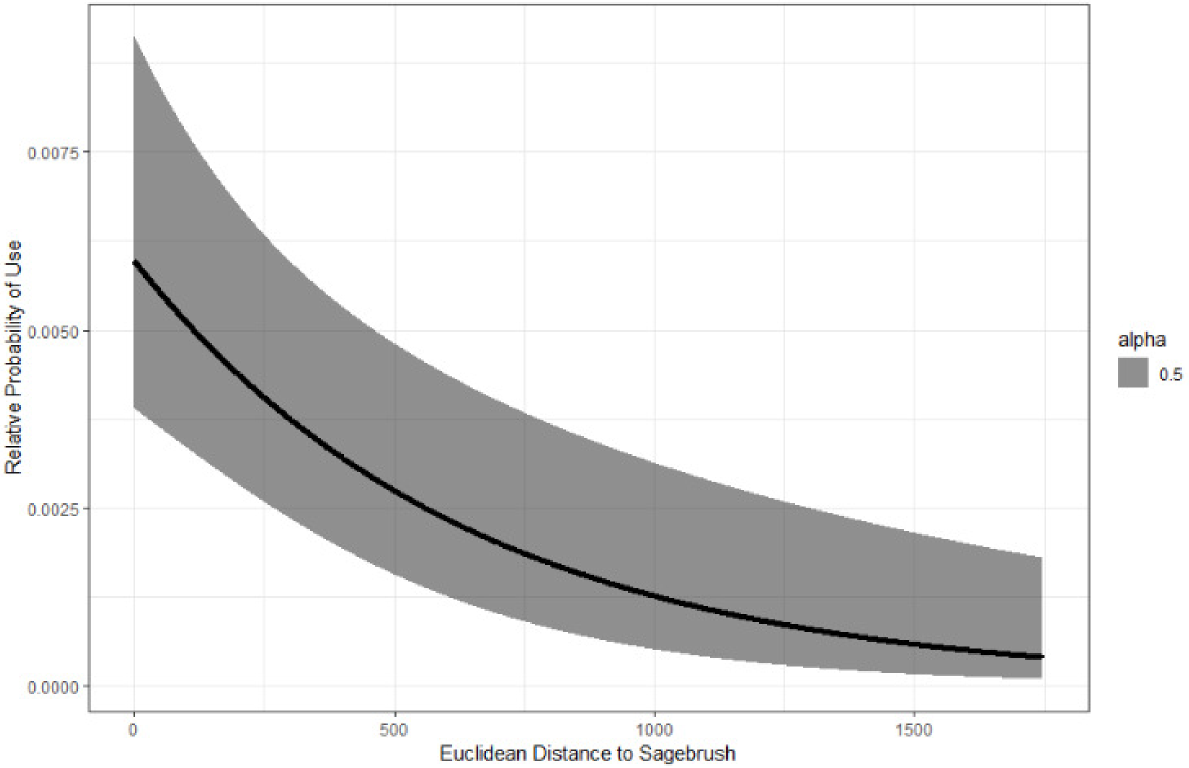
[f] Negative Log Likelihood

Table 5. Standardized coefficient estimates and profile likelihood 95% confidence intervals for top winter RSF model.

	Estimate	**SE**	**2.5%**	**97.5%**
Intercept	-5.284	0.242	-5.767	-4.802
Euclidean Distance to Sagebrush	-0.252	0.074	-0.404	-0.110
Road Density .564 km	-0.327	0.072	-0.480	-0.190
Ruggedness 0.564 km	-2.561	0.286	-3.151	-2.009

Figure 9. Winter RSF coefficient prediction plots from variables included in the top model. Plots are truncated at maximum values observed at used/available sites. All other variables were held at their mean values for predictions.




Relative Probability of Use
0.0000
0.0025
0.0050
0.0075
0
500
1000
1500
Euclidean Distance to Sagebrush
alpha
0.5

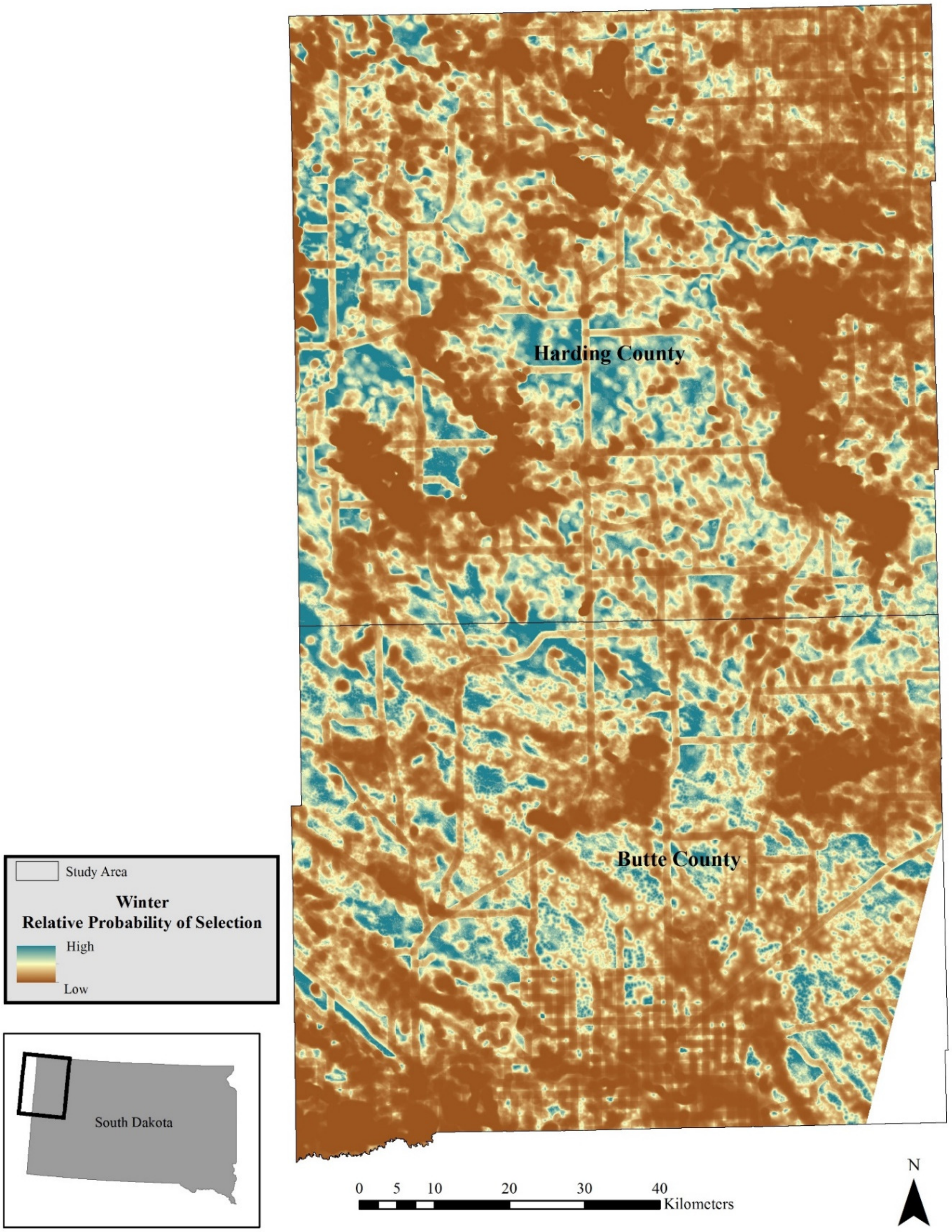


Figure 10. Relative predicted probability of use map for winter. Map was generated from coefficient estimates within the top resource selection function model for winter. Highest values observed were in Montana.

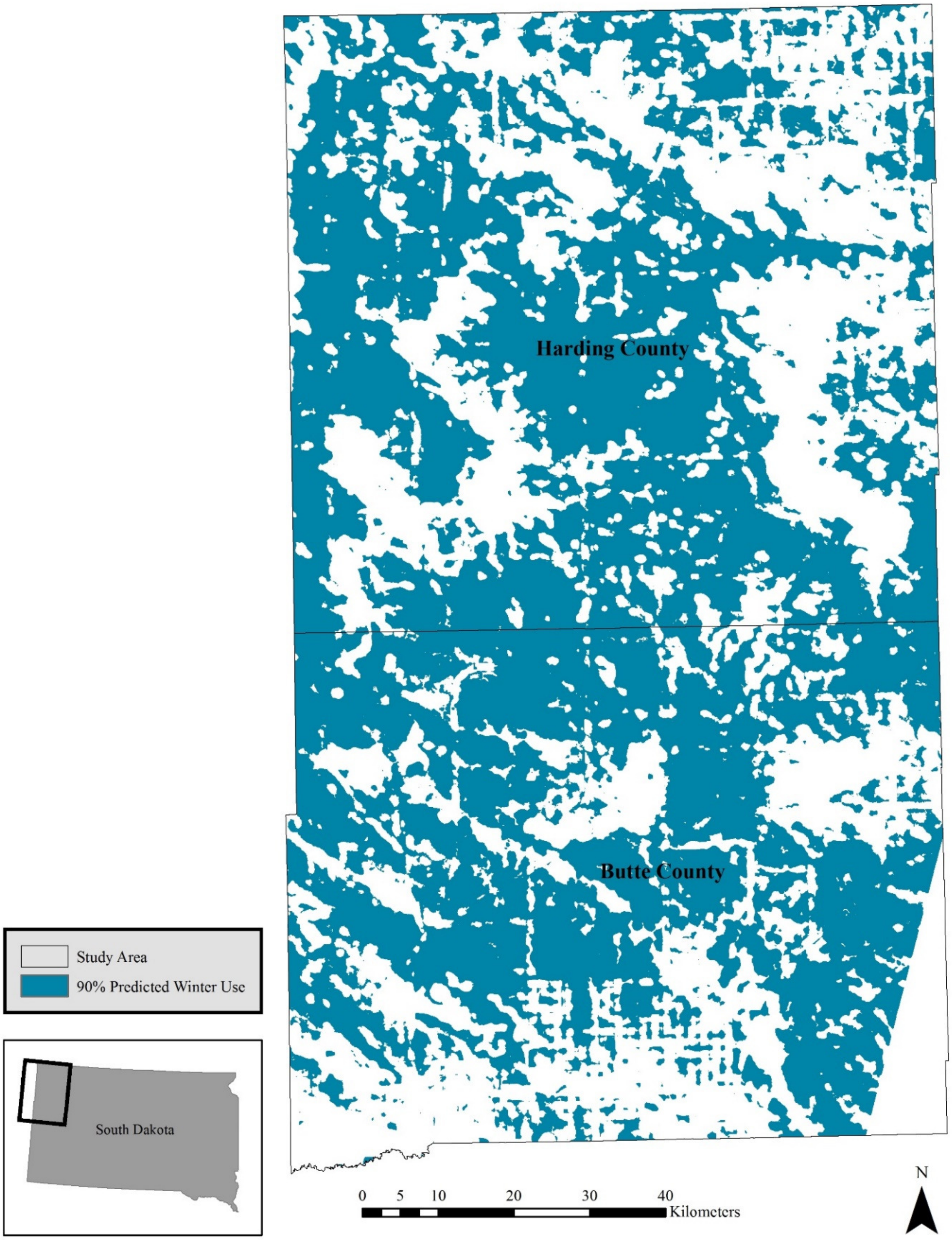


Figure 11. Darkened areas represent area in which 90% of winter use is predicted.

Table 6. Models for nest-site RSF. Only top five models are presented, all possible combinations of 6 variables were evaluated, as well as a null model (n=64).

Model[a]	***K***[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w$_i$***[e]	**–Log Likelihood**[f]
Forest_Dec0.564 + Lek_Dec3.2 + Road_Dens3.2	4	627.0	0	0.22	-309.19
Forest_Dec0.564 + Lek_Dec3.2 + Percent_Water6.44 + Road_Dens3.2	5	627.3	0.33	0.18	-308.2
Percent_Sage6.44 + Percent_Undist3.2 + Road_Dens3.2	5	627.4	0.48	0.17	-308.28
Forest_Dec0.564+ Lek_Dec3.2+ Percent_Water6.44+ Percent_Undist3.2+ Road_Dens3.2	6	628.5	1.57	0.10	-307.64
Forest_Dec0.564 + Lek_Dec3.2 + Percent_Sage6.44 + Road_Dens3.2	5	629.0	2.08	0.08	-309.08

[a] Forest_Dec=Distance to forest with decay function, Lek_Dec=Distance to lek with decay function, Road_Dens= Road density, Percent_Water=Percent water, Percent_Sage= Percent sagebrush, Percent_Undisturbed= Percent unplowed land. Numbers following variables represent moving window radii (km).

[b] Number of parameters

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC$_c$ relative to minimum AIC$_c$

[e] Akaike weight (Burnham and Anderson 2002).

[f] Negative Log Likelihood

Table 7. Full model averaged standardized coefficient estimates and profile likelihood 95% confidence intervals for Nest RSF models.

	Estimate	**SE**	**Adjusted SE**	**2.5%**	**97.5%**
Intercept	-6.059	0.303	0.303	-6.654	-5.465
Forest Distance Decay 0.564 km	-0.984	0.575	0.575	-2.110	0.143
Lek Distance Decay 3.2 km	1.043	0.089	0.089	0.870	1.217
Road Density 3.2 km	-0.945	0.229	0.229	-1.394	-0.495
Percent Water 6.4 km	-0.138	0.230	0.230	-0.589	0.312
Percent Undisturbed 3.2 km	0.125	0.216	0.216	-2.990	0.548

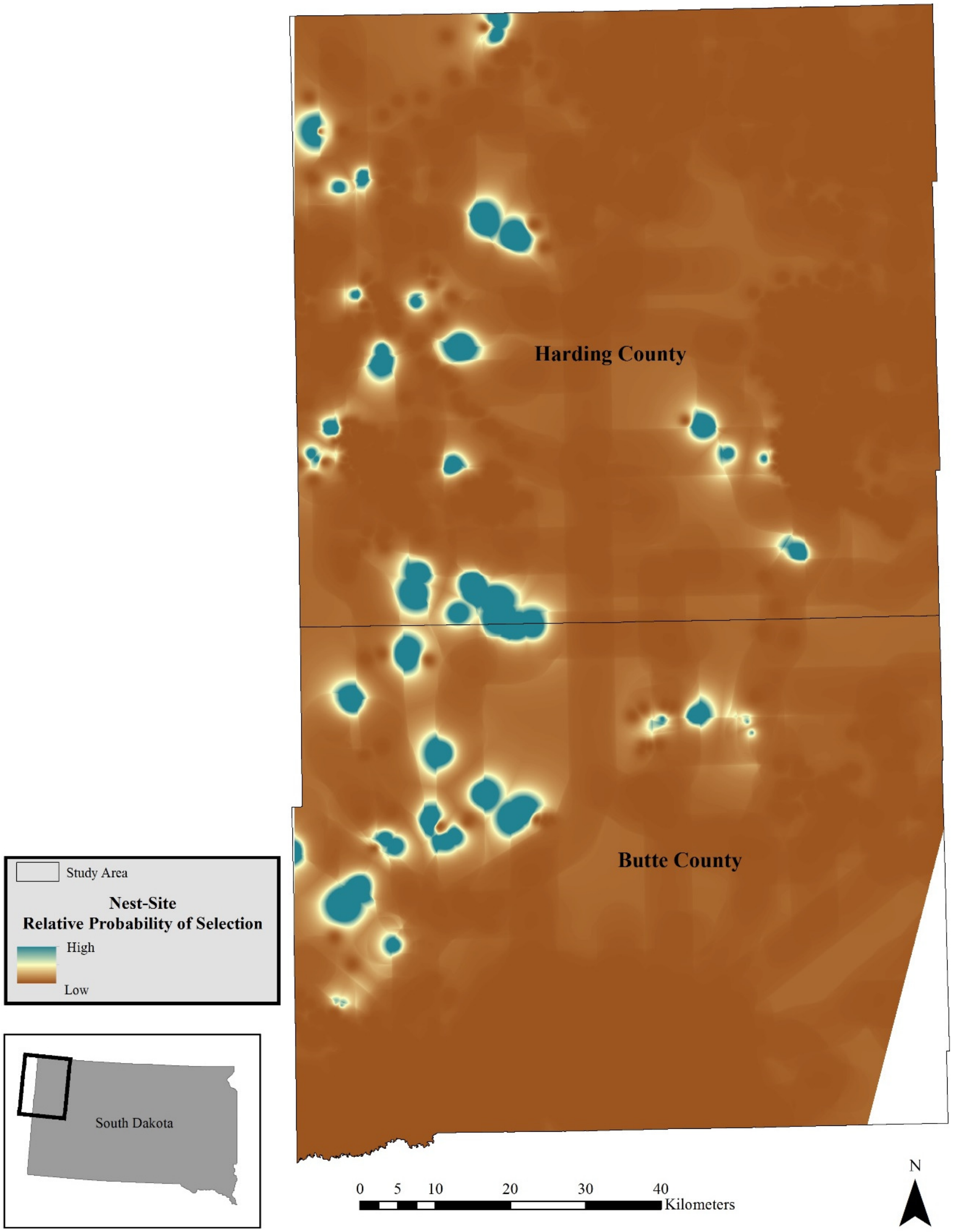


Figure 12. Relative predicted probability of use map for nest-sites. Map was generated from coefficient estimates within the top resource selection function model for nest-sites.

