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Kirol, Christopher, P., Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape, M.S., Department of Ecosystem Science and Management, May 2012.

Landscapes undergoing intensive energy extraction activities present challenges to the persistence of wildlife populations. Much of the oil and gas resources in western North America, underlie sagebrush (*Artemisia* spp.) ecosystems. The greater sage-grouse (*Centrocercus urophasianus*) is a sagebrush obligate that is dependent on this ecosystem for its entire life-cycle. Greater sage-grouse are of concern because they have shown a precipitous decline in numbers and distribution over the last half century. The decline in greater sage-grouse populations is largely attributed to extensive alteration and loss of habitat. As a consequence of this decline, the greater sage-grouse was recently listed under the Endangered Species Act of 1973 as warranted but precluded (USFWS 2010). Oil and gas development has been identified as the one of the leading threats to the species in the eastern portion of its range, which includes Wyoming. Concerns in areas that oil and gas development and greater sage-grouse overlap include direct habitat loss, habitat fragmentation, effective habitat loss due to avoidance behavior, and reduced fitness rates including lower nest success. To address these concern I developed research objectives to: 1) spatially quantify habitat quality for female greater sage-grouse during the reproductive period in the Atlantic Rim Project Area (ARPA) of south-central, Wyoming, which was being developed for coalbed natural gas (CBNG) resources, 2) utilize a non-impacted offsite reference area (Stewart Creek [SC]) to assess factors potentially contributing to changes in habitat quality resulting from energy development during the nesting period, and 3) explore microhabitat conditions that were crucial to female greater sage-grouse reproduction. To achieve

my objectives I monitored radio-marked female greater sage-grouse throughout the reproductive period in 2008 and 2009.

In a geographic information system (GIS) framework, I quantified habitat quality for greater sage-grouse in the ARPA by generating a suite of habitat-specific environmental and anthropogenic variables at three landscape scales. With these variables, I modeled greater sage-grouse habitat occurrence and fitness outcomes for each female life-stage. The final occurrence models were in the form of resource selection functions (RSFs). I modeled fitness as relative survival probabilities and included them in a population growth rate function. The RSFs and population growth rate function were combined into an ecological model predicting sink and source habitats as well as a continuous habitat quality measure on the landscape. My results showed that environmental and anthropogenic variables at multiple spatial scales were predictive of female greater sage-grouse occurrence and fitness. Anthropogenic variables related to CBNG development were predictive in all of the final occurrence models, suggesting that anthropogenic features were resulting in habitat avoidance through all summer life-stages. My fitness modeling illustrated habitat-specific and scale dependent variation in survival across the ARPA landscape. When mapped, the final ecological model identified habitat patches that were contributing the most to population persistence and that source-sink dynamics within the ARPA landscape may be shifting as a result of CBNG development.

Documenting an anthropogenic impact that has already occurred yields limited inference unless a means of comparison is incorporated. I evaluated habitat and demographic responses of greater sage-grouse during nesting by comparing an energy development landscape (ARPA) to a non-impacted landscape (SC). I accomplished this by spatially shifting my nest occurrence and survival models from the ARPA to SC. In addition, I compared nest survival rates between the

areas. My nest occurrence and survival models were predictive in SC without the CBNG predictor variable. Specific environmental variables that were robust predictors of nest occurrence in both areas included big sagebrush canopy cover and litter that represented dead standing woody vegetation and detached organic matter both at a 0.25-km^2 scale. Further, the variability in shrub heights at a 1.0-km^2 scale at was highly predictive of nest survival in both areas. The evidence of the predictive ability of my nest occurrence models in SC and the habitat likeness between areas allowed me to assess what greater sage-grouse nest selection in the ARPA might have looked like prior to the introduction of CBNG development by replacing time (pre-development data) with space (using SC as a spatial control). I modeled the ARPA RSF against the SC nest occurrence data (i.e., nest selection in the absence of CBNG development) and then spatially shifted the adjusted model back to the ARPA. However, the range of variability in habitat conditions between the ARPA and SC caused the spatial shifting of the models to function poorly in practice. This elucidates an important consideration in choosing spatial control related habitat variability and the predictive errors associated with extrapolation out of the range of the data used to train the RSF. Thus for a spatial control to function well, not only do habitat conditions need to be similar to the impacted area but the range of variability in habitat conditions need to also be comparable. Nest survival was significantly higher in SC compared to the ARPA but my nest survival model did not explain this difference. In conclusion, the reference area provided additional information on possible impacts of CBNG development in the ARPA; however, inference was limited without pre-development data.

Understanding habitat selection at macrohabitat and microhabitat scales is critical to conserving and restoring greater sage-grouse habitat. Because of the similar ecological conditions, my microhabitat selection analysis for the greater sage-grouse during the nesting,

early and late brood-rearing periods incorporated both the ARPA and SC. Nest microhabitat selection was positively correlated with mountain big sagebrush (*A. tridentata vaseyana*) and litter cover. I found that female greater sage-grouse preferred areas with greater sagebrush cover and greater perennial grass cover during early and late brood-rearing. However, I did not find forb cover to be predictive of early or late brood-rearing occurrence. My findings suggest that sage-grouse inhabiting xeric sagebrush habitats (≤25 cm annual precipitation) rely on sagebrush cover and grass structure for nesting as well as brood-rearing and that these structural characteristics may be more important than forb availability at the microhabitat scale.

QUANTIFYING HABITAT IMPORTANCE FOR GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) POPULATION PERSISTENCE IN AN ENERGY DEVELOPMENT LANDSCAPE

By

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and the University of Wyoming

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DEDICATION

My wife Sara and daughter Brynn deserve my sincerest gratitude. I wouldn't have made it through this project without my wife's understanding, unconditional love, and unwavering support. My little girl was always happy to see me and remarkably understanding when I had to leave (as understanding as a 2 to 3 year old can be). I thank my parents, Marilyn Townsend and Lance Kirol, my grandpa Lynn Jenkins, my siblings Melanie Kirol, Ashton Kirol, and Jordan Townsend for much encouragement and love. Also, thank you Jordan for the late night math tutorials. I greatly appreciate the hospitality and generosity of my in-laws Mike and Joyce Evans who loaned me a camp trailer, assisted with field work, plant identification, nursed me back to health while I recovered from tick fever, and much more. I thank my late grandparents Bill and Jean Kirol who at a young age introduced me to fly fishing, birding, and Wyoming's natural places. I would like to recognize two amazing teachers in the Cody, Wyoming school system, Dale Ditolla and Dan White, who kindled my interest in biology and wildlife ecology early on in my education.

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CHAPTER 1

INTRODUCTION

Female Sage-Grouse Breeding Ecology

Sagebrush (*Artemisia* spp.) is the most widespread vegetation in the Intermountain lowlands of the western United States (West and Young 2000). Greater sage-grouse (*Centrocercus urophasianus;* hereafter ‘‘sage-grouse’’) are obligates of sagebrush ecosystems, depending on sagebrush for food and shelter throughout the entire year (Patterson 1952, Braun et al. 1977, Swenson 1987). The sage-grouse is a relatively long-lived gallinaceous species (Zablan et al. 1993) with high adult annual survival and low reproductive rates (Connelly et al. 2000). Within the sagebrush ecosystem sage-grouse utilize distinct habitats for nesting, brood-rearing, and wintering life-stages (Patterson 1952, Schroeder et al. 1999, Connelly et al. 2011*a*).

Sage-grouse are a polygamous species that breed on traditional strutting grounds or leks. As a with all lekking birds, males provide neither parental care nor resources (i.e., nesting or foraging sites; Schroeder et al. 1999). Initial breeding dates vary for sage-grouse across their range, but in Wyoming and Montana female sage-grouse generally breed between early and late April, although annual weather variations can cause delays in breeding and nest initiation (Schroeder et al. 1999). Within a few days of being bred, females retire to the locality of their nest site and remain relatively sedentary until they nest (Patterson 1952). Female sage-grouse show high fidelity to nesting areas and often nest close to the previous year’s nest (Patterson 1952, Schroeder et al. 1999, Holloran and Anderson 2005). Sage-grouse begin laying approximately 3 weeks after copulation (Schroeder et al. 1999). The duration of egg laying averages 7 to 10 days and the incubation period ranges between 25–29 days (Schroeder et al. 1999). Depending on the copulation date, hatching can begin as early as April and as late as July

for renests. Sage-grouse clutch size ranges from 6 to 9 eggs and averages 7 eggs (Patterson 1952, Schroeder et al. 1999, Connelly et al. 2011). Nest success ranges from 12 to 86% (Schroeder et al. 1999, Connelly et al. 2011*b*), and is typically lower than other prairie grouse species (Connelly et al. 2000). Further, nest success in relatively unaltered habitats averages 51% while in altered habitats nest success averages 37% (Connelly et al. 2011*b*).

After hatch, females with young move a short distance from their nest for the first few weeks, during which time chicks feed mainly on invertebrates (i.e., early brood-rearing habitat; Hannon and Martin 2006). Later, when the chicks are more mobile and can thermoregulate, the female takes them further from the nest to late brood-rearing locations that provide succulent vegetation and adequate cover (Bergerud and Gratson 1988, Connelly et al. 2000). Late brood-rearing habitats are used until brood breakup in early September (Connelly et al. 2011*a*). Reported chick survival rates are highly variable (Connelly et al. 2011*b*). Chick survival from hatch to breeding age averaged 10% from several studies summarized by Crawford et al. (2004).

Current Status of the Sage-Grouse

Sage-grouse were described as being very plentiful by explorers who visited regions they inhabited prior to European settlement (Coues 1874). Yet, early in the 1900s concern began to arise about observed decreases in sage-grouse populations (Hornaday 1916). Sage-grouse populations have undergone a significant decline over the last 60 years; primarily due to extensive alteration and loss of sagebrush steppe habitat (Connelly and Braun 1997, Connelly et al. 2004). Schroeder et al. (2004) estimated the current extent of sagebrush habitat is 668,412 km^2 or approximately 56% of the presettlement area of 1,200,483 km^2. Historically, sage-grouse occurred in 16 states and 3 Canadian provinces; however, greater sage-grouse have been extirpated from British Columbia and the Gunnison sage-grouse (*C. minimus*) have been

extirpated from Arizona, New Mexico, Oklahoma, and Nebraska (Schroeder et al. 1999). At present, sage-grouse populations occur in 11 states and two Canadian provinces, and many of the remaining populations are isolated (Knick and Connelly 2011). The largest proportion of remaining sagebrush habitats are in Wyoming (Connelly et al. 2004, Doherty et al. 2008).

In response to this downward population trend the greater sage-grouse has been reviewed, by the U.S. Fish and Wildlife Service (USFWS), for listing under the Endangered Species Act four times in the last decade. In 2010, the USFWS concluded that the greater sage-grouse was warranted for protection under the Endangered Species Act of 1973, but currently its listing is precluded because other species are under more immediate threat of extinction. (USFWS 2010). The primary factors identified by the USFWS (2010) as contributing to greater sage-grouse decline include invasive species, infrastructure (i.e. roads, powerlines and pipelines), energy development (mainly oil, gas, and coalbed natural gas [CBNG]), and wildfire.