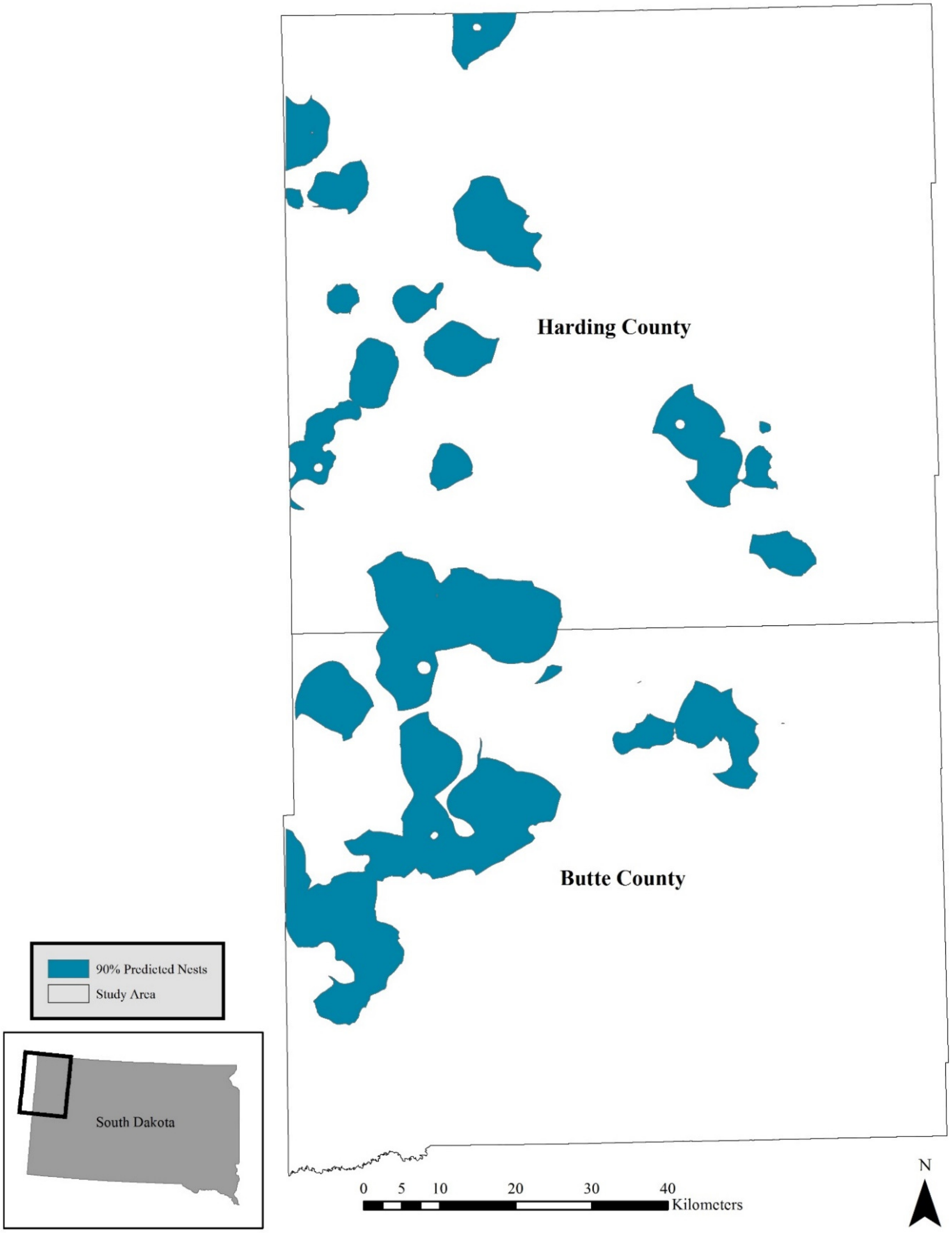


Figure 13. Darkened areas represent area in which 90% of nests are predicted to fall within.

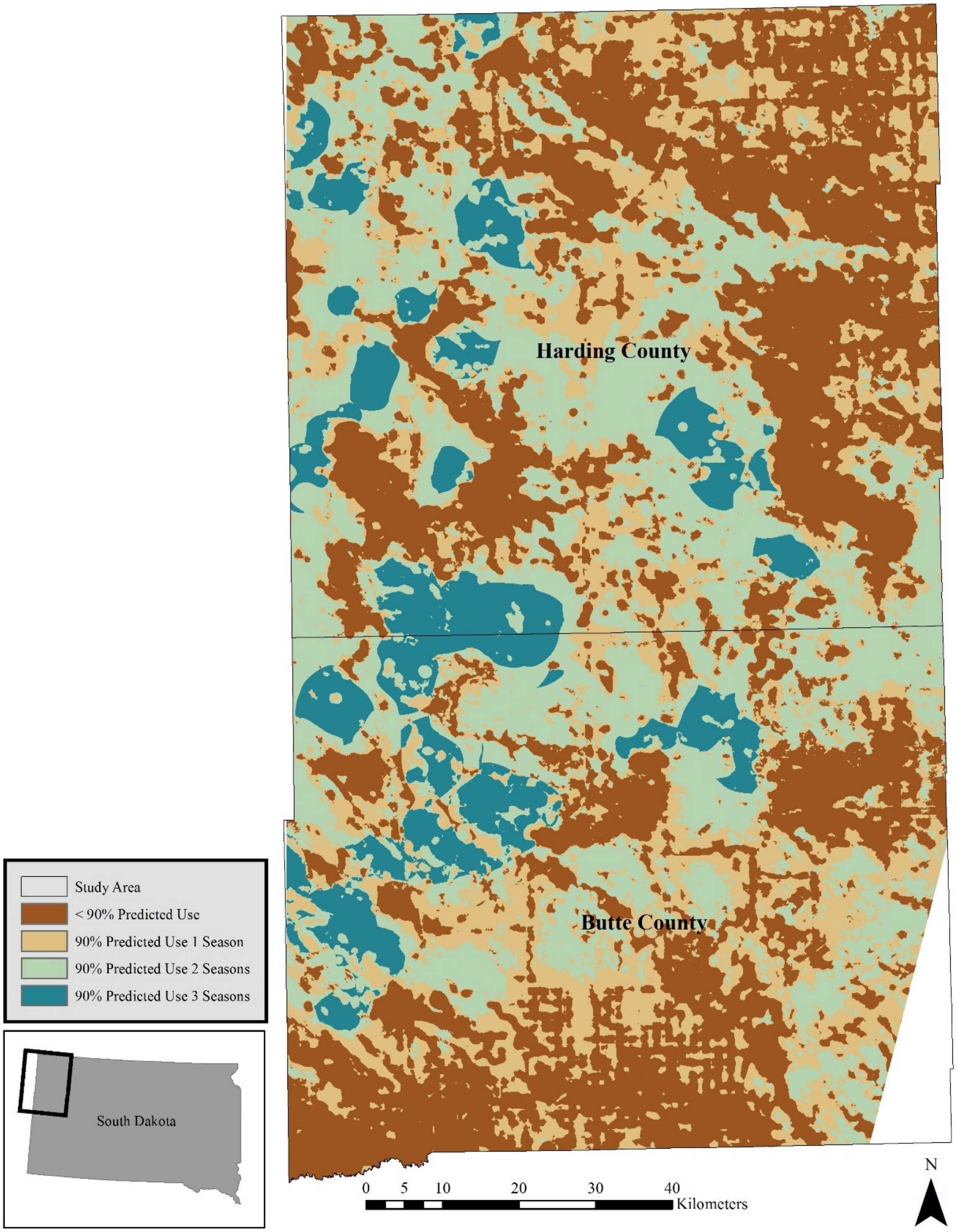


Figure 14. Predicted multi-season use map. Map indicates what areas are used 90% of the time in none, one, two, or all three seasons.

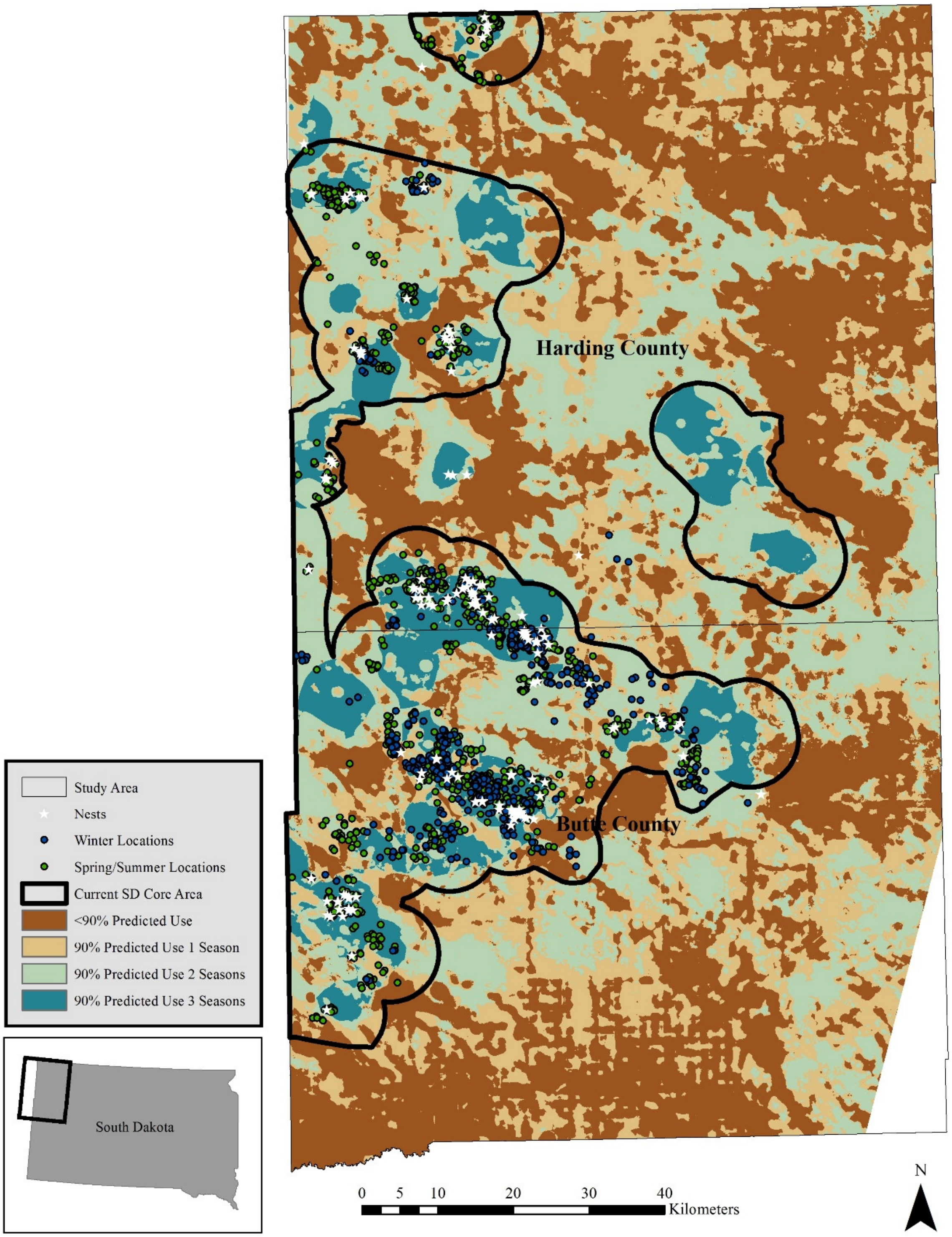


Figure 15. Predicted multi-season use map with outlined area of current South Dakota Core Sage-Grouse Area. Seasons include spring/summer, winter and nesting. Points on map represent documented sage-grouse locations during spring/summer, winter, and nest-sites (n=3,943).

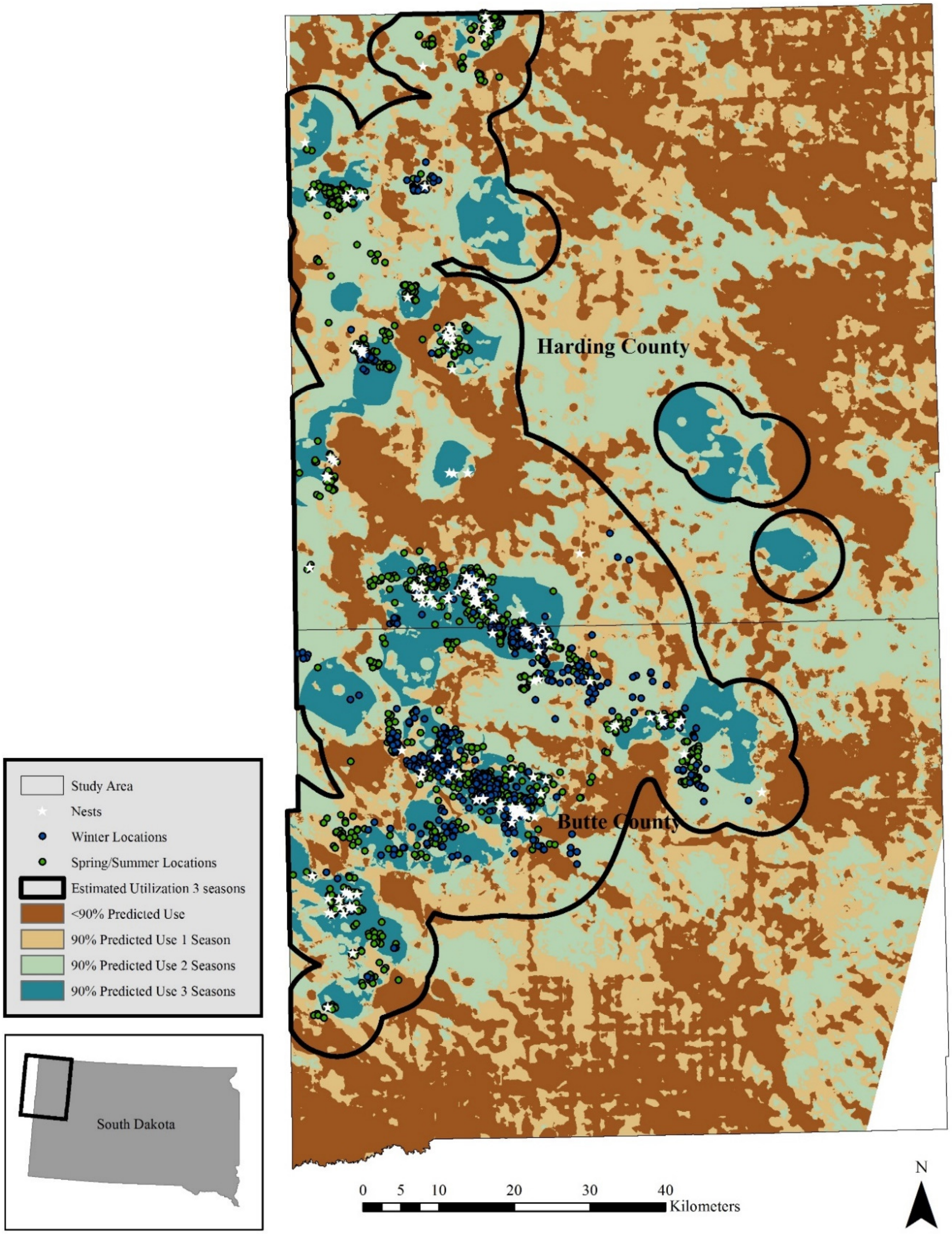


Figure 16. Predicted multi-season use map with outlined area of estimated utilization across three seasons. Seasons include spring/summer, winter and nesting. Points on map represent documented sage-grouse locations during spring/summer, winter, and nest-sites (n=3,943).

CHAPTER 5: GREATER SAGE-GROUSE RESOURCE SELECTION AT MULTIPLE SCALES DURING THE CRITICAL BROOD REARING PERIOD

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) are a species of conservation concern throughout the Intermountain West. Consequently, numerous studies have documented drivers of demographic performance at the core of their distribution; however, relatively few studies have examined sage-grouse inhabiting the eastern extent of their range, in South Dakota. Identifying sage-grouse resource selection during the critical brood rearing period can enhance management of the species and their habitat. We sought to determine selection preferences of female sage-grouse with broods using two types of data at two scales; local (within 50 m) and landscape (45–6440 m). We documented brood-sites and compared each to two paired random locations within 1.55 km of used brood-sites. We analyzed selection using conditional logistic regression and evaluated models using Akaike's Information Criterion corrected for small sample size. At the local scale, we characterized vegetation and arthropod communities. At the landscape scale, we examined features at multiple scales; we determined the scale that best described brood-site selection and populated the landscape model set with variables that represented different scales. In 2016 and 2017, we monitored 26 female sage-grouse with broods. We characterized 76 brood-sites and 152 paired random sites. We found that at a local scale, sage-grouse broods select for higher abundance of Coleoptera and "other" arthropods and avoid sites with high Hymenoptera abundance and high Orthoptera weight. Also, sage-grouse with broods select for areas with high sagebrush (*Artemisia* spp.) canopy cover and tall grass, while avoiding areas with high amounts of grass and

litter cover. At the landscape scale, sage-grouse with broods select for areas near water and away from roads and forests. Land that has been previously plowed has a non-linear (quadratic) response, with high use predicted in areas that are either mostly plowed or mostly unplowed (observed values ranged 30%−100% undisturbed land within 1500 m). To provide quality brood habitat for sage-grouse, wildlife managers should preserve and enhance areas away from roads and forests that are close to open water sources. Although we observed a non-linear response to plowed land, plowing of sagebrush is not recommended due to the long-term impacts to sagebrush plants and our documented selection for high sagebrush cover at the local scale. Also, wildlife managers should seek to provide tall grass within sagebrush stands and avoid accumulation of dead desiccated vegetation (litter) at the local scale.

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a sagebrush (*Artemisia* spp.) obligate species (Wallestad and Eng 1975) that has experienced population declines over the past several decades (Connelly et al. 2004, WAFWA 2015). Currently, the sage-grouse distribution is 56% of the estimated pre-settlement distribution (Shroeder et al. 2004). One critical time period in the life cycle of sage-grouse is brood rearing; chick survival has been identified as the second most important vital rate for sage-grouse population growth in a range-wide assessment (Taylor et al. 2012).

The most common causes of mortality for gallinaceous chicks are; hypothermia, predation, and starvation (Bergerud 1988). Therefore, brood rearing habitat should provide multiple benefits to chicks including; food, vegetation conducive to mobility, protection from the elements, and concealment from predators (Svedarsky 1988). Sage-grouse chicks, and grouse chicks in general, rely primarily on insects during the first weeks after hatch (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994, Hannon and Martin 2006). Insects have been shown to be crucial to sage-grouse chick survival and growth (Johnson and Boyce 1990). Arthropods are consumed in high amounts during the first week of life, after which forbs are the dominant component of sage-grouse chick diets, followed by a transition to sagebrush consumption (Klebenow and Gray 1968, Drut et al. 1994, Peterson 1970).

At a local scale, brood-site selection can be influenced by total vegetation cover (Dunn and Braun 1986, Schrieber et al. 2015); yet, broods seem to avoid dense sagebrush stands (Klebenow 1969, Kaczor et al. 2011) possibly due to the lack of essential forbs in these areas (Klebenow 1969). In a meta-analysis encompassing results from eight brood-site selection studies, sage-grouse selected brood-sites with greater forb and grass cover, taller grass, and less sagebrush cover than random sites (Hagen et al. 2007). On a landscape scale, sage-grouse selected patches with moderate sagebrush cover, and mesic areas closer to water impoundments than found at random (Aldridge and Boyce 2007, Atamian et al. 2010); alternatively, sage-grouse tend to avoid development (human and oil/gas) and cultivation (Aldridge and Boyce 2007).

Sage-grouse in South Dakota are on the eastern fringe of the sage-grouse distribution (Shroeder et al. 2004). Sagebrush plants found in South Dakota are shorter and have less canopy cover than found elsewhere in the sagebrush steppe (Kantrud and Kolgiski 1983, Connelly et al. 2000, Kaczor et al. 2011a). Additionally, sagebrush in

South Dakota do not meet the management recommendations for quality nesting and brood rearing habitat established by Connelly et al. (2000; Kaczor et al. 2011b). Two previous telemetry studies have assessed brood-site selection on the eastern fringe of the distribution, in North and South Dakota (Kaczor et al. 2011a) in 2005−2007. One area of particular interest is Harding County, South Dakota, the area between the two previous studies. Location and resource selection data from this portion of the population is limited. Additionally, there has been no analysis to determine what factors are affecting brood-site selection at a landscape scale on the eastern fringe of the sage-grouse distribution and previous research focused on vegetation and did not assess selection for arthropods (Kaczor et al. 2011a).

Johnson (1980) defines varying scales of selection; we were most interested in the selection of habitat components within the home range (3rd order selection). Therefore, we sought to determine resource selection during brood rearing by comparing sage-grouse brood-sites to available sites. We assessed resource selection at two scales, local and landscape. At the local scale, we evaluated resource selection in terms of vegetation characteristics as well as arthropod communities. At the landscape scale, we evaluated landscape features at multiple scales. Additionally, we wanted to determine if resource selection varied temporally. Specifically, if selection for mesic areas became stronger as those sites became limited later in the brood rearing season.

METHODS

STUDY AREA

Our study took place in Harding and Butte counties of northwest South Dakota. The total area of both counties combined is 12,805 km^2. Land use in the study area is dominated by pastureland (>85%), followed by cropland (10−12%; USDA 2012). The majority of the land in the study area is privately owned (~75–80%; USGS GAP 2016). Annual average temperatures range from -1.7°C–10.6°C with an average of 39 cm of precipitation annually (NOAA, 2019). A majority (84%) of Butte and Harding counties has never been plowed (Bauman et al. 2018).

Our study area represents the eastern edge of the sagebrush distribution where an ecotone between sagebrush steppe and grassland ecosystems occurs (Johnson 1979, Cook and Irwin 1992, Lewis 2004). Common sagebrush species in the study area include silver sagebrush (*Artemisia cana*) and big sagebrush (*Artemisia tridentata;* Johnson and Larson 2007).

FIELD METHODS

We annually captured breeding-age male and female sage-grouse near active leks in March−May, as well as at high sage-grouse use areas in August–September using nocturnal spotlighting and a long-handled net (Giesen et al. 1982, Wakkinen et al. 1992). We aged and sexed captured sage-grouse based on plumage and morphological characteristics (Crunden 1963, Beck et al. 1975, Bihrle 1993). We fit female sage-grouse with a 21.6 g necklace-type Very High Frequency (VHF) radio transmitter (model A4060, Advanced Telemetry Systems, Isanti, MN, USA) as well as a uniquely numbered aluminum butt-end leg band (National Band & Tag Company). We weighed all birds at the time of capture to ensure that radio-transmitters were less than 3% of body weight

(Kenward 2001). All animal handling procedures were approved by the Institutional Animal Care and Use Committee at South Dakota State University (IACUC approval # 15-074A).

We located sage-grouse ≥ 2 times per week from 15 April–15 September using the homing method (Samuel and Fuller 1996, Fuller and Fuller 2012) with a hand-held 3-element Yagi antenna or via fixed-wing aircraft equipped with a 2 element, “H” type antenna on each wing. To identify nests, females were located, and nesting status was determined based on the position of female in relation to surrounding vegetation. Nest remains were used to determine fate of nests (Williams and Wood 2002).

If the nest was successful, daytime brood flush counts were conducted at approximately 21, 35, and 49 days post hatch. If the status of the brood was unknown, female sage-grouse were flushed and the surrounding area searched. If no chicks were found during two consecutive flushes, the brood was considered failed. Each used brood-site was matched with and compared to two random locations within 1.55 km of used site. The distance of 1.55 km was chosen because it is the radius of the estimated mean 50% adaptive kernel home range for broods (7.59 km²) found in a previous South Dakota sage-grouse study (Kaczor 2008) and thus, we considered the area available to broods. Random points were generated using the Create Random Points Tool in ArcGIS.

LOCAL SCALE MODEL VARIABLES

To assess food and cover variables at brood-sites relative to random points, we measured vegetation and collected arthropods. Arthropods were sampled weekly from 1–4 weeks after hatch. Arthropods were sampled in 10 m x 10 m plots containing five pitfall traps, one in the center of the plot, and one 5 m from center in each of the four cardinal directions. Pitfall traps were created using a soil corer to create a hole, which was then fitted with a section of 2 cm PVC pipe. Inside the PVC pipe, an 18 mm glass test tube with a rim was placed and was set flush with the ground. Pitfalls were left open for 48 hours, and each test tube was filled with a 50:50 mixture of 100% propylene glycol and 70% isopropyl alcohol. We also used a 0.38 m diameter sweep net, sweeping 5 m in each cardinal direction from center of the plot at a rate of one sweep/m. After sampling, all collected arthropods were stored in a 50:50 mixture of 100% propylene glycol and 70% isopropyl alcohol until sorting and processing. We sorted arthropod samples into the following Orders; Coleoptera, Hymenoptera, and Orthoptera; all other arthropods were placed into an “other” category (Fischer et al. 1996, Klebenow and Gray 1968). Samples within each Order were counted and weighed. Before weighing, arthropods were dried at 60°C for 24 hours (Leathers 2003). Arthropods were weighed using a DeltaRange® XP26 scale (readability=0.001 mg, repeatability (σ)=0.0007 mg).

Vegetation was indexed weekly from 1−7 weeks after hatch at brood-sites and two associated random sites/used brood-site. Vegetation transects extended 50 m north and 50 m south from brood or random point. Variables included visual obstruction readings (VOR), grass height, and canopy cover estimates. To estimate VOR at brood and random locations, we obtained measurements using a modified Robel pole with alternating black and white bands that were 2.54 cm wide (Robel 1970, as modified by Benkobi 2000). Observers recorded the lowest band that was totally obstructed from a distance of four meters and an eye height of one meter. At each visual obstruction reading location, four readings were taken (one in each cardinal direction) and these four readings were averaged for each sample point along the transect. VOR, along with grass height measurements were taken at the brood use and random locations (0 m), and at 10 m, 20 m, 30 m, 40 m, and 50 m north and south of each brood and random point (n=11).

To estimate canopy cover, we used the Daubenmire method (Daubenmire 1959). Quadrats were 20 cm × 50 cm. Canopy cover was estimated at brood and random locations (0 m), and at 10 m, 20 m, 30 m, 40 m, and 50 m north and south of each brood or random point (n=11). Categories of cover estimated were; total cover, grass, forb, litter, shrub, and annual grass. Litter cover was considered as any residual vegetation that was desiccated and/or not actively growing. All canopy coverages were estimated at one of six cover classes (1=0–5%, 2=5–25%, 3=25–50%, 4=50–75%, 5=75–95%, 6=95–100%). Midpoint values of each cover class were assigned and used for analysis.

Sagebrush density was estimated using the Point Centered Quarter method (Cottam and Curtis 1956). Sample locations were placed at the center, as well as every 10 m along each transect (n=11). At each sampling location, four quadrants were created, and the distance to the nearest sagebrush in each quadrant was measured. Sagebrush was measured to a distance of five meters from each sampling location. For those quadrants where the nearest shrub was >5 m, a default value of 5 m was assigned for calculations. Although this may overestimate shrub density, it is a less severe overestimation, as opposed to neglecting the quadrant when calculating average distance to nearest shrub for each sampling location. Using this altered method, the minimum possible calculated shrub density was 0.04 sagebrush/m^2. If the plot was located in an area with no sagebrush, then sagebrush density was set to a default value of 0 sagebrush/m^2. Each shrub measured for the Point Centered Quarter method also had height recorded that was used to estimate sagebrush height. Sagebrush heights were averaged for each site.

LANDSCAPE SCALE MODEL VARIABLES

We developed landscape variables that were biologically relevant to sage-grouse habitat selection using the Spatial Analyst package in ArcGIS. Variables of interest included; sagebrush, forest, water, roads, ruggedness, undisturbed (unplowed) land, and active oil/gas wells.