Study Justification

The global demand for energy has increased by >50% in the last half-century and is expected to continue at this rate through 2030 (National Petroleum Council 2007). Fossil fuels are expected to continue to account for 83–87% of total world demand with oil, natural gas, and coal being the primary sources (American Gas Association 2005). Sage-grouse populations are often negatively affected by energy development activities (Naugle et al. 2011). Research has demonstrated that impacts of energy development on greater sage-grouse populations include lower male lek attendance and a decline in lek persistence (Holloran 2005, Walker et al. 2007); lower yearling male recruitment to disturbed leks (Holloran et al. 2010); avoidance of critical seasonal habitats (Lyon and Anderson 2003, Doherty et al. 2008); lower nest initiation rates

(Lyon and Anderson 2003); lower annual adult female survival (Holloran 2005, Holloran et al. 2010) and increased chick mortality (Aldridge and Boyce 2007).

Approximately 70% of the remaining sagebrush steppe and the distribution of sage-grouse are on public land with 50% falling under the jurisdiction of the Bureau of Land Management (BLM; Connelly et al. 2004). Mitigation measures in oil and gas fields commonly employed by the BLM and other federal agencies to protect sage-grouse breeding grounds and nesting habitat over the last several years focused on a 3.2-km radius around sage-grouse lekking sites based on earlier research and management recommendations (Braun et al. 1977). Specifically, these mitigation measures included a 3.2 km timing lease stipulation buffer that prohibits surface disturbing activities from March 1 to June 15, while development was allowed in these areas during the remainder of the year. Additionally, a 0.4 km controlled surface use (CSU) stipulation buffer was established around occupied sage-grouse lek sites that precludes infrastructure within the CSU buffer on a year-round basis. However, Aldridge and Boyce (2007) reported that source nesting and brooding habitats were on average ~6 km from active leks and Connelly et al. (2000) suggest that 5-km radii and 18-km radii buffers around active leks may be required to protect reproductive habitats for non-migratory and migratory sage-grouse populations, respectively. Further, Beck (2009) reported that these mitigation measures have been largely ineffective at reducing impacts to sage-grouse in energy development landscapes. Thus, focusing management on a fixed buffer around leks may not be adequate to ensure viability of sage-grouse populations. Due to the impacts of energy development on sage-grouse and an increased demand for domestic fossil fuel production, innovative resource management and extraction processes must be implemented to maintain viable sage-grouse populations within the sagebrush biome.

The dynamics of species at risk of extinction are determined by their demographic characteristics, the distribution and quality of their habitats, and the changes in these factors in response to various natural processes and anthropogenic threats (Akçakaya et al. 2004). Associations between an animal's fitness and their habitats may be used to interpret the effects of habitat disturbance (Kastdalen et al. 2003). To evaluate options for reducing impacts, habitats of high biological value (i.e., critical habitats) need to be identified in areas that are proposed for energy development (Abbitt et al. 2000, Wilson et al. 2005). In a critical review of habitat selection studies in avian ecology, Jones (2001) identified a prevailing issue among researchers studies to not consistently evaluate the behavioral and fitness context of their findings. This is unfortunate, because a complete measure of habitat selection and habitat quality should involve the assessment of whether the identified habitat preferences are adaptive (Jones 2001). Therefore, linking resources to animal occurrence and population fitness is necessary to manage for population persistence (Aldridge and Boyce 2007). Studies that provide a means of quantifying habitat value by incorporating habitat selection and its relationship to fitness outcomes (Van Horne 1983) are essential to conservation planning and management of sage-grouse and other species of conservation concern.

Study Area

My study was conducted in the Atlantic Rim project area (ARPA) that was being developed for coalbed natural gas (CBNG) reserves, and a non-impacted reference area (Stewart Creek [SC]; Fig. 1.1). The majority of land in the ARPA and SC is federally owned and administered by the BLM. The ARPA and SC are dominated by Wyoming big sagebrush (*A. t. wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) communities and provide year-round habitat for sage-grouse (South Central Sage-grouse Local Working Group [LWG] 2007).

The ARPA lies in southern Carbon County, Wyoming and encompasses 1,093 km^2 in Townships 13 through 20 North and Ranges 89 through 92 West. The ARPA lies east of Wyoming Highway 789 between Rawlins and Baggs and includes 64.3% (701.9 km^2) federal, 5.2% (57.0 km^2) state, and 30.5% (334.1 km^2) private lands. The BLM-Rawlins Field Office manages the federal lands as well as 22.6 km^2 of federal mineral estates underlying private land within the study area (BLM 2007). The ARPA and adjacent areas to the west were producing oil and natural gas with large reserves of natural gas occurring in the project area (BLM 2007). Eighty-nine documented sage-grouse leks were distributed throughout the ARPA at a density of 1 lek/13 km^2. Major land uses in the ARPA included energy extraction and livestock grazing.

The SC is approximately 32.2 to 64.4 km north and west of Rawlins and encompassed approximately 820 km^2 of federal (70.0 %), state (5 %), and private (25 %) lands in Sweetwater and Fremont counties, Wyoming. The SC included Townships 23 to 25 North and Ranges 90 to 92 West. Twelve documented leks were distributed throughout the SC with a density of 1 lek/68 km^2. Livestock grazing, primarily cattle, was the main land use within the SC.

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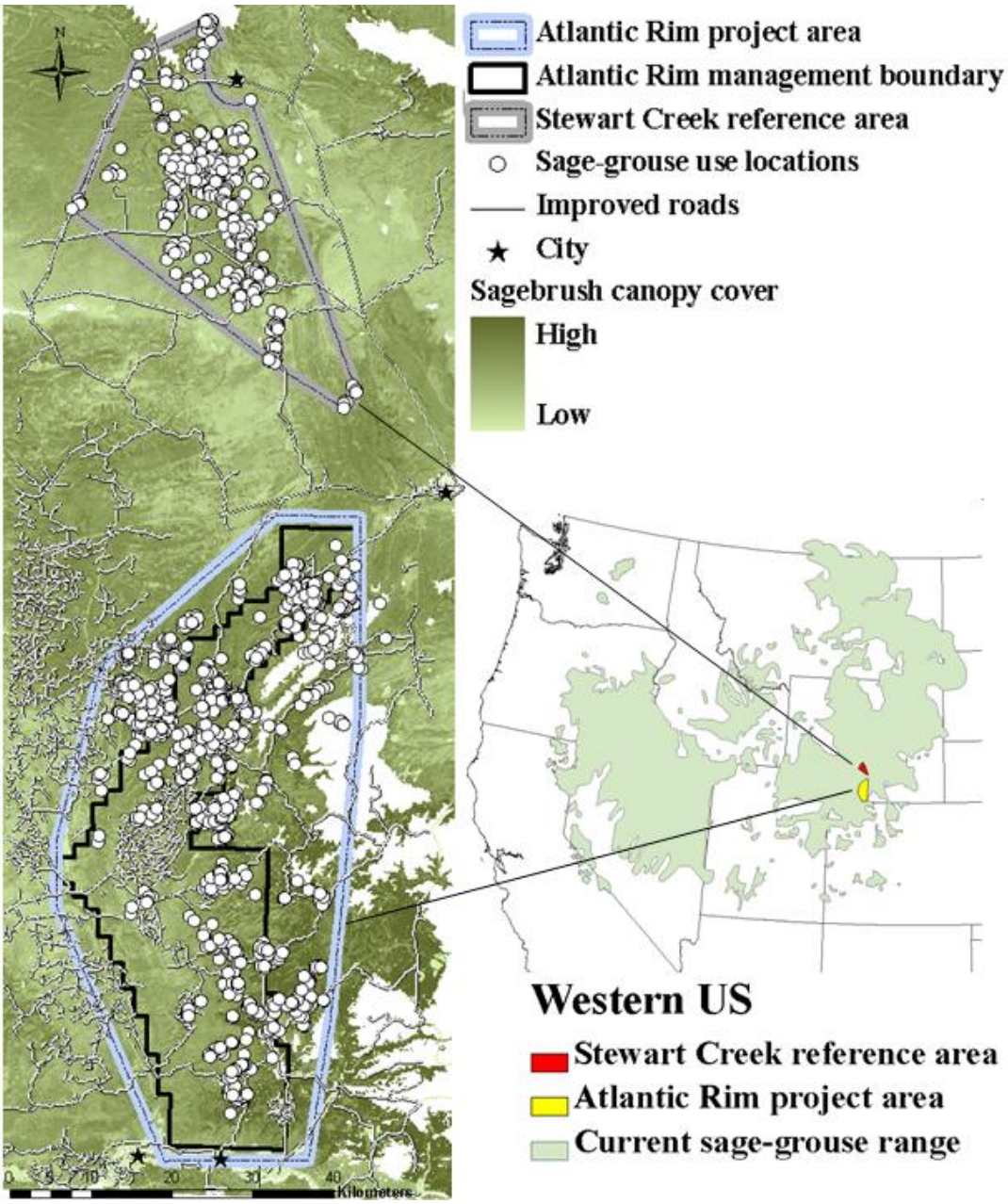

Figure 1.1. The Atlantic Rim and Stewart Creek study areas in relation to the current range-wide sage-grouse distribution. Study areas are located in south-central Wyoming, USA.

CHAPTER 2

Modeling Greater Sage-Grouse Source and Sink Habitats in a Developing Coalbed Natural Gas Field in South-Central Wyoming

In the format for manuscript submittal to the *Journal of Wildlife Management*

ABSTRACT

Although many studies have evaluated habitat selection by animals, few have assessed the relationship between selected habitat characteristics and fitness outcomes. Habitat quality is the ability of the environment to provide conditions suitable for individual and population persistence (Hall et al. 1997). Quality is often compromised when source habitats are lost or fragmented due to energy development, reducing the overall ability of populations to survive and reproduce within altered landscapes. My objective was to model habitat quality and source and sink habitats for greater sage-grouse (*Centrocercus urophasianus*) in the 1,093 km^2 Atlantic Rim Project Area (ARPA) of south-central, Wyoming, which is being developed for coalbed methane natural gas (CBNG) resources. I modeled habitat selection, as resource selection functions (RSFs), and habitat-specific survival using data from n = 167 female sage-grouse monitored from May through August 2008 and 2009. By coupling the final habitat selection models and survival models, in a GIS framework, I spatially predicted habitat quality as well as sink and source habitats on the ARPA landscape. Over the reproductive season, I evaluated relationships between environmental (e.g., percent big sagebrush [*Artemisia tridentata*] cover, percent bare ground, and topographic wetness index) and anthropogenic (e.g., distance to anthropogenic edge, CBNG well density, and linear fence distance) spatial variables and habitat selection and survival at three landscape scales (0.25-, 1-, and 5-km^2 circular scales). Because my analysis was mainly

exploratory I used a sequential modeling approach and Akaike's Information Criterion (AIC) to identify the best-fit models and to make model inferences. I used binary logistic regression and selected best models with AIC adjusted for small samples (AIC_c) to explore habitat selection for nesting, early and late brood-rearing females, and for non-brooding females in early and late summer. Further, I used Cox's proportional hazards modeling, and AIC_{SUR}, an AIC technique adapted for survival analysis, to identify the most predictive variables for nest, brood, and adult female summer survival.

My results demonstrate a suite of environmental and anthropogenic variables at multiple spatial scales that are predictive of occurrence. Sagebrush canopy cover was present in our RSF models throughout every summer female life-stage with the exception of the early non-brooding. Nesting grouse selected habitats with greater litter and big sagebrush cover at the 0.25-km^2 scale. Both early and late brood-rearing hens showed selection for large patches (1-km^2) of moderate sagebrush cover, but avoided areas with the highest sagebrush cover available. Even though there is some habitat overlap, my results show that during the summer, non-brooding females did not select for the same habitat characteristics as females with broods. For example, unlike late brood-rearing, late non-brooding females selected habitats closer to forest edge.