A data layer representing roads included both paved and gravel roads (SD DOT 2018). Ruggedness of the landscape was quantified by using the Benthic Terrain Modeler Toolbox (Wright et al. 2005) with National Elevation Dataset (Gesch et al. 2002) in ArcGIS. We used the Native Lands Data Layer (Bauman et al. 2018), which discriminates between land that has been plowed sometime in the past and unplowed land; we considered unplowed land to be “undisturbed”. Oil and gas facility locations were considered in analyses if their status was injecting or producing during the time of our study (South Dakota Department of Environment and Natural Resources 2018).

We included landcover identified from the 2011 National Land Cover Database (NLCD: Homer et al. 2015) including: sagebrush (NLCD Shrubland Products; USGS 2017), water, and forest (NLCD 2011). The NLCD Shrubland Products, percent sagebrush data layer (NLCD Shrubland Products; USGS 2017), has been shown to accurately represent the presence of sagebrush in South Dakota, but is inaccurate at predicting sagebrush canopy coverage (Parsons et al. *In Review*). Therefore, the percent sagebrush layer was re-classified in ArcGIS to reflect presence or absence of sagebrush at

30 m resolution. Water was defined by combining classes in the NLCD ("Open Water" + "Woody Wetlands" + "Emergent Herbaceous Wetlands"). Forest was defined by combining landcover classes from the NLCD ("Deciduous Forest" + "Evergreen Forest" + "Mixed Forest"). We assessed the influence of both distance to features (with the exception of ruggedness) and the density of each feature at multiple spatial scales (Carpenter et al. 2010, Fedy et al. 2014). All layers were initially generated at a 30 m pixel resolution.

We followed the methods of Fedy et al. (2014) and generated variables of interest at five scales (0.006 km^2, 1 km^2, 7.07 km^2, 32.17 km^2, and 138.67 km^2), which have been shown to be biologically relevant to sage-grouse (Holloran and Anderson 2005, Aldridge and Boyce 2007, Walker et al. 2007b, Carpenter et al. 2010, Doherty et al. 2010, Holloran et al. 2010, Fedy et al. 2012). Mean values or percentages within each scale were calculated for every 30 m pixel using a moving window analysis with the Focal Statistics Tool in ArcGIS. Neighborhood was defined as a circular buffer with a search radius corresponding to each biologically relevant scale (0.006 km^2(0.045 km radius), 1 km^2 (0.564 km radius), 7.07 km^2 (1.5 km radius), 32.17 km^2 (3.2 km radius), and 138.67 km^2 (6.44 km radius; Fedy et al. 2014).

We calculated percentages within each radius for; forest, sagebrush, water and undisturbed layers. We calculated mean values of ruggedness within each radius. Road density was calculated within each scale using the Line Density Tool in ArcGIS by changing the search radius to match each scale. Oil and gas well density was created using the Point Density Tool in ArcGIS.

Distance to features was calculated using the Euclidean Distance Tool in ArcGIS. We also created exponential decays as a function of Euclidean distance (Carpenter 2010, Fedy 2014). Decay function formula was as follows; $e^{(-d/\alpha)}$ where d is the Euclidean distance to feature, and α is the value corresponding with each scale's search radius (0.045 km, 0.564 km, 1.5 km, 3.2 km, and 6.44 km). Decay distance functions allow a non-linear response to distance to features, and values reach 0 after a specified distance; distance decay values are closer to 1 when near to the feature, and values reach 0 as distance increases. Whereas Euclidean distances represent linear responses of distances from features and values continue to increase as distance to feature increases, extending to the extent of the study area. Therefore, interpretation of distance decay coefficients is opposite Euclidean distance coefficients. Distance decay variables were generated using the Raster Calculator Tool in ArcGIS. Euclidean distance and decay function distances were calculated for the following variables; water, forest, sagebrush, undisturbed, oil/gas wells, and roads (Table 1).

TEMPORAL SHIFT IN SELECTION

During brood rearing, sage-grouse will often select for more mesic areas (Klebenow 1969, Wallestad 1971, Connelly and Markham 1983, Gates 1983, Connelly et al. 1988). One way to quantify lush, green areas, is using Normalized Difference Vegetation Index (NDVI; Moderate Resolution Spectrum Radiometer (MODIS)), which is a measure of the "greenness" on the landscape. We hypothesized that selection responses to NDVI may vary temporally, as resources (green areas) become limited throughout the brood rearing season. We downloaded and used NDVI data at a 250 m resolution composited in 8-day time intervals (NASA 2018).

ANALYSIS METHODS

Three model sets were created within two scales (local and landscape). The local model sets included vegetation and arthropods measured at brood and random sites. The landscape scale model set included landscape features (Table 1). We z-standardized all variables before modeling so that parameter estimates of effect sizes would be directly comparable to one another. We modeled the probability of a sage-grouse selecting a brood-site from a set of potential sites with discrete choice models, specifically, conditional logistic regression models (Cooper and Millspaugh 1999, Schreiber et al. 2015, Lehman et al. 2016). We used discrete choice models with one brood-site/stratum; this directly compares each used brood-site to two paired-random sites sampled. This methodology allows for resource availability to vary spatially and temporally, depending on when and where the selected brood-site was located. We used the clogit() function with the Breslow method within the 'survival' R package (Therneau and Lumley 2014). This method creates essentially the same model as a stratified Cox model with one case/stratum, and each group of points (brood-site and two paired random sites) is assigned to a single stratum. We clustered based on individual female to account for dependence among an individual's locations and to calculate robust sandwich variance estimates (White 1980, 1982).

To test for non-linearities of each variable (quadratic, log-transformed), we evaluated univariate models and selected the form with the most explanatory power (lowest AIC_c score; Franklin et al. 2000, Schreiber et al. 2015, Lehman et al. 2016). We used the best fitting univariate forms of each variable within each final model set. We ran all possible additive combinations of variables in each model set.

We tested for correlations between all variables using a Pearson Product Moment correlation. Variables were considered significantly correlated if ($r > |0.7|$). We tested for multicollinearity among variables in the final model set using variance inflation factors (VIF).

Models within the final model set were evaluated using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989, Burnham and Anderson 2002). We considered models ≥ 2 ΔAIC_c units from the top model as candidate models. We examined our candidate model set for nested models including ≥ one additional parameter and essentially the same log likelihood (Burnham and Anderson 2002). Also, we tested for uninformative parameters by calculating 85% confidence intervals around parameter estimates; if 85% confidence intervals overlapped 0, the variable was deemed uninformative (Arnold 2010). However, if model uncertainty existed, all models within 2 ΔAIC_c units from the top model were averaged to generate full model averaged coefficient estimates and standard errors (Burnham and Anderson 2002).

We tested our model fit using Wald tests. Wald tests can simultaneously test multiple parameters against null hypotheses where each variable = 0. We considered our models to be statistically better than a null model if Wald test statistic P-values were <0.05. We used Wald tests rather than likelihood ratio tests because in likelihood ratio tests, independence within clusters (individual females) is assumed. We included clusters to specifically account for non-independence of an individual's brood-sites and therefore, elected to use Wald tests, which accounted for non-independence within clusters. When model averaging was used, we tested each model against the null model before including it in model averaging.

Within our local scale arthropod model set, we sought to select one quantification (count or weight) of each Order. To select the quantification with the most explanatory power, we evaluated univariate models within each Order and selected the quantification with the lowest AIC_c score.

At the landscape scale, we evaluated univariate models to determine the form (percent/mean or distance), scale (0.006 km^2, 1 km^2, 7.07 km^2, 32.17 km^2, and 138.67 km^2), and transformation (untransformed, log-transformed, and quadratic transformed) that best represented each variable in sage-grouse resource selection. We did not assess transformations on distance decay variables, as those variables already represent non-linear responses. We did assess transformations of Euclidean distance to features. By allowing for multiple scales to be simultaneously represented in our landscape model we expected better model performance compared to single scale models (Graf et al. 2005).

Separately, we used the Generalized Linear Model function in R with the binomial family, to determine temporal effects of brood-site selection in terms of “greenness”. For this approach, we combined all brood-sites and all random sites. We examined NDVI using an interaction term with Julian date to assess the possibility that the impact of NDVI on selection varies depending on Julian date. We elected against the conditional approach for this analysis because when comparing the brood-site explicitly to two paired random locations, each with the same Julian date, we were unable to estimate changes through time (via the interaction term). We also used a univariate conditional logistic regression model with NDVI as the only variable to determine if there was selection for NDVI without temporal effects. We evaluated our NDVI models using three methods. For our generalized linear model, we compared AIC_c scores to a fitted null model and also used a Hosmer-Lemeshow Goodness of Fit Test. We evaluated our univariate conditional logistic regression model using significance of the Wald test statistic.

RESULTS

LOCAL SCALE MODELS

In our local scale arthropod model set (Table 2), we included 47 brood-sites from 14 individuals. We found that sage-grouse with broods selected for higher numbers of Coleopterans and “other” arthropods, and selected against high numbers of Hymenopterans and log transformed mass of Orthopterans (Table 3). None of the variables included in the final model set were significantly correlated and all had $VIF \leq 2.5$. Uncorrelated variables used in the final arthropod model set included; Hymenoptera count, natural log of Orthoptera weight, Coleoptera count, “other” count, and natural log of total weight. We observed model uncertainty and therefore, we model averaged models within 2 ΔAIC_c units from the top model (three models; Table 2). Each of the models included in model averaging had significant Wald test scores, indicating they were better than a null model. Variables included in the top three models included; Hymenoptera count, Coleoptera count, “other” count, and the natural log of Orthoptera weight (Table 2). We removed one outlier, which contained an extremely high count of Hymenoptera.

In our local scale vegetation model set (Table 4), we included 76 used brood-sites from 14 individuals. Sage-grouse at the local scale selected for areas with taller grass and greater shrub cover while avoiding areas with greater amounts of grass cover and litter cover (Table 5). Total cover and litter cover were significantly correlated, therefore, we removed total cover from the final model set, as it had a higher AIC_c score than litter cover. After the total cover variable was removed, remaining variables all had $VIF \leq 2.5$. There were eight models within 2 ΔAIC_c units from the lowest AIC_c score and thus, we initially considered all eight as candidate models (Table 4). We observed a set of variables included in all or a majority of the eight candidate models; natural log of grass height (8 of 8), percent litter cover (8 of 8), percent shrub cover (7 of 8), and percent grass (6 of 8). Additional variables in the candidate models (shrub height, percent annual grass, and natural log of percent forbs) were deemed uninformative based on 85% confidence intervals overlapping zero (Arnold 2010). Therefore, we selected our top model as the lowest ranked AIC_c model, which included all four informative variables with no additional variables. Wald test P-value was <0.05 for the top model; therefore, we considered it to be valid. The largest effect was noted for the response to grass height (log transformed), with approximately equal effect sizes for percent litter, percent shrub and percent grass (Table 5).

LANDSCAPE SCALE MODELS

In our landscape model set (Table 6), we included 76 brood-sites from 14 individuals. We found that sage-grouse with broods selected for areas near water and avoided areas near forests and roads, with mixed responses to undisturbed land (Table 7). None of the variables included in the final model set were significantly correlated and all had VIF ≤ 2.5. We evaluated a total of 128 models. We identified six candidate models (models within 2 ΔAIC_c; Table 6). Models that were ranked within 2 ΔAIC_c units from the lowest AIC_c score, and only included one additional parameter were tested to see if the additional variable was informative (85% confidence intervals overlapping zero; Arnold 2010). We found that ruggedness and the natural log of percent sagebrush were both uninformative. This resulted in the top two models as candidate models. The top two models also were nested models, and the model with the lowest AIC_c score contained an additional parameter but also explained additional deviation. Therefore, we selected it as the true top model. Wald test P-value was <0.05 for the top model, and we considered it to be valid.

Parameter estimates from the top model indicated a positive resource selection response to water. We observed negative resource selection responses to; forest and roads and a non-linear response to percent undisturbed land (observed values ranged 30%–100% undisturbed land within 1500 m; Table 7).

TEMPORAL SHIFT IN SELECTION

For our Generalized Linear Regression (logistic) NDVI selection models, we found no evidence of a poor fit with the Hosmer-Lemeshow Goodness of Fit Test (P>0.05), however, our NDVI interaction with Julian Date model did not outcompete a null model. This indicated that our NDVI model did not fit the data better than would be expected at random. Additionally, our univariate conditional logistic regression model including NDVI had a non-significant Wald test statistic; this indicated that we could not reject our null hypothesis which was: selection response to NDVI was constant.

DISCUSSION

In our local scale arthropod selection models, we found that sage-grouse with broods selected areas with higher numbers of Coleoptera and “other” arthropods than random available sites. The high importance of Coleopterans in the diets of sage-grouse chicks has been documented, specifically during early brood rearing (Klebenow and Gray 1968, Peterson 1970). Also, numerous unidentified insects were found in sage-grouse chick diets from 1−12 weeks old (Peterson 1970). The positive response to Coleoptera abundance and abundance of “other” arthropods was likely due to the high importance of both as dietary items during the first four weeks after hatch.

Contrarily, our results indicated a negative selection response to total weight of Orthoptera and number of Hymenoptera. These findings initially seem counterintuitive because arthropods are an important sage-grouse diet component during the first four weeks of life, but similar results were found in Wyoming, where brood-sites had fewer invertebrates than random areas (Thompson et al. 2006). Peterson (1970) found that during the first four weeks, sage-grouse chicks consume Orthopterans; however, Orthopterans only comprised 1% of the volume of their diet during this time. After week four, ≥ 13% of the volume in sage-grouse chick diets consists of Orthoptera (Peterson 1970). Others have found that sage-grouse chicks do not consume Orthopterans until six weeks of age (Klebenow and Gray 1968).

We only sampled arthropods for the first four weeks; thus, the result of sage-grouse avoiding Orthopterans should be interpreted with caution as there may be a shifting selection for Orthopterans as the brood ages. Additionally, sites with high

Orthoptera weight could be the result of sites with large Orthopterans; these large Orthopterans may exceed the gape width of sage-grouse chicks ≤ 4 weeks of age, making them unavailable for actual consumption. We did not measure or analyze individual sizes of arthropods; therefore, we could not explore this possibility.

Sage-grouse chicks frequently consume Hymenopterans during the first four weeks of life (Klebenow and Gray 1968, Peterson 1970). However, we found that sage-grouse broods avoided sites with higher numbers of Hymenoptera than at random available sites; Thompson et al. (2006) found similar results. It is possible Hymenopterans were available in adequate abundance at most sites; if this is true, sage-grouse broods would not seek out sites with high Hymenoptera abundance because they would not be a limiting factor in brood-site selection. Supporting this hypothesis is a study where a prescribed burn created a mosaicked study area that resulted in burned areas containing decreased Hymenoptera abundance. In this example, sage-grouse broods selected areas with higher Hymenoptera abundance (Fischer et al. 1996). This could indicate that Hymenopterans were not available in adequate abundances throughout the burned study area, creating a positive selection pressure. Whereas in our study system, Hymenopterans may be adequately available throughout creating an apparent negative selection response.

Previous research on microhabitat selection during brood rearing indicates different factors affect brood-site selection across the range, with few consistent findings among studies. We found that female sage-grouse with broods select for taller grass and a higher percentage of sagebrush cover. Our finding of a selection preference for taller grass height is supported by several studies conducted across the range (Sveum et al.