Anthropogenic variables related to CBNG development were predictive in all of the final occurrence models, suggesting that anthropogenic features were negatively influencing habitat selection through all summer life-stages of female sage-grouse. Visual well density was negatively correlated with female sage-grouse occurrence during nesting and early brood-rearing at the 1-km^2 scale, and early non-brooding and late non-brooding at the 5-km^2 scale, whereas the percent of surface disturbance was correlated with late brood-rearing occurrence at the 5-km^2 scale. The addition of 1 visible well within 0.564 km decreased the probability of nest

occurrence by approximately 35%. Percent surface disturbance had a quadratic relationship with late brood-rearing occurrence suggesting that moderate disturbance was tolerated, but as disturbance approached 8%, a threshold of tolerance was reached and avoidance began to occur.

My survival results illustrated several habitat-specific and scale dependent variations in survival or risk across the ARPA landscape. Daily nest survival was positively correlated with Wyoming big sagebrush (*A. t. wyomingensis*) cover within a 5-km^2 area. The variability in shrub heights within a 1-km^2 area was predictive of nest, brood, and adult female survival throughout the summer. Because a strong correlation existed between shrub height variability and survival in all of my survival models, it appears that stands with homogenous vertical cover of sagebrush and other shrub species were riskier habitats for females in every summer life-stage. Daily brood survival was negatively correlated with anthropogenic surface disturbance that exceeded approximately 4% within a 1-km^2 area. Yet, daily female survival did not have a negative relationship to anthropogenic edge.

My results demonstrate that habitat quality was not homogenous across the ARPA landscape, but spatially variable among habitat patches. The RSF models for each life-stage were rescaled between 0 and 1 and projected back on the ARPA landscape in GIS to display relative probabilities of occurrence. I then merged the RSF's for each life-stage to produce a final occurrence layer that spatially predicted the areas with the highest and lowest relative probability of use in summer. Also, for each life-stage, survival estimates calculated with the Kaplan-Meier (K–M) product-limit estimator were combined with the variable adjusted survival coefficients derived from Cox's proportional hazards modeling into baseline survival probability functions (SPFs). This enabled us to predict survival in GIS on the basis of habitat-specific landscape-scale variables. I combined SPF's with fixed demographic rates into a lambda model

that I projected back on the ARPA landscape. My lambda layer thus predicted habitats that contributed to population surpluses or deficits. My lambda model predicted that 87% of sage-grouse habitat within the ARPA has the potential to be contributing to a stable or increasing sage-grouse population ($\lambda \geq 1$).

I combined the female summer occurrence layer and lambda layer in GIS and distributed these combined layers into quartiles to predict selected and non-selected source and sink habitats. The source-sink map predicted that of the sage-grouse habitat within the ARPA, 40% was selected source, 42% was non-selected source, 14% was selected sink, and 4% was non-selected sink. My results provide evidence that source-sink dynamics within the ARPA landscape may be shifting as a result of CBNG development. The apparent shift is largely being driven by avoidance or displacement and not fitness consequences. That is, this shift is mainly resulting in selected source becoming non-selected source habitats.

INTRODUCTION

The presence of animals in anthropogenic-dominated landscapes is often neither adaptive nor positively related to fitness outcomes such as reproduction or survival (Van Horne 1983, Jones 2001, Schlaepfer et al. 2002, Aldridge and Boyce 2007). Consequently, density or animal occurrence considered alone is a misleading indicator of population fitness (Van Horne 1983, Chalfoun and Martin 2007, Aldridge and Boyce 2007). A primary goal of modeling wildlife-habitat relationships should be to understand the suite of habitat features that affect occurrence as well as abundance or fitness of a species (Jones 2001, Morrison et al. 2006). Thus a true measure of habitat quality, the ability of the environment to provide conditions suitable for individual and population persistence (Hall et al. 1997), should be based on the combination of occurrence and fitness measures such as survival and productivity.

Source-sink dynamics are predicated on the fact that habitat quality is heterogeneous throughout a landscape and that fitness parameters are often habitat-specific (Falcy and Danielson 2011). Local population persistence depends on a balance between mortality and fecundity in addition to demographic surpluses from adjacent source habitats (Pearson and Fraterrigo 2011). Sink habitats are characteristically substandard habitats where resources are scarce and, consequently, survival is possible, but reproduction (although it may occur) is usually poor (Pulliam and Danielson 1991). Selected sinks termed an "ecological trap" arise when sudden anthropogenic change acts to uncouple the cues that individuals use to assess perceived habitat quality from true quality (Schlaepfer et al. 2002). Source habitats are critical in a landscape being altered by human activity (i.e., developing energy field) because they act as population refugia (Pearson and Fraterrigo 2011). Source habitats are associated with high-quality habitats that tend to yield a surplus of individuals because births exceed deaths, whereas sink habitats on average yield a demographic deficit (births below mortality; Pulliam and Danielson 1991). The finite population growth rate or lambda (λ) is a vital metric for judging local population 'health' and source-sink dynamics (Pulliam 1988, Nichols and Hines 2002). Healthy populations are generally stationary, that is neither growing nor declining [$\lambda = 1$], or increasing ($\lambda > 1$), whereas unhealthy populations are declining ($\lambda < 1$; Gotelli 2008).

Greater sage-grouse (*Centrocercus urophasianus;* hereafter sage-grouse) studies incorporating geographic information systems (GIS) and remote sensing have identified selection at several landscape-scales (e.g., Homer et al. 1993, Wisdom et al. 2002, Aldridge and Boyce 2007, Aldridge and Boyce 2008, Doherty et al. 2008, Doherty et al. 2010). Habitat quality can also vary at different scales (Diez and Giladi 2011). Accordingly, for landscape-scale species with large ecological neighborhoods (Addicott et al. 1987), such as the sage-grouse, variables

should be measured at multiple scales that are biologically relevant to that species (Johnson 1980, Morris 1987, Wiens 1989). In addition, assessing multiple spatial scales allows us to understand how a species occurrence and survival is affected by habitat characteristics at different scales and the interactions across these scales (Wiens 1989). Research has demonstrated the importance of considering multiple scales when evaluating habitat selection (Thompson and McGarigal 2002, Lawler and Edwards 2006, Chalfoun and Martin 2007, Doherty et al. 2010) and fitness (Robinson et al. 1995, Reid et al. 2006, Robinson and Hoover 2011). Further, fragmentation may affect productivity through different mechanisms at different spatial scales (Diez and Giladi 2011). Although others have assessed sage-grouse fitness related to habitat occurrence at a single landscape-scale (Aldridge and Boyce 2007) none have assessed sage-grouse fitness at multiple spatial scales.

The global demand for energy has increased by >50% in the last half-century and is expected to continue at this rate through 2030 (National Petroleum Council 2007). Fossil fuels are expected to continue to account for 83–87% of total world demand, with oil, natural gas, and coal being the primary sources (American Gas Association 2005). Anthropogenic development resulting in changes in land cover can alter abundance and spatial patterns of habitat use and may have negative consequences for population persistence (Lindenmayer and Fischer 2006, Aldridge and Boyce 2007, Naugle et al. 2011) as well as the distribution of source and sink habitats (Pulliam 1988). Specialist species such as sage-grouse are particularly vulnerable to habitat fragmentation contributing to variability in habitat quality (Pearson and Fraterrigo 2011) and researchers are only beginning to understand the response of sage-grouse populations within an entire landscape to anthropogenic change (Connelly et al. 2000). However, the development and subsequent extraction of fossil fuels has been recognized as one of the factors contributing to

the decline of sage-grouse throughout its range (Connelly et al. 2004, Naugle et al. 2011). Research has demonstrated that impacts of energy development on greater sage-grouse populations include lower male lek attendance and a decline in lek persistence (Holloran 2005, Walker et al. 2007, Harju et al. 2010); lower yearling male recruitment to disturbed leks (Holloran et al. 2010); avoidance of critical seasonal habitats (Lyon and Anderson 2003, Doherty et al. 2008); lower nest initiation rates (Lyon and Anderson 2003); lower annual adult female survival (Holloran 2005, Holloran et al. 2010) and increased chick mortality (Aldridge and Boyce 2007). Due to these impacts and an increased demand for domestic fossil fuel production, innovative resource management and extraction processes must be implemented to maintain viable greater sage-grouse populations within the sagebrush biome.

Sage-grouse are a relatively long-lived species (Zablan et al. 1993) with high adult annual survival and low reproductive rates (Connelly et al. 2000), that translates to lower potential growth rates when compared to other gallinaceous species. Sage-grouse rely on contiguous intact expanses of sagebrush for all life-stages (Patterson 1952, Schroeder et al. 1999, Connelly et al. 2004). Sage-grouse utilize distinct habitats within the sagebrush ecosystem for nesting, early brood-rearing, late brood-rearing, and wintering. Extensive loss and fragmentation of big sagebrush (*Artemisia tridentata* spp.) steppe habitat have reduced the current distribution of sage-grouse to about 50% of their original range (Schroeder et al. 2004). The largest proportion of remaining sagebrush habitats are in Wyoming (Connelly et al. 2004, Doherty et al. 2008).

Nest success is a key vital rate for avian species and can be defined as the probability that a nest survives from initiation to completion with at least 1 egg hatching (Rotella et al. 2004). Researchers have suggested that lower nest success in sage-grouse is likely a significant factor in population declines (Bergerud 1988, Crawford et al. 2004, Baxter et al. 2008). Across grouse

species, 50% of chicks, on average, die between hatching and brood breakup in August and September (Bergerud 1988). Findings from many studies suggest grouse population declines may be driven by changes in the production and survival of chicks (Bergerud 1988, Beck et al. 2006, Hannon and Martin 2006), which is particularly true for sage-grouse (Connelly and Braun 1997, Aldridge and Brigham 2002, Crawford et al. 2004). A range-wide life-stage simulation analysis found that sage-grouse chick survival was the second highest contributor to lambda (Taylor et al. 2012). Grouse chick mortality is generally highest during the first 2 weeks post-hatch when the primary causes of mortality include exposure to cold wet weather, predation, lack of food, and poor condition of the chick or female (Hannon and Martin 2006, Gregg et al. 2007).

Adult female survival is often not considered a significant driver of wildlife population persistence, as the emphasis is usually on production of offspring (i.e., nest and brood success); however McDonald and Caswell (1993) describe several studies on avian species including sage-grouse and prairie chickens (*Tympanuchus* spp.) where survival of adult "breeders" was the most significant vital rate for lambda. Population viability analysis for a sage-grouse population in northern Colorado indicated that adult and juvenile survival were the most significant vital rates followed by adult and juvenile fecundity (Johnson and Braun 1999). Further, a recent range-wide sage-grouse population growth assessment found that when compared to all other vital rates female survival had the greatest influence on lambda (Taylor et al. 2012). Mortality in adult female sage-grouse appears to be dictated by seasonal patterns (Connelly et al. 2000, Moynahan et al 2006), suggesting the need to understand mortality for sage-grouse on a seasonal basis.