1998, Aldridge and Brigham 2002, Hagen et al. 2007). Also, our finding of sage-grouse with broods selecting for higher sagebrush canopy cover is supported by other research (Aldridge and Brigham 2002, Thompson et al. 2006, Herman-Brunson 2007, Kirol et al. 2012) with few contradictory findings indicating an avoidance of higher percent of sagebrush canopy cover (Klott and Lindzey 1990, Hagen et al. 2007).

Conflicting results regarding the selection preference of sagebrush canopy cover could be a function of sage-grouse with broods selecting for an optimal amount of sagebrush cover. In some study areas, the optimal amount is less than sagebrush canopy cover observed at available sites. Our study site is at the fringe of the sagebrush and sage-grouse distribution; sagebrush in our study site is shorter and has lower percent canopy cover than found elsewhere in the sagebrush-steppe (Kantrud and Kolgiski 1983, Connelly et al. 2000, Kaczor et al. 2011b). Therefore, it seems that in our study system, the optimal amount of sagebrush canopy cover is higher than available at random; indicating a positive selection response. This finding mirrors the selection preferences for a sage-grouse population on the northern fringe of the sage-grouse distribution in Canada, where the landscape also is characterized by lower sagebrush canopy cover than found elsewhere within the sage-grouse distribution (Aldridge and Brigham 2002).

We found that sage-grouse broods avoided areas with high percent grass cover and high percent litter cover. These results contradict previous research in South Dakota (Kaczor et al. 2011a) and across the range (Thompson et al. 2006, Hagen et al. 2007, Kaczor et al. 2011a, Kirol et al. 2012). Neither grass nor litter are food components within sage-grouse diets; however, grass and litter may provide cover to sage-grouse. We found that visual obstruction was not a significant variable in our models, indicating that sage-grouse may not be seeking hiding cover during brood rearing in our study system. It is possible that hiding cover is indeed important, but that it was adequately available at both our used and random sites, and therefore we did not find a significant difference between the two. If sage-grouse are not selecting for hiding cover, then there may be no other reason to select areas with high amounts of grass and litter cover.

We found several variables were not important to brood-site selection (visual obstruction, percent forb cover, shrub density, shrub height, annual grass). It is possible that sage-grouse are selecting for these variables at a large scale, and we could not detect this large-scale selection with the methods used. For example, sage-grouse may select pastures or tracts of land with high amounts of hiding cover at a scale ≥ 1.55 km; however, because our paired random available sites were all within 1.55 km of the used site, we could not detect this preference. Data pertaining to our local scale variables were not available at larger scales (via remote sensing) and therefore, we could not assess selection for these variables at the landscape scale.

At the landscape scale, sage-grouse with broods selected areas away from forests. Forested areas provide none of the brood rearing habitat requirements of sage-grouse and their avoidance of forested areas is well documented (Doherty et al. 2008, Atamian et al. 2010, Doherty et al. 2010). Sage-grouse also avoided areas near roads; as distance from roads increases, so does probability of selection. There are multiple reasons sage-grouse may avoid roads including; noise (Blickley et al. 2012), risk of vehicle collision (Trombulak and Frissell 2000), tall structures associated with roads being used as raptor perches (Manier et al. 2014, DeGregorio et al. 2014), or roads serving as travel corridors for predators (Lariviére and Messier 2000, Ruiz-Capillas et al. 2013).

Sage-grouse exhibited a non-linear response to undisturbed land within 1500 m. This response indicates that sage-grouse selected areas with high amounts of plowed land (up to 70% plowed), and also high amounts of unplowed land (100% unplowed) within 1500 m. Areas of lowest selection probability had amounts of disturbed land between the two extremes (values ranged between 30% and 100% undisturbed). The Native Lands Data Layer used for determining plowing history does not distinguish between type of vegetation that is currently present on the landscape; only if the land has ever been plowed or "disturbed". However, a *post hoc* analysis indicated that a majority (74%) of disturbed land identified by the Native Lands Data Layer in Butte and Harding counties is currently grassland/pasture (38%), other hay/non-alfalfa (23%), and alfalfa (13%; USDA CDL 2019). It has been documented that during late summer, both adult sage-grouse and sage-grouse chicks consume alfalfa and spend time in alfalfa fields consuming other forbs (Peterson 1970, Wallestad and Eng 1975, Wallestad 1975). If sage-grouse are indeed selecting for alfalfa within our system, it could explain the dichotomy within the non-linear selection relationship for lands that are mostly "disturbed" and those that are not; especially since we found a positive selection for sagebrush cover within our local scale analysis.

We found no support for our hypothesis regarding a shifting preference towards green areas as they become limited; this indicates sage-grouse are not making resource selection decisions based on NDVI values at a 250 m scale. Similar findings have indicated NDVI may not be an efficient predictor of sage-grouse population dynamics (Blomberg et al. 2012). Blomberg et al. (2012) noted that plant species other than sagebrush (such as trees and grass) have NDVI values but can affect sage-grouse in different ways. Therefore, NDVI values only representing greenness may elicit different responses by sage-grouse depending on the actual landcover causing the "greenness". Additionally, NDVI has been shown to be less predictive in shrublands, compared to grasslands (Paruelo and Lauenroth 1995). We did find that sage-grouse selected areas near water during brood-rearing, which also has been shown elsewhere (Klebenow 1969, Wallestad 1971, Connelly and Markham 1983, Gates 1983, Connelly et al. 1988). Therefore, our hypothesis may be plausible, but using NDVI as an indicator may be inappropriate.

To provide quality brood habitat for sage-grouse, wildlife managers should provide areas away from roads and forests that are close to open water sources. Plowing of sagebrush is not recommended due to the long-term impacts to sagebrush plants, and the documented selection for sagebrush cover at the local scale. At the local scale, wildlife managers should seek to provide tall grass within sagebrush stands, and avoid accumulation of dead, desiccated vegetation (litter).

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Table 1. Variables used in brood-site selection models. Two scales of third order selection were examined (local and landscape). At the landscape scale, within each model set, variables were tested using univariate models to determine scale/form that best described brood-site selection.

Local Scale (≤50 m radius)		**Landscape Scale (45 m−6.4km radius)**
Vegetation	**Arthropods**	**Landscape features**
Grass Height	Coleoptera Count	Undisturbed (unplowed)
Visual Obstruction Reading (VOR)	Orthoptera Count	Sagebrush
Shrub Density	Hymenoptera Count	Forest
Shrub Height	"Other" Count	Water
Total Cover	Total Count	Ruggedness
Grass Cover	Coleoptera Weight	Oil/Gas Wells
Forb Cover	Orthoptera Weight	Roads
Litter Cover	Hymenoptera Weight	NDVI
Shrub Cover	"Other" Weight	
Annual Grass Cover	Total Weight	

Table 2. Models for arthropod selection at the local scale (within 5 m of used or random site). Only top ten models are presented, all possible combinations of five variables were evaluated (n=32).

Model[a]	***K***[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w_i***[e]
Hymenoptera Ct + Orthoptera Wt (log) + Other Ct	3	95.6	0	0.18
Hymenoptera Ct + Orthoptera Wt (log) + Other Ct + Coleoptera Ct	4	95.8	0.21	0.16
Hymenoptera Ct + Orthoptera Wt (log) + Coleoptera Ct	3	96.2	0.63	0.13
Hymenoptera Ct + Orthoptera Wt (log) + Other Ct + Total Wt (log)	4	97.8	2.22	0.06
Hymenoptera Ct + Orthoptera Wt (log) + Coleoptera Ct + Total Wt (log) + Other Ct	5	98.1	2.47	0.05
Hymenoptera Ct + Other Ct	2	98.1	2.53	0.05
Hymenoptera Ct + Coleoptera Ct + Orthoptera Wt (log) + Total Wt (log)	4	98.4	2.79	0.04
Hymenoptera Ct + Coleoptera Ct + Other Ct	3	98.5	2.86	0.04
Orthoptera Wt (log) + Other Ct	2	98.6	3.04	0.04
Hymenoptera Ct + Coleoptera Ct	2	99.2	3.57	0.03

[a] Cole = Coleoptera, Hymenop = Hymenoptera, Orth= Orthoptera, Other = All arthropods not identified within other three orders, log= natural log transformation of variable, Ct= Count, Wt= Weight

[b] Number of parameters

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC$_c$ relative to minimum AIC$_c$

[e] Akaike weight (Burnham and Anderson 2002).

[f] Negative Log Likelihood

Table 3. Full model averaged standardized coefficient estimates and 95% confidence intervals for local scale Arthropod selection.

	Estimate	**SE**	**2.5%**	**97.5%**
Hymenoptera Count	-0.72	0.29	-1.3	-0.15
Orthoptera Weight (log)	-0.56	0.42	-1.4	0.27
Other Count	0.35	0.34	-0.32	1.03
Coleoptera Count	0.25	0.26	-0.27	0.77

Table 4. Models for vegetation characteristics at the local scale (within 50 m of used or random site). Only top 10 models are presented, all possible combinations of 9 variables were evaluated (n=512). Models within 2 ΔAIC_c from the top model were model averaged.

Model[a]	***K***[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w_i***[e]
Natural log Grass Height + %Litter + %Shrub + %Grass	4	135.1	0	0.07
Natural log Grass Height + %Litter + %Shrub + %Grass + Shrub Height	5	135.4	0.23	0.06
Natural log Grass Height + %Litter + %Grass + Shrub Height	4	136.6	1.4	0.03
Natural log Grass Height + %Litter + %Shrub + %Grass + %Annual Grass	5	136.6	1.42	0.03
Natural log Grass Height + %Litter + %Shrub + %Grass + Natural log %Forb	5	136.6	1.46	0.03
Natural log Grass Height + %Litter + %Shrub + %Grass + Shrub Height + %Annual Grass	6	136.7	1.57	0.03
Natural log Grass Height + %Litter + %Shrub	3	136.9	1.78	0.03
Natural log Grass Height + %Litter + %Shrub + %Annual Grass	4	137.0	1.86	0.03
Natural log Grass Height + %Litter + %Shrub + %Grass + %Litter + Shrub Height + Natural log %Forb	6	137.2	2.02	0.02
Natural log Grass Height + %Litter + %Shrub + %Grass + VOR	5	137.2	2.07	0.02

[a] %Grass = percent grass cover, %Litter = percent litter cover, Grass Height(log)= grass height, log transformed, %Shrub= percent shrub cover, Shrub Height=average shrub height, %Annual Grass= percent annual grass cover, %Forb(log)= percent for cover, log transformed, VOR= Visual obstruction reading

[b] Number of parameters

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC$_c$ relative to minimum AIC$_c$

[e] Akaike weight (Burnham and Anderson 2002).

Table 5. Standardized coefficient estimates and 95% confidence intervals for top local scale vegetation model.

	Estimate	**Robust SE**	**2.5%**	**97.5%**
Natural Log Grass Height	1.06	0.35	0.37	1.75
Percent Litter	-0.72	0.25	-1.21	-0.22
Percent Shrub	0.50	0.21	0.08	0.92
Percent Grass	-0.58	0.32	-1.20	0.04

Table 6. Models for features selected at the landscape scale (45 m–6440 m of used or random site). Only top 10 models are presented, all possible combinations of 7 variables were evaluated (n=128). Models within 2 ΔAIC_c from the top model were model averaged.

Model[a]	***K***[b]	**AIC*c***[c]	**ΔAIC*c***[d]	***w*_i**[e]
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + EucDist Road	5	121.51	0	0.17
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m	4	122.03	0.51	0.13
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + EucDist Road + Ruggedness 564 m	6	122.05	0.53	0.13
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + EucDist Road + Natural Log %Sage 564 m	6	123.05	1.54	0.08
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + Ruggedness 564 m	5	123.1	1.59	0.08
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + Natural Log %Sage 564 m	5	123.32	1.8	0.07
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + EucDist Road	7	123.68	2.16	0.06
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + EucDist Road + Natural Log %Sage 564 m + Ruggedness 564 m	7	123.8	2.28	0.05
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + Oil Density 6440 m + Oil Density² 6440 m	6	124.24	2.73	0.04
%Undisturbed 1500 m + %Undisturbed² 1500 m + DecDist Forest 564 m + DecDist Water 6440 m + Natural Log %Sage 564 m + Ruggedness 564 m	6	124.5	2.98	0.04

[a] %Undisturbed = percent undisturbed (unplowed) land, DecDist Forest = decay distance to forest, DecDist Water= decay distance to water, EucDist Road= Euclidean distance to road, Ruggedness=heterogeneity of slope and aspect, Natural Log % Sage= percent sage cover, log transformed, Oil Density= active oil/gas well density, "2"= quadratic transformation, numbers following variables represent moving window radii (km).

[b] Number of parameters

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC_c relative to minimum AIC_c

[e] Akaike weight (Burnham and Anderson 2002).

Table 7. Standardized coefficient estimates and 95% confidence intervals for top landscape scale model.

	Estimate	**Robust SE**	**2.5%**	**97.5%**
Percent Undisturbed (1500 m)	3.08	1.24	0.65	5.51
Percent Undisturbed² (1500 m)	1.28	0.43	0.43	2.13
Decay Distance Forest (564 m)	-4.76	1.75	-8.20	-1.32
Decay Distance Water (6440 m)	0.8	0.31	0.20	1.40
Euclidean Distance Road	0.74	0.52	-0.27	1.75

CHAPTER 6: LINKING SAGE-GROUSE NESTING ECOLOGY COMPONENTS; NEST-SITE SELECTION, NEST PREDATION, AND NEST SURVIVAL

ABSTRACT

The greater sage-grouse (*Centrocercus urophasianus*) is a sagebrush (*Artemisia* spp.) obligate species that typically selects nest-sites under sagebrush. Nest success has been defined as one of the primary drivers in sage-grouse populations, and predation has been documented as the leading cause of nest failure. We sought to link these critical components in sage-grouse nesting ecology; nest-site selection, nest predation, and nest success. We fit 76 female sage-grouse with VHF radio-collars during 2016 and 2017, in South Dakota. We detected a total of 71 nests. Overall nest initiation was 89% in 2016 (n=19) and 100% in 2017 (n=38). Average distance of nest to nearest active lek was 2.5 km (SE=0.3 km, range=0.6–12.2 km). Most nests (90%) were found within 3.5 km of an active lek. We used conditional logistic regression to model nest-site selection as a function of vegetation covariates. We found sage-grouse selected vegetation components at a relatively small scale (within 5 m of nest) and tended to select for taller nest shrubs, taller maximum grass height, and higher percent shrub cover; sage-grouse avoided areas with higher percent grass and annual grass cover than found at paired-random sites. To determine primary sage-grouse nest predators in our study system, we deployed remotely triggered cameras at 48 of 71 nests (68%). Cause-specific nest failures could be determined for 12 of the 25 failed nests with cameras. American badger (*Taxidea taxus*) depredation caused 50% of known cause nest failures (n=6), followed by coyote (*Canis latrans*) depredation (n=2), and abandonment (n=2). Once we determined that American badgers were the leading sage-grouse nest predator, we modeled the occurrence of

American badger using presence only data and landscape variables in MAXENT. Values of predicted probabilities of American badger presence were extracted for each nest and used as a variable in daily nest survival modeling. Additionally, in an attempt to link resource selection and fitness, we assessed variables selected for or avoided by sage-grouse at nest-sites at both the local and landscape scale and assessed if any impacted daily nest survival. None of the vegetation characteristics at nest-sites influenced daily nest survival. However, features important to sage-grouse nest-site selection at the landscape scale were significant in determining the fate of nests. We found that sage-grouse daily nest survival was negatively impacted when the nest-site was closer to an active lek. Also, nest survival was positively impacted when nests were nearer to forests, roads, and in areas with higher percentages of undisturbed (unplowed) land. These results indicate a possible ecological trap, as the resources selected are creating negative fitness consequences. Our model averaged estimate for daily nest survival rate was 0.96±0.01; when extrapolated for the 28-day incubation period, we estimated nest success at 29% (95% CI=20%–42%). By better understanding the vegetative characteristics sought out by sage-grouse when selecting a nest-site, wildlife managers can create attractive habitat without negatively impacting daily nest survival. Further research needs to be conducted to identify underlying factors contributing to the mismatch between nest-site selection and fitness consequences at the landscape scale.