My research was conducted in the Atlantic Rim project area (ARPA), which is a coalbed natural gas (CBNG) field in the early stages of development, in south-central, Wyoming, USA. The BLM Record of Decision (ROD) for the Atlantic Rim Natural Gas Field completed in 2007

describes the development of 2,000 natural gas wells, in addition to 116 exploration wells that were already drilled (BLM 2007). Well field development for the ARPA includes the drilling of 1,800 coalbed natural gas wells and 200 deep natural gas wells at a down spacing of 32.4 ha (80 ac) per well (BLM 2007). Development and drilling began in 2007 and will continue for approximately 20 years, with the project life expected to range from 30 to 50 years (BLM 2007). Various drilling and production related facilities (e.g., roads, pipelines, water wells, disposal wells, compressor stations, and gas processing facilities) will also be constructed within the ARPA (BLM 2007). At the conclusion of my field research in August 2009, approximately 600 natural gas wells were established in the ARPA. The ARPA supports a substantial sage-grouse population and has one of the highest lek densities in Wyoming with 89 documented sage-grouse leks at a density of 1 lek/13 km^2.

Because habitat quality is a function of a habitats conduciveness to survival and production, my primary research objective was to spatially quantify sage-grouse habitat quality in GIS on the basis of occurrence and fitness models containing the most predictive landscape variables. This approach offers a means of prioritizing habitat importance related to sage-grouse population persistence. As my primary goal was to predict and map habitat quality, I designed my analysis to identify the best-supported landscape predictor variables, but not to identify all landscape variables that potentially may be correlated to occurrence or survival (Arnold 2010) in the ARPA. Earlier attempts at identifying critical sage-grouse habitat have focused on nesting and brood-rearing habitats exclusively (e.g., Aldridge and Boyce 2007, Aldridge and Boyce 2008) and identified sink and source habitats based on these life-stages (e.g., Aldridge and Boyce 2007). However, one cannot truly estimate habitat quality and identify sink and source habitats without integrating a population growth estimate (λ) into the analysis. That is, knowing that a

habitat has a lower quality does not provide an indication of the population or fitness consequences. In addition, by definition source habitats should yield a demographic surplus (Pulliam and Danielson 1991). Specific objectives of my research were to 1) generate resource selection functions (RSFs) for the life-stages specific to female sage-grouse reproduction, 2) use survival modeling to produce habitat-specific survival models for nests, broods, and adult females over the reproductive period and express these models as survivorship functions, 3) quantify habitat as it relates to λ; thus, predicting habitats that contribute to population sources or sinks, and 4) in a GIS framework combine habitat-specific occurrence probabilities with predicted λ values to spatially identify sink and source habitats as well as critical and/or limiting reproductive habitats to determine which areas, if protected, have the highest potential to contribute to persistence of sage-grouse populations in the ARPA landscape.

STUDY AREA

The ARPA lies in southern Carbon County, Wyoming and encompasses 1,093 km² in Township 13 through 20 North and Ranges 89 through 92 West. The ARPA extends approximately 77 km north and south between Rawlins and Baggs, and includes 64.3% (701.9 km²) federal, 5.2% (57.0 km²) state, and 30.5% (334.1 km²) private lands. The BLM-Rawlins Field Office manages the federal lands as well as 22.6 km² of federal mineral estates underlying private land within the study area (Bureau of Land Management [BLM] 2007). Major land uses in the APRA include energy extraction (see Introduction), livestock grazing, and hunting.

The ARPA is within the semi-desert grass-shrub zone in the Cool Central Desertic Basin and Plateaus major land resource area (Natural Resources Conservation Service [NRCS] 2006). The semi-desert grass-shrub zone is characterized by a vast sagebrush steppe with low average annual precipitation–between 18.0 to 30.5 cm (NRCS 2006). The region encompassing the

ARPA normally has cool temperatures with average daily temperatures ranging between a low of –16 degrees (°) C and a high of 0.5°C in midwinter and between 13°C and 24°C in midsummer (BLM 2006). Temperature extremes range from –46°C to 38°C with the frost-free period generally occurring from mid-May to mid-September. Precipitation is evenly distributed throughout the year with minor peaks in May, July, and October. The snowiest months are in December and January with an average of 98.6 cm of snow falling during the year (BLM 2006). Because of the wide variation in elevation and topography within the ARPA, site-specific climatic conditions vary.

The northern portion of the ARPA (approximately 20%) lies within the Great Divide Basin. The Great Divide Basin is a closed basin, which splits the Continental Divide and has no hydrologic outlet. The southern portion of the ARPA is situated within the Yampa watershed, a tributary of the Colorado River. The ARPA is bisected by the southern margin of the Continental Divide and the northern portion of the ARPA parallels the western margin of the Continental Divide (BLM 2006). The Atlantic Rim forms a portion of the southern margin of the Continental Divide and is the most significant topographic feature within the study area. The southern portion of the ARPA is characterized by fairly rough terrain bisected by deep drainages with prominent hogback ridges, knolls, and escarpments. The northern portion of the ARPA contains less severe terrain and is characterized by drainage basins, rolling hills, hogback ridges and escarpments with the prominent Atlantic Rim to the east. The major drainages within the ARPA include Fillmore Creek draining to the north and Muddy Creek, Cow Creek, Wild Cow Creek, Cherokee Creek, and Deep Creek draining to the south. Elevations within the study area range from 1982 to 2529 m (BLM 2006).

Vegetation communities occupying a significant portion of the ARPA include Wyoming big sagebrush (*A. t. wyomingensis*), Wyoming big sagebrush/bitterbrush (*Purshia tridentata*), mountain big sagebrush (*A. t. vaseyanas)*, mountain big sagebrush/bitterbrush, alkali sagebrush (*A. arbuscula longiloba*), basin big sagebrush (*A. t. tridentata*), silver sagebrush (*A. cana*)/bitterbrush, greasewood (*Sarrcobatus vermiculatus*)/basin big sagebrush, Utah juniper (*Juniperus osteosperma*) woodland, and aspen (*Populus tremuloides*) woodland (BLM 2006).

Mountain (50%) and Wyoming (34%) big sagebrush are the dominant vegetation types in the ARPA (BLM 2006). The mountain big sagebrush cover type is mainly distributed along the foothills at higher elevations within the study area. Bitterbrush, chokecherry (*Prunus virginiana*), alderleaf mountain mahogany (*Cercocarpos montanus*), Douglas rabbitbrush (*C. viscidiflorus*), rubber rabbitbrush (*E. nauseosus*), Saskatoon serviceberry (*Amelanchier alnifolia*), and mountain snowberry (*Symphoricarpos oreophilus*) are other common shrubs within this cover type. A variety of forb and grass species compose the understory within the mountain big sagebrush cover type. Common forbs include arrowleaf balsamroot (*Balsamorhiza sagittata*), beardtongue (*Penstemon* spp.), bluebells (*Mertensia* spp.), buttercup (*Ranunculus spp*.), false dandelion (*Agoseris glauca*), geranium (*Geranium richardsonii*), groundsel (*Senecio* spp.), Indian paintbrush (*Castilleja* spp.), locoweed (*Astragalus* spp.), phlox (*Phlox multiflora*), sego lily (*Calochortus nuttallianum*), silky lupine (*Lupinus sericeus*), sulfur buckwheat (*Eriogonum umbellatum*), and wild onion (*Allium* spp.; BLM 2006). Common grasses associated with mountain big sagebrush communities include bluebunch wheatgrass (*Pseudoroegneria spicata*), bottlebrush squirreltail (*Elymus elymoides*), green needlegrass (*Nassella viridula*), Idaho fescue (*Festuca idahoensis*), little bluegrass (*Poa secunda*), mutton bluegrass (*Poa fendleriana*), needle-and-thread (*Hesperostipa comata*), oniongrass (*Melica*

bulbosa), prairie junegrass (*Koeleria cristata*), spike fescue (*Leucopoa kingii*), and thickspike wheatgrass (*Elymus macrourus;* BLM 2006).

Wyoming big sagebrush dominates the more arid lower elevations within the ARPA. Other shrub species associated with this cover type include broom snakeweed (*Gutierrezia sarothrae*), cotton horsebrush (*Tetradymia canescens*), Douglas rabbitbrush, rubber rabbitbrush and winterfat (*Krascheninnikovia lanata*). Major forbs comprising the understory include beardtongue, hollyleaf clover (*Trifolium gymnocarpum*), Hood's phlox (*Phlox hoodii*), hooker sandwort (*Arenaria hookeri*), locoweeds, goldenweed (*Happlopappus* spp.), low buckwheat (*Eriogonum ovalifolium*), spring parsley (*Cymopterus acaulis*), and wild onion. Common grasses in Wyoming big sagebrush communities include bottlebrush squirreltail, Indian ricegrass (*Achnatherum hymenoides*), little bluegrass, needle-and-thread, thickspike wheatgrass, threadleaf sedge (*Carex filifoli*), and western wheatgrass (*Pascopyrum smithii*; BLM 2006).

METHODS

Radio-marking and Monitoring

I captured female sage-grouse from 14 leks in the ARPA in 2008 and 2009 using established spot-lighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992). Selected leks were evenly distributed throughout the ARPA to ensure equal capture effort across the study area and to obtain a random sample of the population (Manly et al. 2002). I attached VHF radio transmitters (Model A4060; Advanced Telemetry Systems Incorporated, Isanti, Minnesota, USA) to females with a PVC-covered wire necklace. Transmitters weighed 22 g (~1.4% of mean female sage-grouse body mass); had a battery life expectancy of 789 days; and were equipped with motion-sensors (i.e., radio-transmitter pulse rate increased in response to inactivity after 8 hours). I classified sage-grouse as yearlings (first breeding season) or adults

(second breeding season or older) based on the shape, condition and coloration of the outermost wing primaries, and the outline of the primary tail feathers (Eng 1955, Dalke et al. 1963). I weighed each grouse to the nearest 1 g and collected a blood sample for genetic analyses. Blood samples were obtained by clipping a vestigial toenail from a metatarsus and storing blood samples on Whatman (2008) FTA micro cards; blood samples were collected for genetic analyses not associated with my study. Female sage-grouse were captured and handled according to University of Wyoming Institutional Animal Care and Use Committee approved protocols (03032009).

I located sage-grouse on the ground using hand-held receivers and 3-element Yagi antennas. I used ground telemetry to monitor radio-marked females through the nesting (May–June), and early and late brood-rearing periods (late June–August). Sage-grouse locations were recorded in Universal Transverse Mercator (UTM) coordinates using a hand-held 12 channel Global Positioning System (GPS; Garmin Etrex; Garmin International, Olathe, Kansas, USA). To minimize stress to the female, I recorded locations for newly discovered nests by projecting the point with the GPS from a distance of ≥20 m. I obtained locations of radio-marked birds by circling the signal source until the surveyor could either visually observe the bird on a nest or with her brood or isolate the female to a few shrubs. To not be perceived as a threat, I mimicked the mooing sounds and loud movements of cattle when approaching a radio-marked bird (Walker 2008). My field observations suggest that this technique reduced the frequency of bird flushing. After recording a nest location, I retreated in a meandering or zig zagging pattern to prevent predators from following human scent to the nest.

Nest monitoring.—I located radio-marked female sage-grouse at a frequency of ≤7 days throughout the nesting season. I monitored nests until the conclusion of the nesting effort once a

female was observed on a nest or triangulated to the same location over 2 visits. I used triangulation to monitor nests from a distance of ≥30 m to minimize human-induced nest predation or nest abandonment. The fate of the nest was later determined by the condition of the eggshells and shell membranes (Wallestad and Pyrah 1974). When nest fate could not be determined, I monitored females to assess whether they were brooding; a brooding female indicated a successful nest. If possible, I determined the number of hatched eggs by counting the number of egg shell caps. I considered a nest successful if ≥1 egg hatched. The hatch date was estimated as the day midway between consecutive visits unless other diagnostic signs allowed for a better approximation. A nest was considered to be successful if it hatched by approximately 28 days (Schroeder et al. 1999); otherwise it was recorded as naturally abandoned, abandoned due to researcher disturbance, nest predation, or unknown fate. If a nest was depredated I noted diagnostic evidence such as nest bowl disturbance, eggshell remains, scat, or tracks at the nest site to determine whether avian or mammalian predation occurred (Thirgood et al. 1998).