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a sagebrush (*Artemisia* spp.) obligate species (Wallestad and Eng 1975) that typically selects nest-sites under sagebrush (Wallestad and Pyrah 1974). Nest success has been identified as a primary driver of sage-grouse populations (Taylor et al. 2012). Therefore, factors affecting nest-site selection and nest success are of high interest. More specifically, the variables important in nest-site selection may impact nest success, thus these specific variables are of particular interest.

Interactions between resource selection and its effect on individual fitness has been a subject of interest (Rosenweig 1991), and multiple research projects have attempted to link resource selection and fitness consequences for sage-grouse (Aldridge and Boyce 2007, Casazza et al. 2011), and other wildlife species (McLoughlin et al. 2005, Arlt and Pärt 2007, Long et al. 2016).

When features are selected during a resource selection process, and this selection is assumed to be free of cost, selection choices should result in positive fitness consequences for the individual (MacArthur and Pianka 1966, Rosenweig 1974). Sometimes, an individual makes a selection choice that, based on their evolutionary history, should result in a positive fitness consequence; however, with a changing landscape, the positive fitness consequence is now a negative fitness consequence. This phenomenon has been termed an ecological trap.

The concept of an ecological trap was first defined by Gates and Gysel (1978), and is loosely defined as resources that are attractive, and thus, selected for use by an individual; however, the individual experiences negative fitness consequences from use of the selected feature. It is important to identify ecological traps when considering management actions, that may make areas enticing for a species to use yet may not result in an increase in fitness.

For sage-grouse, predation has been shown to be the leading cause of nest failure (Moynahan 2007, Herman-Brunson et al. 2009). Predation has most likely driven the evolution of nest-site selection (Martin 1993), as the nest-site can provide visual, scent, and physical barriers that can protect against depredation (Bowman and Harris 1980, Redmond 1982, DeLong et al. 1995, Holloran and Anderson 2003, Conover et al. 2010). It has been shown that sage-grouse select nest-sites that provide greater visual cover, as opposed to sites that provide greater olfactory concealment from predators (Conover et al. 2010). Because sage-grouse nests are exposed to diverse predator communities, knowing the predator community is crucial to identifying the search mechanisms being used to detect nests. If the search mechanisms of the primary nest predators can be identified, wildlife managers can use proper management tools to increase nest success (Thomson 2007, Benson 2010, Coates and Delehanty 2010). For example, if the primary predator is known to search primarily using visual cues, then increasing visual cover may become more important than providing olfactory concealment. Although predators are a major component in sage-grouse nest-success and adult survival, there is little evidence that predation is the limiting factor in sage-grouse populations (Connelly and Braun 1997).

We had multiple nested objectives, but overall, our goal was to link nest-site selection factors at multiple scales, and the effects of those resources on daily nest survival (similar to Casazza et al. 2011). Additionally, we wanted to identify the primary sage-grouse nest predators and link probability of nest predator occurrence with nest success. First, we modeled nest-site selection at a local scale. Second, we determined sage-grouse nest predators. Third, we modeled probability of occurrence for the identified primary sage-grouse nest predator. Fourth, we modeled daily nest survival using vegetation and landscape features that were selected for or avoided, along with values from our predicted predator occurrence map.

METHODS

STUDY AREA

Our study took place in Harding and Butte counties of northwest South Dakota. The total area of both counties combined is 12,805 km^2. Land use in the study area is dominated by pastureland (>85%), followed by cropland (10−12%; USDA 2012). Over 84% of the study area has never been plowed (Bauman 2018). The majority of the land in the study area is privately owned (~75–80%; USGS GAP 2016). Annual average temperatures range from -1.7°C–10.6°C with an average of 39 cm of precipitation annually (NOAA 2019).

Our study area represents the eastern edge of the sagebrush distribution where an ecotone between sagebrush steppe and grassland ecosystems occurs (Johnson 1979, Cook and Irwin 1992, Lewis 2004). Sagebrush communities found in South Dakota are shorter and have a lower percent canopy cover than found elsewhere in the sagebrush steppe (Kantrud and Kolgiski 1983, Connelly et al. 2000b, Kaczor et al. 2011). Common shrubs in the study area include silver sagebrush (*Artemisia cana*) and big sagebrush (*Artemisia tridentata*; Johnson and Larson 2007).

Common mammalian nest predators found in the study area include; coyote (*Canis latrans*), red fox (*Vulpes vulpes*), American badger (*Taxidea taxus*), raccoon (*Procyon lotor*), and striped skunk (*Mephitis mephitis*). Both Butte and Harding counties undergo predator control efforts conducted by a Multi-County Predator Control District, South Dakota Game, Fish and Parks, and the USDA Wildlife Services. Over 2,600 coyotes and red foxes (combined) were removed from the study area during the fiscal years of 2016 and 2017 via South Dakota Game, Fish and Parks' wildlife damage specialists and USDA Wildlife Services staff (SD GFP 2017).

FIELD METHODS

We annually captured breeding-age female sage-grouse near active leks March–May, as well as at high sage-grouse use areas in August and September using nocturnal spotlighting and a long-handled net (Giesen et al. 1982, Wakkinen et al. 1992a). We aged and sexed captured sage-grouse based on plumage and morphological characteristics (Crunden 1963, Beck et al. 1975, Bihrle 1993). We fit female sage-grouse with a 21.6 g necklace-type Very High Frequency (VHF) radio transmitter (model A4060, Advanced Telemetry Systems, Isanti, MN, USA) as well as a uniquely numbered aluminum butt-end leg band (National Band & Tag Company). We weighed all birds at the time of capture to ensure that radio-transmitters were less than 3% of body weight (Kenward 2001). All animal handling procedures were approved by the Institutional Animal Care and Use Committee at South Dakota State University (IACUC approval # 15-074A).

We located sage-grouse ≥ 2 times per week from 15 April–15 September using the homing method (Samuel and Fuller 1996, Fuller and Fuller 2012) with a hand-held 3-element Yagi antenna or via fixed-wing aircraft equipped with a 2 element, "H" type antenna on each wing. To identify nests, females were located, and nesting status was determined based on the position of female in relation to surrounding vegetation. Nest remains were used to determine success or failure of nest (Williams and Wood 2002).

NEST INITIATION AND NEST DISPERSAL

Nest initiation was calculated by dividing the number of females observed nesting by the total number of radio-collared females present during nesting season. We determined female nesting status by locating radio-collared females ≥ 2 times per week with VHF equipment. We used binoculars to visually locate radio-collared female sage-grouse. Nesting status was determined based on proximity to surrounding shrubs and vegetation as well as behavior. If female was in a different location at the subsequent visit, but a nest was suspected at prior visit, previous site was examined for presence of a nest.

Female sage-grouse were excluded from analysis if they were missing for a period of 14 days or more. This was due to the possibility of researchers failing to detect an initiated nest during the that time period. Females also were excluded if they died during nesting season before a nest was detected (15 Apr–31 May). One hen was captured late in nesting season and had an apparent brood patch. This individual was included due to an assumption that the female had lost a previous nest and was returning to the lek to breed again. Nest initiation estimates likely underestimate actual nests, due to nest depredations occurring before incubation begins, or nests being depredated during the first days of incubation before nest is detected by researchers. Nest dispersal was quantified by measuring the proximity of each nest to the nearest active lek. Lek locations were obtained from South Dakota Game, Fish and Parks.

VEGETATION SAMPLING

Within seven days after estimated or actual hatch date, vegetation was indexed at nest-sites and at two paired random locations within 3.3 km of nest-sites. To compare successful and failed nests without bias, vegetation must be sampled at the same relative time for each (each nest's hatch date or estimated hatch date; Smith et al. 2018). It has been shown that most vegetation components are relatively similar at this time to when the female initiated the nest ~35 days earlier (Hausleitner et al. 2005). However, grass height and grass cover change significantly from initiation to hatch (Hausleitner et al. 2005). The buffer distance of 3.3 km for our random locations was chosen because it was the average distance from nest to nearest active lek in a previous South Dakota sage-grouse study (Kaczor 2008) and therefore, the area within 3.3 km was considered available to a female sage-grouse when selecting a nest-site.

Random points were generated using the Create Random Points tool in ArcGIS. Vegetation sampling was centered at the nearest shrub to the random point if in shrubland, and if located in grassland, then vegetation sampling was centered on the nearest grass or forb bunch to the random point. Transects extended 50 m in each cardinal direction from the nest or random point. Variables measured included; nest shrub height, length, and width, visual obstruction readings (VOR), grass height, canopy cover estimates and sagebrush density.

To estimate VOR at nest and random locations, we obtained measurements using a modified Robel pole with alternating black and white bands 2.54 cm wide (Robel 1970, modified by Benkobi 2000). Observers recorded the lowest band totally obstructed from a distance of four meters and an eye height of one meter. At each VOR sampling point, four readings were taken (one in each cardinal direction) and averaged to a single value. VOR and grass height measurements were taken at the nest or random location (0 m), 1 m, 5 m, 10 m, 30 m and 50 m in each cardinal direction (n=21).

To estimate canopy cover at nest and random locations, we used the Daubenmire method (Daubenmire 1959). Quadrats measured 20 cm x 50 cm. Canopy cover was estimated at nest (0 m), 1 m, 5 m, 10 m, 30 m, and 50 m in each cardinal direction (n=24). Categories estimated consisted of; total cover, total grass, forb, litter, shrub, and annual grass. Annual grass was classified as such if it was either *Bromus japonicus* or *Bromus tectorum*. Canopy coverages of each category were estimated at one of six cover classes (1=0–5%, 2=5–25%, 3=25–50%, 4=50–75%, 5=75–95%, 6=95–100%). Midpoint values of each cover class were assigned and used for analysis.

Sagebrush density was estimated using the Point Centered Quarter method (Cottam and Curtis 1956). Sample locations were placed at the center, as well as every 10 m along each transect (n=21). At each sampling location, four quadrants were created, and the distance to the nearest sagebrush in each quadrant was measured. Sagebrush was measured to a distance of 5 m from each sampling location. For those quadrants where the nearest shrub was >5 m, a default value of 5 m was assigned for calculations. Although this may overestimate shrub density, it is a less severe overestimation, opposed to neglecting the quadrant when calculating average distance to nearest shrub for each sampling location. Using this altered method, the minimum possible calculated shrub density was 0.04 sagebrush/m^2. If the sampling plot was located in an area with no sagebrush, density per square meter was set to a default value of 0 sagebrush/m^2. Each shrub to which distance was measured also had height measured. Sagebrush heights were averaged for each site.

CAMERA DEPLOYMENT AT NEST-SITES

Methods of identifying nest predators via the traditional methods of examining remains of predated nests, along with other signs left at predated nests, have been shown to be inaccurate and misleading (Lariviere 1999, Pietz and Granfors 2000, Williams and Wood 2002, Staller et al. 2005). Using camera technology at nests is a more effective method for identifying nest predators than an analysis of nest remains (Richardson et al. 2009), and, if properly implemented, cameras do not impact nest predation rates for grassland ground nesting birds (Pietz and Granfors 2000, Herranz et al. 2002) or sage-grouse (Coates et al. 2008, Coates and Delehanty 2010, Lockyer et al. 2013).

We deployed Moultrie M-888 motion triggered mini game cameras at nest-sites. Cameras were equipped with an infrared flash capable of reaching >21 m. Cameras were set to take a photo at the onset of motion, with a 30 second delay between detections. Passive infrared sensor (PIR) sensitivity was set to high or low based on researcher discretion. Cameras were not deployed during inclement weather due to possibility of flushing female sage-grouse resulting in egg chilling. If a female sage-grouse flushed from the nest and did not return within two hours, all camera equipment was removed from nest. In 2016, we deployed cameras as soon as nests were detected. In 2017, a new protocol was put in place to minimize abandonment. The new protocol restricted placing cameras until females had been incubating for a minimum of 5–7 days.

It should be noted that photometric analysis is somewhat subjective. On multiple occasions predators were detected on cameras, yet the nest remained intact. Due to these observations, it was difficult to assign cause of nest failure based on a predator detection event at a nest. Final conclusions were based on timing of predator detection and timing of nest being unoccupied by female based on VHF signal. For example, if an American badger was detected on camera, yet we know the female was present on the nest following the time of the American badger observation based on VHF signal, we eliminated that particular American badger observation as the nest-predation event. If multiple predators were detected on a single nest camera, we used multiple sources of information to inform our decision as to which predator likely caused the depredation. Sources of information included images of; female sage-grouse attempting to defend nest, timing of known incubation based on VHF signal, timing of female sage-grouse incubation break photos relative to each predator's detection, and if available, photos of predator physically inside nest bowl.

ANALYSIS NEST-SITE SELECTION

Habitat selection is defined as use of a resource at a rate greater than its availability (Johnson 1980, Garshelis 2000). Johnson (1980) defines varying scales of selection including: the species' geographic range, the individual's home range, habitat components within the home range, and specific food items within the selected habitat components. We analyzed nest-site selection at the third order; habitat components within the individual's home range (Johnson 1980).

We z-standardized all variables before modeling so parameter estimates of effect sizes would be directly comparable to one another. We modeled the probability of a sage-grouse selecting a nest-site from a set of potential sites with discrete choice models, specifically, conditional logistic regression models (Cooper and Millspaugh 1999, Schreiber et al. 2015, Lehman et al. 2016). We used discrete choice models with one nest-site/stratum; this directly compares each nest-site to two paired-random sites sampled. This methodology allows for resource availability to vary spatially and temporally, depending on when and where the selected nest-site was located. We used the clogit() function with the Breslow method within the 'survival' R package (Therneau and Lumley 2014). This method creates essentially the same model as a stratified Cox model with one case/stratum, and each group of points (nest-site and two paired random sites) is assigned to a single stratum. We clustered based on individual female to account for dependence among an individual's nests (re-nests and nests from same individual in both years) and to calculate robust sandwich variance estimates (White 1980, 1982).

We tested for correlations between all variables using a Pearson Product Moment correlation test. Variables were considered significantly correlated if $r > |0.7|$. We tested for multicollinearity among variables in the final model set using variance inflation factors (VIF).

Models were evaluated using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). We considered models ≤ 2 ΔAIC_c units from the top model as candidate models. We examined our candidate model set for nested models including $\geq$ one additional parameter and essentially the same log likelihood (Burnham and Anderson 2002). Also, we tested for uninformative parameters by calculating 85% confidence intervals around parameter estimates; if 85% confidence intervals overlapped zero, the variable was deemed uninformative (Arnold 2010).