Brood monitoring.—I monitored females that successfully hatched chicks at a frequency of ≤7 days to assess brood-rearing habitat use and brood fate through August 2008 and 2009. At each visit, I attempted to determine if the female was still with her brood by visually locating the chicks with binoculars or by observing brooding behavior (e.g., distraction displays, feigning injury, clucking, and hesitation to flush). I considered the brood the experimental unit, rather than individual chicks. Therefore, a brood was considered to have survived if I observed ≥1 chick at approximately 40 days post-hatch. Forty days post-hatch is used as a cut-off for late brood-rearing success because the majority of chick mortality has already occurred by this age; consequently, chicks are more likely to survive to breeding age after this date (Aldridge 2005,

Gregg et al. 2007, Walker 2008). For the survival analysis, I estimated dates of brood loss at the mid-point between the last date observed with a brood and the first date without. Females thought to no longer be with brood were checked twice after the initial determination to confirm brood loss. I conducted back-to-back night-time spotlight counts (Walker 2008) between 36 and 40 days post-hatch to verify brood fate. This back-to-back method allowed us to determine brood fate more conclusively. Conducting the count at night is less error-prone when compared with day-time flush counts because mothers actively brood their chicks for warmth and protection at night, making chick presence much easier to determine. Furthermore, Dahlgren et al. (2010) estimated 100% chick count accuracy using night-time spotlight counts. In addition, an observer can accurately determine brood presence, while avoiding the significant disturbance caused by day-time flush counts. I considered the duration of the early brood-rearing period from hatch to 14 days and late brood-rearing period >14 days posthatch (Connelly et al. 1988, Thompson et al. 2006, Connelly et al. 2011).

Female monitoring.—I monitored female survival by field observation from early May through August 2008 and 2009. I located nesting and brooding females at a frequency of ≤7 days and non-brooding females ≤14 days post nest or brood loss, or after it was determined they did not initiate a nest. In addition, aerial telemetry flights were conducted almost monthly throughout the year, providing further information on summer female survival in addition to winter female survival data. I did not include females in the survival analysis for a period of 2 weeks after radio-marking to account for trapping stress and collar adjustment (Winterstein et al. 2001). A female was considered to have survived the summer if she survived to 110 days, corresponding to approximately the end of August depending on the collaring date and/or the first ground-telemetry location. If the female did not survive, dates of mortality were estimated

at the mid-point between the last date detected alive and the first date detected dead. In some cases, date of mortality was estimated more accurately on the basis of diagnostic signs (e.g., fresh or decomposed body) or flight data (i.e., mortality signals).

Spatial Predictor Variables

I considered predictor variables on the basis of *a priori* information from previous landscape-scale research (Homer et al. 1993, Aldridge and Boyce 2007, Doherty et al. 2008, Carpenter et al. 2010, Doherty et al. 2010) as well as hypothesized predictors of ecological relationships. These variables encompassed environmental and anthropogenic categories that I evaluated at 3 spatial scales (0.282-km radii [0.25-km^2], 0.564-km radii [1-km^2], and 1.260-km radii [5-km^2]) based on the biology of sage-grouse. I performed spatial analyses with ArcGIS 9.3 software (Environmental Systems Research Institute, Redlands, California, USA). I calculated summary statistics for most of the continuous predictor variables for each scale using a moving window function in GIS.

Modeling distribution or occurrence of organisms can be highly sensitive to scale (Pearce and Boyce 2006); I thus theorized that this was also true for survival. Correspondingly, I assessed 3 spatial scales, 1 patch scale defined as a contiguous area of one habitat type, and 2 landscape-scales defined as a mosaic of patches, on the basis of sage-grouse ecology and previous research (Meyer et al. 2002, Aldridge and Boyce 2007, Doherty et al. 2010). The radii for the largest landscape-scale, 1.260-km radii, was equal to the average movement distance between successive locations for all females within each month, which was equal to the median of these monthly movement distances over the duration of the May–August 2008 and 2009 reproductive season. The second landscape-scale of 1-km^2 (0.564-km radii) was based on research conducted by Aldridge and Boyce (2007) who found a strong relationship between

landscape features and sage-grouse selection and survival in southern Alberta, Canada within a 1-km^2 area during nesting and brood-rearing period. Further support for this intermediate scale came from Berry and Eng (1985) who found that female sage-grouse in southwest Wyoming nested an average of 0.552 km from the preceding year's nest. The biological relevance of my patch scale, 0.25-km^2 or 0.282-km radii, is supported by research conducted by Holloran and Anderson (2005) on sage-grouse nest site fidelity in Wyoming. They found that the median distance between successful nests over consecutive years was 0.283 km. Thus, it reasons that nest-site selection by sage-grouse in Wyoming occurs at approximately this scale. Moreover, a scale of 0.35- km radii, proved predictive of nest-site selection in the Powder River Basin, Wyoming (Doherty et al. 2010). The suite of environmental and anthropogenic spatial predictor variables I examined in occurrence and survival modeling are described in Table 2.1.

Environmental predictor variables.—The importance of sagebrush for sage-grouse reproduction and survival is well documented (Dunn and Braun 1986, Connelly et al. 2000, Braun et al. 2005, Holloran et al. 2005, Aldridge and Boyce 2007, Hagen et al. 2007, Doherty et al. 2008, Carpenter et al. 2010**),** as is the importance of herbaceous cover (Holloran et al. 2005, Hagen et al. 2007, Connelly et al. 2011) and litter (Kaczor 2008, Kirol et al. 2012). Using remotely sensed sagebrush products developed by Homer et al. (2012) for Wyoming, I assessed 8 habitat characteristics: percentage bare ground, herbaceous cover, litter, an estimate of shrub height, and percentage canopy cover of sagebrush, big sagebrush, and Wyoming big sagebrush. Litter was defined as an estimate of detached plant and animal organic matter as well as dead standing woody vegetation (Homer et al. 2012). With this spatial data I calculated the standard deviation (SD) as a proxy for the amount of habitat diversity or heterogeneity (Kastdalen et al.

2003, Carpenter et al. 2010) at each scale for herbaceous cover, sagebrush cover, big sagebrush cover, Wyoming big sagebrush cover, and shrub height.

I generated a Normalized Difference Vegetation Index (NDVI) from national agriculture imagery program (NAIP) color aerial imagery (U.S. Department of Agriculture [USDA] 2010). NDVI is a measure of surface greenness, generally correlating well with live green vegetation and above-ground biomass. The NDVI was calculated using the red and near infra-red bands of the four-band NAIP imagery and rescaled between 0 and 1. Values close to 1 represent greener vegetation whereas values close to 0 generally are associated with bare ground. The NAIP imagery was from August 2009, which corresponded to the end of the field portion of my study. Furthermore, I derived a categorical (0 or 1) mesic habitat variable from NDVI by reclassifying it into mesic or non-mesic based on ground-truthing and verified with NAIP imagery. Mesic habitats mainly represented riparian areas along stream channels, ponds, and wet meadows containing abundant herbaceous cover and few shrubs. Research has shown that sage-grouse demonstrate avoidance of coniferous habitats (Commons et al. 1999, Doherty et al. 2008). Using NW ReGap data (Lennartz 2007), I classified conifer stands to create a categorical variable I termed Forest. The variable Forest was verified using NAIP imagery. Utah juniper (*Juniperus osteosperma*) was the dominant conifer in my study area.

I compiled topographic variables including slope (Slope), topographic wetness index (TWI; Theobald 2007), and vector roughness measure (VRM; Sappington et al. 2007) utilizing a 1/3-arc-second National Elevation Dataset (NED; 10-m DEM). TWI is a form of compound topographic index (CTI) that predicts surface water accumulation on the basis of landscape concavity and hydrology (Theobald 2007). On the landscape-scale, CTI has proved predictive of sage-grouse selection (Aldridge and Boyce 2008; Carpenter et al. 2010) and survival (Aldridge

and Boyce 2007) in southern Alberta, Canada. Research has demonstrated that sage-grouse select for less-rugged terrain with moderate slopes in winter (Doherty et al. 2008 and Carpenter et al. 2010) and during nesting (Doherty et al. 2010). I used VRM, a terrain roughness index that measures the heterogeneity of the terrain because it is not directly correlated with slope as with other roughness measures such as the land surface ruggedness index and terrain ruggedness index (Sappington et al., 2007).

Anthropogenic predictor variables.—It has been demonstrated that anthropogenic activities such as fossil fuel development and extraction negatively affect sage-grouse through avoidance and reduced fitness rates (Holloran 2005, Walker et al. 2007, Holloran et al. 2010, Lyon and Anderson 2003, Doherty et al. 2008, Aldridge and Boyce 2007). I quantified anthropogenic variables independent of scale including distances (km) from grouse use and random available locations to anthropogenic edge (Distedge), nearest improved gravel road (Disthaul), nearest unimproved road (two-trackdist), nearest fence (Distfence), and nearest energy well (Distwell). At each spatial scale I quantified total linear distances (km) for fences (Fence), improved gravel roads (Haulrd), and unimproved roads (two-track), as well as counts of energy wells (Well), visual energy wells (Vwell), and the percentage of total surface disturbance ($Dstbarea^2$) within each scale.

Energy well data, including type, location, status, production, and spud date, were derived from the Wyoming Oil and Gas Conservation Commission database (2009). I evaluated potential influences of energy infrastructure and access roads in a temporal context because energy development was ongoing over the duration of my field research. Thus, variables associated with energy development including Distedge, Disthaul, Distwell, Dstbarea, Haulrd, Well, and Vwell were time-stamped based on the spud dates of wells associated with these

variables to accurately characterize when they were established on the landscape. I batched these time-stamped infrastructure data into monthly increments and conducted all spatial analyses based on monthly increments. The spatial analysis for each month only included infrastructure that was established on the ground prior to that month. This enabled us to depict temporal additions to human infrastructure and avoid potential biases resulting from infrastructure being included in the analysis prior to it actually existing on the ground. In addition, I used 2009 NAIP imagery to inspect the analysis area to validate well and road locations. I compiled linear distance variables (Haulrd, two-track, and Fence) using Geospatial Modeling Environment (GME) tools (Beyer 2010).

I determined wells visible from any given location (Vwells) by using the ArcView Spatial Analyst 9.3 Viewshed tool. The viewshed analysis allowed us to classify well sites that were visible from each cell on the landscape. I used 3 m as the standard well height for this analysis because this is a standard height for the structure at most CBNG wells in the ARPA. Visible wells were then summed for each spatial scale surrounding used or available locations.

I separated roads into improved (i.e., improved gravel, improved dirt) and unimproved (i.e., high clearance 4WD or two-track) roads. Improved roads were mainly used for access to energy fields and well sites and thus termed haul roads. Unimproved roads were numerous throughout my study area.

I quantified the human footprint or percentage surface disturbance, that is, areas of bare ground resulting from complete vegetation removal in my study area. To accomplish this, I created a disturbance layer that consisted of all energy infrastructure including well pads, compressor sites, transfer stations, and haul roads as well as a minimal number (n = 2) of

unoccupied human dwellings. I digitized energy infrastructure and dwellings using NAIP imagery and buffered haul roads at 10-m representing the average road width in the study area.

The study area contained approximately 31 grazing allotments. Because sage-grouse mortalities due to fence strikes have been extensively documented (Connelly et al. 2011), I assessed possible relationships between fences and survival and occurrence. Fence data were provided by the BLM-Rawlins Field Office and consisted of grazing allotment boundary and cross fences.

Experimental Design and Statistical Analysis

Occurrence analysis.—I employed a use versus availability design (Manly et al. 2002) with binary logistic regression (Boyce and McDonald 1999) to estimate each RSF. An RSF estimates the probability of a habitat unit being selected relative to its availability (Manly et al. 2002, Johnson et al 2006). The RSFs took the following form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots\ldots + \beta_k x_k) \qquad \ldots\ldots(1)$$

Where w(x) is the RSF (probability proportional to use [Manly et al. 2002]) for each cell in the landscape for the environmental and anthropogenic predictor variables, x_i and the β_i's are coefficient estimates for each predictor variable.

I incorporated a Type I Design where I pooled used locations across individual grouse and evaluated habitat availability for all grouse with pooled random locations to represent a population level response to habitat variables (Manly et al. 2002, Thomas and Taylor 2006). I constrained random locations within 100% minimum convex polygons specific to each life-stage (Manly et al. 2002) to allow female sage-grouse use to determine availability (Thomas and Taylor 2006). I explored 5 distinct female life-stages during the May–August, 2008 and 2009 reproductive periods. The life-stages included nesting, early brood-rearing, late brood-rearing,

early non-brooding, and late non-brooding. Non-brooding females that were unsuccessful nesters or lost their broods were modeled over the same temporal period as early and late brood-rearing females to assess whether they were using different habitats or showing similar selection patterns as brooding females. I employed Wyoming sagebrush products (Homer et al. 2012) to constrain the random locations to sagebrush habitats by excluding areas within the minimum convex polygons that were inappropriate to be considered as available habitat such as exposed rock, open water, and conifer stands. To ensure a representative sample of available habitats, I generated random points at a ratio of 5 times the number of used points (Aldridge and Boyce 2007, Carpenter et al. 2010). To account for possible over representation bias of available units (i.e., random locations greater in number than used locations) in my logistic regression analyses I down weighted available units to be proportional to used units (Aldridge and Boyce 2007, Carpenter et al. 2010).

I used a 2nd-order Akaike's Information Criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989) to assess model support. In my decision to use AIC_c, I followed the tenet that $n/K < 40$, where n was the sample size, and K was the number of parameters for model selection. In my analyses, n was generally small (< 40) compared to K because of down-weighting of available units that reduced the relative sample size. For all scale dependent variables, I examined the 3 spatial scales described above to determine the scale that was most correlated to occurrence by testing each variable scale individually and comparing AIC_c scores (Arnold 2010, Carpenter et al. 2010, Doherty et al. 2010). For each variable I retained the scale with the lowest AIC_c score corresponding to the greatest predictive potential (Burnham and Anderson 2002). After the selection of the appropriate scale, I removed unsupported variables based on whether 85% confidence intervals (CIs) around parameter estimates included 0

(Hosmer and Lemeshow 2000, Arnold 2010). A parameter estimate of 0 indicates no significant difference between used and available habitat units (Hosmer and Lemeshow 2000). I used variable screening to remove unsupported predictor variables, thereby reducing the likelihood of overfitting models in my model selection process (Burnham and Anderson 2002, Arnold 2010).

I computed a Pearson's correlation matrix to test for multicollinearity among predictor variables and omitted one of each correlated variable when correlation coefficients (r) were $\geq |0.6|$. To assess multicollinearity beyond variable pairs, I inspected variance inflation factor (VIF) scores and tolerance (t) values and removed one of the correlated variables when (t) $\leq |0.40|$ (Allison 2009, SAS Institute 2009). I checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($|0.3| \leq r \leq |0.6|$). Undetected correlations between variables can cause instability in the signs of coefficients and also result in inflated standard errors (Doherty 2008). Generally, if variables were correlated, the variable with the lowest AIC_c score was retained. On occasion, findings from previous research informed the decision to retain a variable (Aldridge and Boyce 2007, Doherty et al. 2010). I did not permit correlated variables to compete in the same model at any level of model selection.

Survival analysis.—I explored relationships between landscape-scale predictor variables and sage-grouse survival or risk for 3 distict life-stages: nest, brood, and adult (including yearling) female summer survival. In general, survival analyses are used for investigating time to event data. Cox's proportional hazards regression model (hereafter Cox model [Cox 1972]) is a robust survival model that provides a method of estimating the effect of variables on time to an event such as death. For example, in this analysis "time" refers to the approximate date of nest initiation and the "event" is the approximate date of nest failure. If the nest hatched successfully then it did not have an "event" and was censored. The Cox model allows for incorporating time-

dependent variables or variables that change with time and space, and right and left censored survival data (Hosmer and Lemeshow 1999). Right and left censoring allows for incorporating individuals into the model that may not be observed for an entire period or those whose event is unknown. I used the Cox model to fit my nest survival, brood survival, and adult female survival data to spatial predictor variables (Hosmer and Lemeshow 1999), which allowed us to explore those habitat features that had the greatest impact on survival. Furthermore, the Cox model produces a risk ratio that is used to assess the effect of a predictor variable on relative risk of the event while controlling for other variables in the model (Hosmer and Lemeshow 1999). The risk ratio was thus used to compare the influence of unit change in a variable on the risk of death (Winterstein et al. 2001). The Cox model took the following form in my analysis:

$$h(t|x_t) = h_0(t)\exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \ldots \beta_{ik} x_{ik}) \qquad \ldots\ldots(2)$$

where β_i's are the regression coefficients for the x_i variables, and $h_0(t)$ is the baseline hazard. The baseline hazard is unspecified but the effects of the variables are still estimated. Environmental and anthropogenic predictor variable effects were interpreted as hazard ratios ($\exp[\beta_i]$). Thus, each cell in the landscape had a value in terms of a hazard ratio.

My survival analysis periods (t) for nests, broods, and summer females were t = 28 days, t = 40 days, and t = 110 days, respectively. For the nest survival analysis, I assessed fixed-variables in the Cox model because the variables were not changing over time due to the fixed location of the nest. However, time-dependent variables were incorporated into the female and brood survival models because they experienced exposure to different habitat characteristics as they moved through the landscape. To account for time-dependence and discontinuous intervals of risk in my female and brood Cox models, a "counting-process" method was used that allowed time-dependent variables to be distributed into time intervals (Allison 2010). I assigned variable

information across intervals centered at the observation time to the midway point of the next observation when the variable information changed. This allowed us to incorporate changing exposure to habitat features across the survival period for each demographic rate. Unlike previous research on landscape scale sage-grouse survival, that generally only takes into account variable exposure at the time of event (Aldridge and Boyce 2007), I took another step to more accurately relate time-dependent variables to survival by averaging the exposure to variables over the survival time specific to each individual, which I termed average accumulative exposure. That is, the variables that correspond to an event in the Cox model were an average of the variable exposure from $t = 0$ to the time of the event. I believe this is an important step because an event such as brood loss is more likely a consequence of accumulative exposure to habitat features than exposure at the point of death. This approach accounts for possible errors associated with determining the exact point of an event but also incorporates the point of the event in the analysis. For example, a female may be depredated by a red fox (*Vulpes vulpes*) and be moved from the original location of the event prior to the location being recorded on the ground or females may be consistently loosing chicks as they move through riskier landscapes. When the fate of an individual or brood was unknown they were right-censored.

I calculated survival estimates for each of these demographic rates with the Kaplan-Meier (K–M) product-limit estimator (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989). In addition, K-M adult female winter survival estimates to $t = 242$ days were calculated from the Atlantic Rim that included data from 3 winters (2007–2008, 2008–2009, 2009–2010) to be incorporated into a model of population growth. Following the fitting of the Cox model and after calculating K-M survival estimates for each demographic rate, I estimated the baseline survivorship function (hereafter; survival probability function [SPF]) of the

proportional hazards model (Hosmer and Lemeshow 1999): The SPF function took the following form:

$$S(t, \mathrm{x}, \beta) = [S_0(t)]^{\exp(\mathrm{x}'\beta)} \qquad \ldots\ldots(3)$$

Where, $S_0(t)$ is the K-M survival estimate at the end of the survival period for that demographic rate (nest [t = 28 days], brood [t = 40 days], and female summer [t = 110 days]), and x´β is the variable adjusted coefficient from the Cox model. The SPF allowed me to transform daily risk (e.g., daily risk of nest loss in terms of a hazard ratio) derived from the Cox models, to survival probabilities corresponding to the entire demographic period that I was able to map back on the landscape.

I calculated influence statistics for each variable to determine if any observations were unusually influential in survival models because they had inflated residuals or leverage (Hosmer and Lemeshow 1999, Allison 2010). I did not remove any observations following this diagnostic procedure. I used a derivation of the AIC technique adapted for survival modeling (AIC_{SUR}) to select the best supported models of survival (Liang and Zou 2008). In the same manner as my occurrence modeling effort, I examined 3 spatial scales to determine the scale that best explained survival by testing each variable-scale individually and comparing (AIC_{SUR}) scores (Arnold 2010, Carpenter et al. 2010, Doherty et al. 2010) for scale-dependent variables. I retained the variable scale with the lowest (AIC_{SUR}) score. After selection of the appropriate variable scale, I screened variables by removing unsupported variables having parameter estimates with 85% CIs that included 0 (Le 1997, Hosmer and Lemeshow 1999, Arnold 2010). For the remaining variables, I assessed multicollinearity with a Pearson's correlation matrix and variance inflation factor (VIF) scores combined with tolerance (t) values. I omitted variables from correlated groups when (r) was $\geq |0.6|$ or (t) was $\leq |0.4|$ (Allison 2009, SAS Institute 2009). Finally, I

checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($|0.3| \leq r \geq |0.6|$). When variables were correlated, the variable with the lowest AIC_{SUR} score was retained unless findings from previous research informed my decision to retain a certain variable (Aldridge and Boyce 2007). I did not permit correlated variables to compete in the same model at any level of model selection.

In general, the Cox model assumes that the hazard remains constant over time; thus, a variables' influence is proportional over time (Le 1997, Hosmer and Lemeshow 1999). I tested the variables in my top survival models individually for proportionality (Le 1997) and I assessed log (-log(survival) by log(time)) plots to confirm that the proportional hazards assumption was not violated.

Model Development

My modeling objective was to use my sample of female sage-grouse from the ARPA population to find the best-supported predictor variables. Consequently, I used the variables with the most predictive potential to make population-level inference regarding occurrence and survival; therefore, my final RSFs or SPFs contained only the most predictive variables (Boyce et al. 2002). I evaluated the relative importance of predictor variables for occurrence and survival at 3 spatial scales and within 2 variable subsets. Because my research was mainly exploratory, I used a sequential modeling approach (Arnold 2010) consisting of two steps. As described previously the most informative scale for each variable was selected and uninformative variables were removed prior to modeling. In the first level of model selection, environmental and anthropogenic model subsets were modeled separately and within these subsets I explored all variable combinations (Burnham and Anderson 2002). At this stage, I considered models with AIC_c or AIC_{SUR} scores in the range of 2–7 units (Burnham and Anderson 2002) to be

competitive with the top model. However models with AIC scores effectively equivalent (<2 AIC_c or AIC_{SUR}) to the null model were not considered competitive (Allison 2010, Doherty et al. 2010). To address model selection uncertainty, I used additional metrics to assess variable importance because variables with poor explanatory power may have support only because they were added to an otherwise good model (Burnham and Anderson 2002, Arnold 2010). Thus, in addition to AIC_c or AIC_{SUR} scores I checked for models with essentially the same maximized log-likelihood values to assess if the model was only competitive because of the addition of a single uninformative variable (Burnham and Anderson 2002:131). Also I assessed variable importance by summing Akaike model weights across models that included the variable of interest (Arnold 2010). I brought forward the variables with the greatest potential as predictors of occurrence or survival within each subset to the final level of model selection. In a few cases, no models in the subsets were better than the null model (≥2 AIC_c or AIC_{SUR}); thus, considered uninformative (Burnham and Anderson 2002, Doherty et al. 2010). When this occurred, no models from that subset were brought forward to the final level of model selection.