If model uncertainty existed, all models within 2 ΔAIC_c units from the top model were averaged to generate full model averaged coefficient estimates and standard errors (Burnham and Anderson 2002). Model averaging reduces bias which may occur when a top model is selected, and in fact it is not the true top model. Model weights were re-assigned within the candidate model set, so that total model weights summed to 1 prior to model averaging. We based inference off of full model averaged coefficient estimates; models that exclude a certain variable had a coefficient value of zero assigned for that variable whereas models that included the same variable had the estimated coefficient value from the model assigned. For each model, the coefficient values estimated (or assigned values of 0) along with that model's weight were used to generate weighted average coefficient values also termed full model averaged coefficient estimates.

We tested our model fit using Wald tests. Wald tests can simultaneously test multiple parameters against null hypotheses where each variable equals zero. We considered our models to be statistically better than a null model if Wald test statistic P-values were <0.05. We used Wald tests rather than likelihood ratio tests because in likelihood ratio tests, independence within clusters (individual females) is assumed; our models were defined using clusters and thus, did not meet independence assumptions required for likelihood ratio tests.

We were unsure at which scale sage-grouse may be making selection decisions; therefore, we tested two different scales of each vegetation variable, mean value within five meters of nest or random location, and mean values within 50 m of nest or random location. We compared univariate models of each scale for every variable, and selected the scale of each variable with the lowest AIC_c score to use in our models.

Variables considered in nest-site selection included; VOR, maximum grass height, percent total cover, percent grass cover, percent forb cover, percent litter cover, percent annual grass cover, sagebrush density, average shrub height, nest shrub height.

AMERICAN BADGER SPECIES DISTRIBUTION MODEL

The American badger has been identified as a common sage-grouse nest predator (Coates et al. 2008, Parsons 2019 Chapter 6). We assessed our hypothesis that sage-grouse nests may have higher or lower probability of success dependent upon the modeled probability of occurrence of American badgers at each nest-site. We used American badger location data collected via remotely triggered camera stations located approximately 6.68 km apart (Mitchell 2018) across Butte and Harding counties in the summer/fall of 2016. Cameras were operated for six nights at each site. We used presence only data to model American badger habitat suitability using MAXENT (Phillips and Dudik 2008, Phillips et al. 2018).

Variables used to model American badger suitability included; landcover, distance to development (National Land Cover Dataset 2011), distance to road (U.S. Census Bureau, TIGER 2015 Roads), elevation, slope, aspect, and ruggedness (USGS, National Elevation Dataset). The MAXENT model was replicated 15 times using the bootstrapping method. We evaluated the model using a receiver operator characteristic (ROC) curve and assessed the “area under the curve” (AUC). The modeled landscape was originally generated at 30 m pixel resolution but was re-sampled in ArcGIS using cubic convolution to 100 m pixel resolution. Probability of American badger occurrence values were extracted for each nest-site and used as a covariate in nest success models.

NEST SUCCESS

Nest success was calculated using the R interface, RMark (Laake 2013) with program MARK (White and Burnham 1999). Initially, two *a priori* models were evaluated: constant survival (β_0) and a model using "Year" as a covariate ($\beta_0 + \beta_1$YEAR). Models were evaluated using AIC$_c$ (Burnham and Anderson 2002). If there was no support for the model including "Year" (indicating no difference in Daily Survival Rate (DSR) between years), nests were pooled across years. If we experienced model uncertainty, all models within 2 ΔAIC$_c$ units from the top model were averaged to generate full model averaged DSR estimates and standard errors (Burnham and Anderson 2002).

We evaluated three model sets quantifying factors affecting nest success. Our first model set consisted of vegetation characteristics measured and averaged within 50 m of the nest. We included the following variables; total cover, grass cover, shrub cover, grass height, visual obstruction, shrub density, shrub height, and predicted probability of American badger occurrence. We evaluated all possible combinations of these variables.

Our next two model sets consisted of variables found to be important in nest-site selection at two different scales. We assessed these variables to determine if factors that were specifically selected or avoided when sage-grouse were selecting nest-sites had an impact on the fate of nests, and thus, fitness. In other words, we wanted to determine if the selection choices made by sage-grouse at nest-sites had fitness consequences.

We evaluated vegetation characteristics found to be important to nest-site selection at a local scale (identified within the nest-site selection portion of this chapter's analysis). We evaluated all possible combinations of these variables. Additionally, in a separate model set, we used the landscape variables shown to be important to sage-grouse nest-site selection at a landscape scale (Parsons 2019; Chapter 4). Those variables included; distance to forest with a decay function at 564 m, distance to lek with a decay function at 3.2 km, road density within a 3.2 km search radius, percent undisturbed (unplowed) land within 3.2 km, and percent water within 6.44 km. We evaluated all possible combinations of these variables.

RESULTS

NEST INITIATION AND NEST DISPERSAL

We captured and radio-collared a total of 76 female sage-grouse. We detected a total of 71 nests, one of which was abandoned due to camera deployment/observer. Overall nest initiation was 89% in 2016 (n=19) and 100% in 2017 (n=38). Re-nest initiation rate was 40% in 2016 (n=10) and 55% in 2017 (n=22). In 2016 and 2017, when initial and re-nest attempts were combined, 7 of 19 (37%) and 18 of 38 (47%) females, respectively, successfully hatched a nest.

Combining all nests found in 2016 and 2017, the average distance of nest to nearest active lek was 2.5±0.3 km, range = 0.6–12.2 km (n=71). Most nests (90%) were within 3.5 km of an active lek and 93% of all nests found were within 4 km of an active lek.

NEST-SITE SELECTION

We found that sage-grouse were selecting vegetative characteristics at a small scale (within 5 m of nest), as our 0–5 m average values outcompeted the 0–50 m values for every variable in the univariate models. We experienced little model uncertainty (Table 1). The top model contained all variables used in the other competitive model with the addition of one variable; all variables were significant when we examined 85% confidence intervals (none overlapped zero). Five variables were found to be important in sage-grouse nest-site selection; nest shrub height, percent annual grass cover, maximum grass height, percent grass cover, and percent shrub cover. Sage-grouse selected for taller nest shrubs, taller maximum grass height, and more shrub cover than was available at random sites; sage-grouse avoided areas with high grass cover, and more specifically, annual grass cover (Table 2). Litter and total cover were significantly correlated, and because total cover had a lower AIC_c score, we retained it to use in our models. Similarly, nest shrub height and VOR were significantly correlated. Nest shrub height had a lower AIC_c score, and so we retained it in our models. All remaining variables had $VIF \leq 2.5$. The top model that we used to make inferences from had significant Wald test scores, and we considered this to be a valid model.

CAUSE-SPECIFIC NEST FAILURE

Infrared cameras were deployed on 48 of 71 nests (68%). During the 2016 and 2017 nesting seasons, 234,521 photos were taken. Causes for not deploying infrared cameras included; camera removal if female did not return within two hours of deployment (n=3), improper vegetation characteristics to properly conceal camera (n=2), nest was depredated before camera could be deployed (n=17), and camera was not placed due to high risk of abandonment (n=2).

Of the failed nests (n=46), cameras were deployed on 25 (Table 3). Cause-specific nest failures could be determined for 12 of the 25 failed nests with cameras. American badger depredation caused 50% of known cause nest failures (n=6), followed by coyote depredation (n=2), and abandonment (n=2). One nest was depredated by a striped skunk and one nest was found intact, but the female sage-grouse had been predated.

AMERICAN BADGER SPECIES DISTRIBUTION MODEL

We created an American badger species distribution model for our study site (Figure 1) using 41 detection locations. The road distance variable had the highest percent contribution to model (49.4%) followed by, landcover, slope, ruggedness, and aspect (19.9%, 11.8%, 8.8%, 7.6%, respectively). Lastly, distance to development and elevation had little contribution to model development (2.5% and 0.1% respectively). We considered our model to be valid; our average training AUC value was 0.90, SD=0.014. Thus, our model was adequate to use as a covariate in sage-grouse daily nest survival models.

NEST SUCCESS

We did not find a significant impact of year on daily nest survival, therefore, we combined both years and used a total of 70 nests to estimate nest success; 25 were successful (36%). In the first model set, evaluating vegetation characteristics within 50 m of nest-site, the more complex models did not outcompete the null model. This indicates that none of the vegetation variables within this model set significantly contributed to explaining additional variation within the data.

In the second model set, we evaluated vegetation characteristics found to be important in nest-site selection at the local scale. Variables within this model set included; nest shrub height, percent annual grass cover, maximum grass height, percent grass cover, and percent shrub cover; variables were averaged within 5 m of nest-site. None of the more complex models outcompeted the null model, indicating none of these variables significantly contributed to explaining additional variation within the data. Additionally, these vegetation variables did not make a significant difference in determining whether or not a nest was successful.

We experienced model uncertainty in our model set containing variables important in nest-site selection at the landscape scale (Table 4). Therefore, we used model averaging with all models within 2 ΔAIC_c units from the top model (six models). We found that sage-grouse daily nest survival declined as nest-sites were closer in proximity to an active lek (Table 5). Also, daily nest survival increased when nests were closer to forests, in higher road density areas, and in areas with higher percentages of undisturbed (unplowed) land (Table 5).

We elected to make inferences based on our full model averaged estimates of DSR. We calculated DSR using model averaging within the landscape scale nest-site selection model set (Table 4) and our DSR estimate using these models was 0.96±0.01.

When extrapolated for the 28-day incubation period, our modeled nest success estimate was 29% (95% CI=20%–42%).

We used distance decay functions for distance to forest and leks. Distance decay functions allow a non-linear response to distance from features, and values range from 1–0. Areas near to features have higher values and as distance to feature increases, values reach 0. Distances at which values decrease more rapidly (thresholds) are dependent upon the scale's search radius used in the decay equation. Distance decay values are closer to 1 when near to the feature, as distance increases, values reach 0. Interpretation of distance decay coefficients is opposite Euclidean distance coefficients. Also, because of the non-linear response of distance decay variables, it is difficult to define changes in nest success using standard distance units. Therefore, we elected to make comparisons between the minimum and maximum distances from features observed.

We found a positive effect of forest on DSR. The nearest nest to forest was 948 m. Using an exponential distance decay for forest at 0.564 km, values reached 0 at 9.5 km; a total of 20 nests had forest distance decay values of 0 (≥ 9.5 km from forest). By calculating the odds ratio between the nearest observed nest to forest (948 m) and those ≥ 9.5 km, the odds of a nest succeeding are 74% lower for the farthest nests, compared to the nearest nest to forest.

Using the lek distance decay variable at 3.2 km, values reached 0 around 47 km, and therefore none of our nests had lek distance decay values of 0. The nearest nest to a lek was 524 m and the farthest was 12.2 km. By calculating the odds ratio for the nearest observed nest to a lek (524 m) and the farthest one (12.2 km), the odds of a nest succeeding are 49% lower for the nearest nest, compared to the farthest we observed.

We found a positive effect of road density on nest success. The highest road density value observed was from a nest that was within 281 m from the nearest road, but also within a 3.2 km vicinity of three additional roads. We observed 15 nests with road density values of 0. Using the odds ratio for the nest with the highest observed road density and the nests with the lowest observed road density (0), we found the nest in high road density is 29% more likely to be successful compared to nests located in areas with no roads within 3.2 km.

We observed a positive nest success response to percent undisturbed land within 3.2 km; however, the variable was only in one of the six models used in model averaging. We observed percent undisturbed land within 3.2 km of nests range from 59%–99%. Using our calculated odds ratio, we would expect to see a 4% increase in the odds that a nest is successful if it had 99% undisturbed land within 3.2 km of nest compared to 59% undisturbed land within 3.2 km of a nest.

These results indicate a mismatch between features selected, and their fitness consequences in terms of nest success. To clarify, sage-grouse tend to select nest-sites in areas farther from forests, nearer to leks, and in areas with low road density; all of these features result in higher probability for nest failure. The positive selection response for a higher percentage of undisturbed land results in a positive fitness consequence, as the percent undisturbed land has a positive effect on nest survival.

DISCUSSION

NEST INITIATION AND NEST DISPERSAL

We observed generally high nest initiation during both years of the study (89% and 100%). The lower nest initiation rates observed in 2016 could be due to the fact that we radio-collared a higher proportion of yearling female sage-grouse in 2016. It has been documented that yearling sage-grouse have lower nest initiation rates than adults (Connelly et al. 1993, Taylor et al. 2012). In a range-wide assessment, Taylor et al. (2012) documented yearling nest initiation to be 89% and adult nest initiation to be 96%. Therefore, it appears that our nesting rates are within the typical range of nest initiation values.

We found that >90% of nests were within 3.5 km of an active lek. Nest-lek distances are highly variable across the sage-grouse distribution. In western Wyoming and Idaho, >90% of nests were within 8.5 km, and 3 km, respectively, of an active lek (Wakkinen et al. 1992b, Holloran and Anderson 2005). Previous research in South Dakota indicated 97% of nests were within 7 km of an active lek (Kaczor et al. 2011, SD GFP 2014). When we included all nests documented in South Dakota (Parsons 2019; Chapter 4) we found that 90% of nests were within 6 km of an active lek. This particular study was focused in Harding County, whereas the previous research was focused primarily in Butte County and occurred ~ 10 years prior. The difference in nest-lek distances between studies could be an artifact of temporal or spatial differences between studies.

NEST-SITE SELECTION

We found that sage-grouse are exhibiting a stronger selection response for vegetation variables close to the nest-site (within 5 m of nest) opposed to mean values within 50 m of nest-site. We found that sage-grouse were selecting for taller nest shrubs, taller maximum grass height, and higher percent shrub cover. Our finding of sage-grouse selecting for higher amounts of shrub cover is supported by other research (Gregg 1994, Holloran et al. 2005, Aldridge and Brigham 2007, Kaczor et al. 2011, Lockyer et al. 2015). Our finding of sage-grouse selecting for taller grass at nest-sites also has been supported by previous research (Aldridge and Brigham 2002, Holloran et al. 2005, Kaczor et al. 2011). We found that VOR within five meters of the nest-site was highly correlated with nest shrub height; VOR was shown to a predictor of nest success in the previous North and South Dakota studies (Herman-Brunson et al. 2009, Kaczor et al. 2011). Therefore, even though the previous studies in the Dakotas did not evaluate nest shrub height, it likely has a similar impact on nest-site selection as VOR, because the two were found to be highly correlated.

We found that sage-grouse avoid areas with high amounts of grass cover, and also high amounts of annual grass cover when selecting nest-sites. Many studies showed no effect or mixed effects of grass cover (Gregg 1994, Popham and Gutiérrez 2003). In our study system, we observed a majority of sites with high amounts of total cover. Therefore, it is possible that this observation is a direct tradeoff between shrub cover and grass cover; sage-grouse are selecting for higher amounts of shrub cover and in turn, avoiding high percent grass cover sites, which are readily available.