After determining the best supported model(s) in each variable subset (e.g., anthropogenic and environmental), I allowed models to compete across subsets to see if additional information produced a more parsimonious model (Arnold 2010). I judged improvements in model parsimony or fit by the weight of evidence (w_i) and difference between AIC_c or AIC_{SUR} for the top model and AIC_c or AIC_{SUR} for the *i*th candidate model ($\Delta_{i;}$ Burnham and Anderson 2002). For example, I explored whether the final model(s) from the environmental subset had the most support when held in isolation, or if a combination of top models from environmental + anthropogenic subsets produced a model with greater support. When a single top model was not apparent based on AIC_c or AIC_{SUR} scores (≤7 units considered

competitive) I used multi-model inference to calculate final parameter coefficients, 95% confidence intervals, odds ratios, and risk ratios within confidence sets. I determined confidence sets for those models where Akaike weights were within 10% of the top model (Burnham and Anderson 2002). I explored quadratic transformations because the quadratic form of a variable can often identify non-linear relationships that would otherwise go undetected. I followed the convention that the linear term was always included in the model with the quadratic. At the final level of model selection I further filtered variables with poor support for a true statistical difference between groups that had parameter estimates with 95% CIs that considerably overlapped 0 (Hosmer and Lemeshow 1999; 2000). Yet, in a few instances I retained variables in the RSF or SPF with 95% CIs around parameter estimates that only slightly included 0 and were noticeably skewed because they indicated support for an apparent relationship (Le 1997).

My brood survival data contained a low number of events (n = 11). A large number of predictor variables fitted to too few events in the Cox model can result in data that are too sparse to accurately estimate parameters (Hosmer and Lemeshow 2000). Consequently, I modified selection of brood survival models by taking a conservative approach and only fitting ≤3 variable models to maintain acceptable model performance (Vittinghoff and McCulloch 2006) at both levels of model selection.

Model Validation

I assessed goodness-of-fit for my final occurrence and survival models using the likelihood ratio χ^2 test statistic (Hosmer and Lemeshow 1999, 2000). I did not have independent data to test the predictive accuracy of my final models. As such, for my occurrence models, I performed an area-adjusted 5-fold cross validation to evaluate the predictive performance of these models (Boyce et al. 2002). For each of the 5 data folds (bins) the withheld set was assessed against the

model predictions of that training data set using correlations between bin ranks of the RSF values. A high score corresponds to good predictive performance (Boyce et al 2002). In addition, I assessed the area under the receiver operator characteristic (ROC) curve as another indicator of model performance. Specifically ROC measures the true positive accuracy or ability to correctly classify subjects into one of two categories, termed the model discrimination ability (Rushton et al. 2004). Because model accuracy is more complex when censoring is involved, I used an extension of the ROC statistic, named the overall *C* statistic (*C* index), designed specifically for survival models to assess the discrimination ability of my final survival models (Pencina and D'Agostino 2004). For both the ROC and *C* statistic, values between 0.7 and 0.8 are considered to have acceptable discrimination, while values between 0.8 and 0.9 have excellent discrimination. Conversely, a value ≤ 0.5 indicates that the model predicts the outcome no better than chance (Hosmer and Lemeshow 2000). I conducted all statistical analyses with Statistical Analysis Software (SAS), version 9.2 (SAS Institute 2009). I report all K-M survival estimates as estimate ± standard error [SE]).

Mapping Ecological Models on the ARPA Landscape

I mapped my final occurrence and survival models onto the landscape in a GIS framework. The maps or layers were in a raster format with 30-m cell resolution. For interpretation, the final occurrence RSF models were mapped with values rescaled between 0 and 1, where 1 represents the highest and 0 represents the lowest predicted probability of occurrence.

For each RSF I distributed my predicted occurrence probabilities into quartiles on the basis of percentile breaks in predicted probabilities (Sawyer et al. 2006). I classified areas as high occurrence (highest 25% of predicted probabilities for summer occurrence**)** that were assigned a value of 4, moderate-high (51 to 75% predicted probabilities for summer occurrence)

that were assigned a value of 3, moderate-low (26 to 50% predicted probabilities for summer occurrence) that were assigned a value of 2, and low (lowest 25% of predicted probabilities for summer occurrence) were assigned a value of 1. Then RSF layers for each life-stage, now containing occurrence probability values grouped into quartiles with values from 1 to 4, were added into a single layer; thus, every cell contained a summer occurrence probability score providing a means to classify habitat importance on the basis of female occurrence during all summer life-stages. This layer was then rescaled between 0 and 1 to form the female summer probability of occurrence map. Thus, every cell in the female summer occurrence map had an occurrence probability based on the combined values derived from each of the life-stage layers.

Holloran and Anderson (2004) provided a model that combines sage-grouse demographics into an estimate of λ while conducting research near Jackson Hole in western Wyoming. In forming this model, they relied on knowledge of sage-grouse population dynamics as well as matrix population modeling (see Johnson and Braun 1999, Hagen 2003, Holloran 2005; M. J. Holloran, Senior Ecologist, Wyoming Wildlife Consultants LLC, personal communication, 2011). In following with my research objective to identify habitats contributing to sage-grouse population persistence in the ARPA, I incorporated this model to predict habitat quality on the landscape in terms of population growth. Thus I integrated my SPFs specific to nests, broods, and adult female summer as well as my K–M female winter survival estimates and nest initiation rates into the λ model that took the following form:

$$\lambda = [(\textit{Nest Initiation} \times \textit{Nest Survival} \times \textit{Brood Survival}) \times ♀\textit{Chick} \times \textit{Chick Winter Survival}] + (♀\textit{Adult Summer Survival}) \times (♀\textit{Adult Winter Survival}) \quad \ldots\ldots(4)$$

Where, *Nest Initiation* was a fixed value from the mean of my initiation rates from 2008 and 2009. *Nest Survival* was a dynamic value, based on the final predictor variables, from my nest

SPF; *Brood survival* was a dynamic value from my brood SPF; ♀*Chick* was a fixed value of female chicks produced annually derived from a combination of the average brood size of 6.4 (7.5 eggs and 94.3% hatchability; Crawford et al. 2004), a brood sex ratio of 54.6 females to 45.4 males (Swenson 1986), and a mean chick survival rate of 0.296 to 56 days (Aldridge and Boyce 2008); *Chick Winter Survival* was a fixed value from a chick winter survival estimate of 0.80 (Beck et al. 2006); ♀*Adult Summer Survival* was a dynamic value from my female summer SPF*;* and ♀*Adult Female Winter Survival* was a fixed value from my K-M female winter survival estimate. For the demographic rates that did not come directly from my research (♀*Chick* and *Chick Winter Survival*), I was conservative in my estimation of λ by using the lower estimates available in the sage-grouse literature. Even though these were lower estimates, all were within the breadth of values found in other studies (Schroeder et al. 1999, Holloran and Anderson 2004, Connelly et al. 2011).

The final nest, brood, and, adult female summer SPFs, were incorporated with my K-M female winter survival estimate and nest initiation rate in addition to demographic rates from the sage-grouse literature into the λ model (Equation 4). The λ model was then mapped onto the ARPA landscape to predict λ as a function of variability in habitat quality. The map was adjusted per each 30-m cell as a result of changing λ model values that were driven by habitat-specific changes in the SPFs for nest, brood and female summer.

The combination of my female summer occurrence map and λ map formed my final ecological maps that spatially predicted sage-grouse habitat quality on the ARPA landscape in 2 ways. First, the sage-grouse habitat quality map displays habitat quality in quartile bins derived from the distribution of predictions from the summer occurrence map and λ map. I classified areas as high quality (highest 25% of predicted probabilities for summer occurrence and λ**)**,

moderate-high quality (51 to 75% predicted probabilities for summer occurrence and λ), moderate-low quality (26 to 50% predicted probabilities for summer occurrence and λ), and low quality (lowest 25% of predicted probabilities for summer occurrence and λ). Second, predicted sink and source habitats were mapped on the ARPA landscape by grouping occurrence and survival into quartiles based on the λ threshold of 1 (e.g., predicting a stable population) and a binary measure of occurrence probability with the break at the mean value between high and low predicted probability (Table 2.2). These source-sink habitat categories include selected source, non-selected source, selected sink, and non-selected sink habitats.

RESULTS

In spring 2007 and 2008 I captured and radio-marked 90 female sage-grouse. In 2009, I captured 71 female sage-grouse and included those birds with 6 birds from 2007 and 2008 that still had functioning transmitters for a total of 77 birds. During 2008 and 2009 I identified and monitored 93 nests, 68 early brood-rearing locations, 69 late brood-rearing locations, 134 early non-brooding locations, and 158 late non-brooding locations. The average recorded nest initiation for 2008 and 2009 was 59%.

Occurrence

Nest occurrence.—The predictor variables that formed the best approximating environmental model represented 2 spatial scales. At the patch scale (0.25-km^2, 0.282 km radius), big sagebrush canopy cover (Bsage) and litter (Litter) were strongly correlated with nest occurrence (Table 2.8). Within this radius around nests, big sagebrush canopy cover averaged 13.5 ± 0.4% compared to 11.8 ± 0.2% at available locations and litter averaged 23.7 ± 0.2% compared to 21.1 ± 0.5% at available locations. At the largest landscape scale (5-km^2), the likelihood of nest occurrence decreased as the variation in NDVI (NDVIsd) increased. Accordingly, the odds of

nest occurrence decreased by approximately 20% with every 100 unit increase in the standard deviation of NDVI. Model support greatly increased (w_i = 0.77) with the addition of the anthropogenic model (environmental + anthropogenic; Table 2.3). The final anthropogenic model contained the visible well count (Vwell) variable at the 1-km^2 scale. Visible well count was inversely correlated with nest selection. The addition of 1 visible well within a 1-km^2 area reduced the odds of nest occurrence by approximately 46%. Available locations averaged 0.29 ± 0.04 visible wells per km^2 while nest locations averaged 0.06 ± 0.03 visible wells per km^2. The environmental and anthropogenic predictor variables, Bsage_0.25, Litter_0.25, NDIVsd_5.0, and Vwell_1.0, formed the final nest RSF model that was then rescaled and mapped onto the landscape to depict probability of nest occurrence (Fig. 2.1). The likelihood ratio χ^2test statistic suggested that the nest RSF model had good fit (χ^2_4 = 33.80, P < 0.001). The ROC statistic indicated acceptable discrimination (0.73) and, based on 5-fold cross-validation, the predictive ability of the nest RSF model was excellent (r_s = 0.96, P < 0.001, n = 10).