The avoidance of annual grasses has been documented elsewhere (Lockyer et al. 2015) but is often times not a variable used in nest-site selection analyses. The invasion of exotic grasses (annual grasses) has been documented as a range-wide threat to the breeding habitat of sage-grouse (Connelly et al. 2000, Crawford et al. 2004). Although annual/exotic grass invasion is documented as a threat to sage-grouse on a large scale, at a local scale, sage-grouse may avoid areas with high amounts of annual grass because it has no biological value to sage-grouse. Sage-grouse do not consume grass (Patterson 1952, Wallestad and Eng 1975). Also, annual grasses are typically shorter and provide less cover than other available native vegetation.

It is important to note that by measuring vegetation at actual or estimated hatch date, we measured vegetation conditions > 30 days after the female sage-grouse had selected the site and began laying eggs. This was necessary to avoid disturbing incubating female sage-grouse. Hausleitner et al. (2005) found that estimating vegetation post-hatch adequately described selection for shrub height, visual obstruction, percent shrub cover, percent litter cover, and percent forb cover; grass height and percent grass cover significantly changed between initiation and hatch, therefore those values should be viewed relatively. In other words, our finding of sage-grouse selecting for taller grass is valid, however managers should make grass height recommendations based off of grass heights observed at initiation dates rather than hatch dates; our measurements were collected at hatch date.

CAUSE-SPECIFIC NEST FAILURE

We were able to identify nest predators at nearly half of the nests that had cameras deployed and failed. However, we missed opportunities to identify nest predators at 13 failed nests with cameras deployed. Reasons for failed depredation detections included vegetation growth covering camera, power loss, insufficient memory, camera was not triggered, or poor camera angles. Although we used radio-signals to determine date of females leaving nests along with camera data, there was still possible bias associated with detecting predators on camera and associating depredation events with particular individuals.

Another technique used to identify nest predators includes molecular testing of predator saliva on nest remains to isolate DNA and identify type of predator (Hopken et al. 2016). This method has proven difficulties detecting avian predator DNA due to the co-amplification of avian prey DNA from nests, but it can be successful (Vestheim and Jarman 2008, Steffens et al. 2012). It appears that the most effective method of accurately identifying nest predators at this time includes using a molecular approach along with remotely triggered cameras at nests (Steffens et al. 2012, Hopken et al. 2016). This approach would reduce bias associated with both methods employed individually, such as DNA contamination from subsequent nest visitors/scavengers, as well as multiple predators captured on cameras without sufficient data to identify the true nest predator.

We determined primary nest predators in our study system and knowing the predator community is crucial to managing for higher nest success, specifically in order to identify the search mechanisms being used to detect nests (Thompson 2007, Benson 2010).

NEST SUCCESS

Our modeled nest survival estimate using model averaged estimates, was 29%; our raw observed nest success was 36%. Previous studies in the Dakotas estimated nest success to be 30–53% (Herman-Brunson et al. 2009, Kaczor et al. 2011), varying between years and study sites. Across the range, sage-grouse nest success has a wide range, from 14.5% (Gregg et al. 1994) to 86.1 % (Trueblood 1954). Mean nest success across the range is estimated at 47.3% and 47.7% using 14 and 16 studies, respectively (Connelly et al. 2004, Crawford et al. 2004). These data indicate that our nest success rate was below range wide average, and among the lower range wide observations of nest success (Connelly et al. 2004).

We found several landscape features that impacted daily nest survival rate; distance to forest, distance to lek, road density, and percent undisturbed land. More interesting, is the fact that forest, leks, and roads exhibit opposite selection and fitness responses, indicating a potential ecological trap. Often, ecological traps are developed from anthropogenic altered landscapes that create a mismatch between attractive habitat and habitat that is dangerous. These altered landscapes can change quickly; more quickly than evolutionary responses can be developed. The only factor we found to be important that was associated with human disturbance was road density, whereas lek locations and forest are natural features. Even so, leks and forests can be considered an ecological trap because of the mismatch of responses between selection and fitness.

It is important to note that we only examined fitness consequences related to nest success. Immediately after a nest hatches, chick survival becomes important; chick survival is also a component of an individual's fitness. Therefore, although we found negative fitness consequences in terms of nest success, sage-grouse could be experiencing an overall increase in fitness, if the variables in question increase chick survival or adult survival.

Sage-grouse nest survival increases as nests are located nearer to forests. This could be a response of changing predator communities between forested areas and the sagebrush steppe. Also, we found decreasing nest survival as nests are located closer to leks. We know that sage-grouse typically nest within 3.5 km of leks, and it is possible that as nest densities are higher in these areas, predation pressure is higher; predators are optimizing search efforts and focusing on these areas. It is also possible that features that determine an optimal lek site are also optimal for certain nest predators, creating a high amount of overlap in these areas (Coates and Delehanty 2010). We found that as road density increased, so did daily nest survival. This result is counterintuitive, especially because our predicted probability of American badger occurrence model indicated that American badger occurrence is more likely near roads. It is possible that predators are displaced near roads, where human activity is prevalent; if so, these areas could create a spatial refuge from predation (Mulhy et al. 2011, Burr et al. 2016).

Lastly, we found increased daily nest survival with increasing percent undisturbed land. This could indicate that intact native sagebrush stands and grasslands function better in providing nesting habitat for sage-grouse. Unplowed lands may naturally be more heterogeneous relative to land that has been plowed and potentially planted to a monoculture. It has been found that ground nests in heterogeneous habitat patches are more likely to be successful compared to homogeneous habitat (Mankin and Warner 1992, Churchwell et al. 2010). Heterogeneous habitat can result in less efficient search efforts for predators, and likely less efforts put into searching these areas by predators (Bowman and Harris 1980). Additionally, if a greater proportion of the land is unplowed, patch sizes may be larger; larger patch sizes have been shown to have a positive impact on nest success of ground nesting birds (Paton 1994, Sovada 2000).

Local scale vegetation components did not have an impact on daily nest survival rates. This finding differs from previous research conducted in South Dakota that found grass height and litter cover impacted daily nest survival. One major difference between the design of our study and the previous work is the timing at which vegetation was measured. We measured vegetation within one week of estimated or actual hatch date, so that all nests (successful and failed) had vegetation measurements at the same relative time to one another. The previous research conducted vegetation surveys “after fate was determined” (Kaczor et al. 2011). The design implemented in the previous study, which measures successful nests later in relative time than failed nests, has been shown to be biased based on phenology affecting grass height (Smith et al. 2018). This could be the sole explanation for grass height being non-significant in our daily nest survival models, whereas in previous studies in South Dakota, it was significant.

MANAGEMENT IMPLICATIONS

Wildlife managers should seek to provide habitat which is likely to be selected and used by sage-grouse when selecting a nest-site. Therefore, managers should attempt to provide sites with high sagebrush cover, and tall grass. Managers should make efforts to control the invasion of annual grasses, as they are avoided by sage-grouse and can contribute to altered fire regimes. Although it is important that we identified the primary nest predator of sage-grouse as the American badger, there is little direct evidence that controlling predators has a positive impact on sage-grouse populations. There has been no research to our knowledge conducted specifically on American badger removal and its impacts. Therefore, predator control is not recommended without further specific research on American badger removal and its impacts to sage-grouse nest success.

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Table 1. Models for vegetation characteristics predicting nest-site selection. Only top 10 models are presented, all possible combinations of 7 variables were evaluated (n=128).

Model[a]	K[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	w_i[e]
Nest Height + %Annual Grass + Grass Height + % Grass + % Shrub	5	86.07	0	0.28
Nest Height + %Annual Grass + Grass Height + % Grass	4	87.93	1.86	0.12
Nest Height + %Annual Grass + % Grass + % Shrub	4	88.23	2.16	0.10
Nest Height + %Annual Grass + Grass Height + % Grass + % Shrub + % Total Cover	6	88.46	2.39	0.09
Nest Height + %Annual Grass + Grass Height + % Forb + % Grass + % Shrub	6	88.46	2.39	0.09
Nest Height + %Annual Grass + % Grass	3	89.88	3.81	0.04
Nest Height + %Annual Grass + % Forb + Grass Height + % Grass	5	90.02	3.95	0.04
Nest Height + %Annual Grass + Grass Height + % Grass + % Total Cover	5	90.17	4.1	0.04
Nest Height + %Annual Grass + % Grass + % Shrub + % Total Cover	5	90.19	4.12	0.04
Nest Height + %Annual Grass + % Forb + %Grass + % Shrub	5	90.52	4.45	0.03

[a] Nest Height=maximum height of nest shrub or other vegetation covering nest, % Annual Grass = percent cover of *Bromus japonicus* or *Bromus tectorum*, Grass Height= maximum grass height, % Grass= percent grass cover, % Shrub=percent shrub cover, % Total Cover= percent total cover, % Forb= percent forb cover

[b] Number of parameters

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC$_c$ relative to minimum AIC$_c$

[e] Akaike weight (Burnham and Anderson 2002).

Table 2. Sage-grouse nest-site selection top model's standardized coefficient estimates with robust standard error estimates and 95% confidence intervals.

	Estimate	**Robust SE**	**2.5%**	**97.5%**
Nest Height	1.4413	0.3323	0.79	2.09
% Annual Grass Cover	-1.1965	0.3573	-1.90	-0.50
Maximum Grass Height	0.6497	0.3475	-0.03	1.33
% Grass Cover	-0.9449	0.3173	-1.57	-0.32
% Shrub Cover	0.5095	0.2461	0.03	0.99

Table 3. Summary of overall nest fates in relation to infrared camera deployment.

	Nest Fate	
	Successful	Unsuccessful
Camera	23	25
No-Camera	2	21

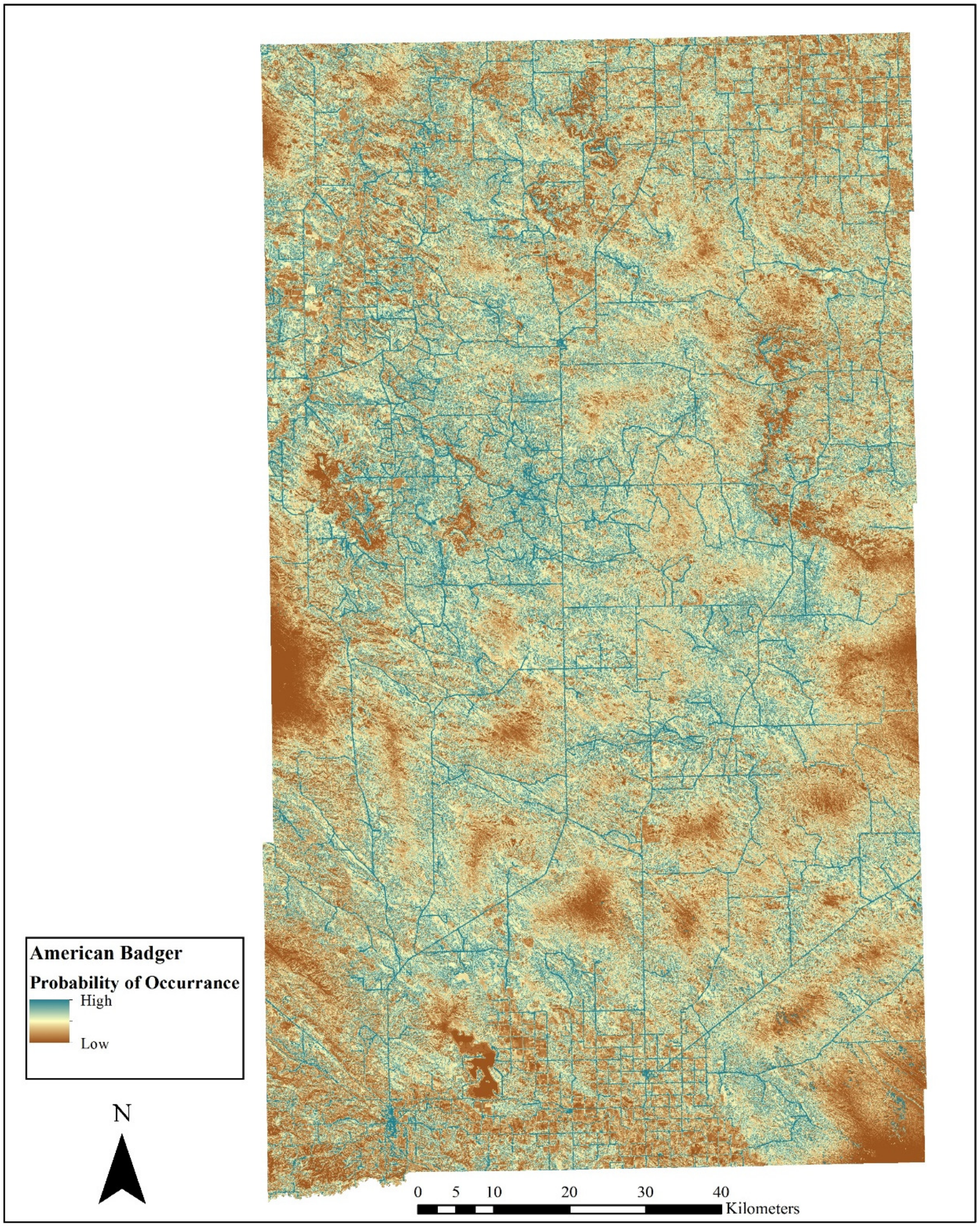

Figure 1. Map of predicted probability of American badger occurrence. Values from this output were extracted for each nest-site and used as covariate in nest success models.

Table 4. Model set for daily nest survival using variables found to be important to nest-site selection at the landscape scale. All possible combinations of five variables were used in models with the addition of an intercept only model (n=32); only the top 10 models are presented here.

Model[a]	***K***[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w_i***[e]	**Deviance**[f]
FOREST + LEK	3	249.7	0.00	0.11	243.62
FOREST	2	250.0	0.32	0.10	245.95
FOREST + ROAD	3	250.0	0.36	0.09	243.98
FOREST + LEK + ROAD	4	250.6	0.95	0.07	242.55
LEK	2	250.7	1.06	0.07	246.69
FOREST + LEK + UNDIST	4	251.4	1.76	0.05	243.37
FOREST + LEK + WATER	4	251.7	2.02	0.04	243.62
FOREST + ROAD + WATER	4	251.9	2.26	0.04	243.87
FOREST + WATER	3	251.9	2.27	0.04	245.89
FOREST + ROAD + UNDIST	4	251.9	2.29	0.04	243.89

[a] FOREST= Distance to forest with decay function at 564 m, LEK= Distance to lek with decay function at 3.2 km, ROAD= Road density within 3.2 km search radius, UNDISTURBED= Percent unplowed land within 3.2 km, WATER= Percent water within 6.44 km.

[b] Number of parameters plus intercept

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[d] Difference in AIC$_c$ relative to minimum AIC$_c$

[e] Akaike weight (Burnham and Anderson 2002).

[f] Negative Log Likelihood

Table 5. Full model averaged unstandardized coefficient estimates and 95% confidence intervals for daily nest survival models using landscape scale covariates.

	Estimate	**SE**	**Adjusted SE**	**2.5%**	**97.5%**
Intercept	3.232	0.804	0.805	2.19	4.28
Forest Distance Decay 0.564 km	6.365	4.762	4.766	-0.89	13.56
Lek Distance Decay 3.2 km	-0.804	0.959	0.959	-1.87	0.25
Road Density 3.2 km	707.5	1402.0	1403.0	-401.33	1784.25
Percent Undisturbed 3.2 km	0.001	0.006	0.006	-0.002	0.004