Female early brooding and early non-brooding occurrence.—The best supported models for early brood-rearing females (early brooding) and non-brooding females (early non-brooding) during the same period (approximately early June to early July) did not have any environmental predictor variables in common. The differences between these models suggest that brooding and non-brooding females were selecting different habitats during this period. Consequently, I formed RSF models specific to each of these life-stages.

The final environmental model for early brooding female occurrence contained the quadratic form of percent sagebrush canopy cover (Sage + Sage^2) and the variability in herbaceous cover (Herbsd) from the 1-km^2 landscape scale (Table 2.8). The variability in percent herbaceous cover within a 1-km^2 area (0.564 km radius) was negatively correlated with

selection during the early brood-rearing period, suggesting selection for habitats with more homogenous herbaceous cover. Within 0.564 km of early brood-rearing locations the standard deviation of percent herbaceous cover averaged 4.2 ± 0.2% versus 5.0 ± 0.1% at available locations. The importance of the quadratic form of percent sagebrush cover (quadratic relationship; Sage = 1.60 + $Sage^2$ = –0.06) implies that early brood-rearing females were selecting for large areas containing moderate sagebrush cover and avoiding the highest cover areas. Unlike the variable Bsage (big sagebrush species) predictive in the nest occurrence model, the variable Sage includes all sagebrush regardless of the species or subspecies (Table 2.1).

The anthropogenic model combined with the environmental model substantially increased model support (w_i = 0.99; Table 3.4). The final anthropogenic model for early brooding included Vwell at the 1-km^2 scale, total linear distance of unimproved road (Two-track_5.0) within 5-km^2, and distance (km) to nearest unimproved road (Two-trackdist). Female early brood-rearing locations were negatively correlated with the number of visible wells within 0.564 km with the model predicting a 50% decrease in occurrence with the addition of 1 visible well. Early brood-rearing locations were positively related to both the distance to the nearest unimproved road and unimproved road density at the 5-km^2 scale. As the distance to an unimproved road increased by 1 km, the odds of occurrence of an early brood-rearing female decreased by almost 2-times. Furthermore, with a 1 km increase in unimproved road density within a 1.260-km radius of a location, the odds of early brooding female occurrence increased by 15%. At early brooding locations, Two-trackdist averaged 143.4 ± 15.1 m and Two-track_5.0 averaged 12.5 ± 0.4 km compared to 192.5 ± 8.7 m and 11.4 ± 0.2 km at available locations, respectively. The final environmental (Herbsd, Sage2) and anthropogenic (Two-trackdist, Two-

track_5.0, Vwell_1.0) variables formed the early brood RSF model that was rescaled and mapped to spatially display the predicted probability of occurrence (Fig. 2.2).

Female sage-grouse without broods (early non-brooding) during the same time interval as early brood-rearing females were selecting habitats with greater litter within 0.282 km (Litter_0.25), less variability in NDVI values (NDVIsd_1.0) and lower terrain roughness values (VRM_1.0) within 0.564 km (Table 2.8). The combination of the final environmental model and the final anthropogenic model produced a model with substantially more support (w_i = approx. 1.0; Table 2.5). Similar to the early brood-rearing anthropogenic model, visual well count (Vwell_5.0) and distance to unimproved road (Two-trackdist) were important predictors. However, some of the mechanisms appeared to be different as Vwell was at a larger scale (5-km^2) and Two-trackdist was in the quadratic form. I rescaled and mapped the final early non-brooding RSF model including the above mentioned environmental and anthropogenic variables to the ARPA landscape (Fig. 2.3). The differences in the predicted probability of habitat selection between the early non-brooding RSF and the early brood-rearing RSF are evident in Figures 2.2 and 2.3. Within 0.282 km of early non-brooding locations, litter averaged 22.9 ± 0.6% compared to 22.2 ± 0.3% at available locations. Terrain roughness (VRM) within a 1-km^2 area surrounding early non-brooding locations averaged $5.1 \times 10^{-4} \pm 4.4 \times 10^{-5}$ versus $9.0 \times 10^{-4} \pm 2.9 \times 10^{-5}$ at available locations. Because VRM measurement units are small, I rescaled them by multiplying the original values by 1000 for interpretation. Thus, with a 1000 unit increase in VRM the likelihood of early non-brooding occurrence decreased by approximately 50%. Early non-brooding females did not seem to be showing avoidance of forest edge. The quadratic term for distance to an unimproved road (Two-trackdist = –4.1 + Two-trackdist^2 = 5.6) suggests a concave relationship. Specifically, the probability of early non-brooding female occurrence

initially decreased as the distance from an unimproved road increased, but at approximately 0.5 km the relationship changed and the probability began to increase as the distance to nearest unimproved road increased. Within a 5-km^2 area, as the number of visual wells increased by 1 the probability of occurrence by early non-brooding females decreased by approximately 24%.

For the early brooding and early non-brooding RSFs, the likelihood ratio indicated good model fit, $\chi^2_6 = 29.30$, $P < 0.001$ and $\chi^2_6 = 63.07$, $P < 0.001$, respectively. The ROC statistic for early brooding (0.74) and early non-brooding (0.76) showed acceptable discrimination. Predictive ability, assessed by 5-fold cross-validation, for the early brood ($r_s = 0.95$, $P < 0.001$, $n = 10$) and early non-brood ($r_s = 0.97$, $P < 0.001$, $n = 10$) RSF models was excellent.

Female late brooding and late non-brooding occurrence.—Similar to early brood-rearing and early non-brooding female selection, I found that habitat selection by late brood-rearing females and late non-brooding females also diverged (Table 2.8). Because of the predicted differences in occurrence based on my modeling, I formed RSF models specific to each of these life-stages. The duration of the late brood-rearing period (>14 days post-hatch) over the course of our research extended from early July to late August 2008 and 2009.

The final late brood-rearing (late brooding) environmental model was very similar to the final environmental model for early brooding. The final late brooding environmental model included Herbsd_5.0 and Sage^2_1.0. The only difference from the final early brooding environmental model was the scale at which Herbsd was most predictive. As such, late brooding female occurrence was negatively correlated with the variability in the percent herbaceous cover within 1.260-km. Herbsd_5.0 averaged 4.7 ± 0.2% at late brood-rearing locations compared to 5.4± 0.1% at available locations. As with early brood-rearing selection, sagebrush cover, regardless of sagebrush species, was an important predictor of occurrence in the quadratic form

(Sage = 2.19 + Sage^2 = –0.09). This finding suggests that females during the late brood-rearing period were strongly correlated with moderate sagebrush canopy cover, but avoided areas with the highest sagebrush canopy cover available at the 1-km^2 scale. The addition of the anthropogenic model moderately increased model support (w_i = 0.54), but I believe the increase was sufficient to justify including these anthropogenic variables in the final RSF model (Table 2.6). The final anthropogenic model for late brooding included the quadratic form of the percent surface disturbance area within the 5-km^2 scale (Dstbarea^2_5.0), the distance to the nearest improved road (Hauldist), and the distance to the nearest unimproved road (Two-trackdist). The quadratic form of Dstbarea^2 (Dstbarea = 0.02 + Dstbarea^2 = 0.0001) suggests that at the 5-km^2 scale, late brood-rearing females were using habitats with surface disturbance (e.g., well pads and improved roads), but avoided habitats when a surface disturbance threshold of approximately 8% was surpassed. Late brooding occurrence was positively correlated with improved roads. Accordingly, as the distance to an improved road decreased by 1 km the probability of late brood occurrence increased by 48%. For late brooding and available locations the average distance from improved roads was 1.1 ± 0.01 km compared to 1.4 ± 0.01 km, respectively. Late brooding females were also positively correlated with distance to the nearest unimproved road. Two-trackdist for late brooding locations averaged 147.0 ± 19.4 m versus 196.3 ± 9.8 m at available locations. The predictor variables Herbsd_5.0, Sage^2_1.0, Dstbarea2_5.0, Hauldist, and Two_trackdist formed the final late brooding RSF that was rescaled and mapped on the ARPA landscape (Fig. 2.4).

Multiscale environmental predictor variables were supported in my late non-brooding modeling including Forestdist and Sage_0.25. The distance to forest edge was positively correlated with late non-brooding female occurrence. That is, with a 1 km decrease in distance

to forest edge the probability of late non-brooding occurrence increased by approximately 49%. The distance to forest edge averaged 1.50 ± 0.01 km at late non-brooding locations compared to 2.10 ± 0.01 km at available locations. Percent sagebrush canopy cover was important at the patch scale and positively correlated with female late non-brooding occurrence. With every 1% increase in sagebrush canopy cover within 0.282 km (Sage_0.25) the probability of late non-brooding female occurrence increased by 55%. At late non-brooding locations sagebrush canopy cover averaged 14.1 ± 0.3% versus 12.6 ± 0.1% at available locations. The final late non-brooding anthropogenic model substantially improved model fit (w_i = 0.79) when combined with the environmental model (Table 2.7). The late non-brooding model contained the variables Two-trackdist and Vwell_5.0. Vwell density was strongly correlated with late non-brooding female occurrence at the largest landscape scale (5-km^2). That is, the odds of late non-brood occurrence decreased by approximately 57% with the addition of 1 visible well within a 1200 m radius on the ARPA landscape. Unlike early brooding and late brooding, distance to nearest unimproved road (Two-trackdist) was negatively correlated with late non-brooding occurrence. Hence, with a 1 km increase in distance to nearest unimproved road the probability of occurrence increased by about 75%. At late non-brooding female locations Two-trackdist averaged 213.5 ± 15.4 m compared to 181.2 ± 5.7 m at available locations. Predictor variables, forestdist, herbsd_5.0, Sage_0.25, Two-trackdist, and Vwell_5.0, formed the final late non-brooding RSF that was rescaled and mapped on the ARPA landscape (Fig. 2.5). Differences in spatial selection patterns are evident when comparing the mapped late non-brooding RSF with the late brooding RSF (see Fig. 2.4 and Fig. 2.5).

The likelihood ratio test specific to late brooding and late non-brooding indicated that the models had good fit, $\chi^2_6 = 20.83$, $P < 0.002$ and $\chi^2_4 = 23.23$, $P < 0.001$, respectively. The ROC

statistic for the late brooding RSF model (0.70) was acceptable. However, the ROC score for the late non-brooding RSF (0.62) indicated poor discrimination ability. Predictive ability measured by 5-fold cross-validation for the late brooding RSF model (r_s = 0.93, P < 0.001, n = 10) was excellent. Yet, 5-fold cross-validation for the late non-brooding RSF model (r_s = 0.70, P < 0.033, n = 10) indicated only moderate performance.

Survival

Nest survival.—Nest survival modeling identified 3 environmental variables at 3 different scales that were strongly correlated with 28-day nest survival. The predictive variables included variability in shrub height at the 1-km^2 scale (Shrbhgtsd_1.0), terrain wetness index at the 0.25-km^2 scale (TWI_0.25), and percent Wyoming big sagebrush canopy cover at the 5-km^2 scale (Wysage_5.0; Table 2.11). Daily nest survival increased with an increase in Shrbhgtsd_1.0. Thus, habitats at the 1-km^2 scale with homogenous shrub heights were riskier habitats for nesting. A 5 cm increase in the variability in shrub height corresponded to about a 41% decrease in the probability of daily nest loss (Fig. 2.7). Shrbhgtsd_1.0 at successful nests averaged 8.2 ± 0.4 cm compared to 7.4 ± 0.3 cm at unsuccessful nests. Similarly, the percent Wysage_5.0 was positively correlated with nest success. With a 1% increase in Wyoming big sagebrush canopy cover within a 1.260-km radius surrounding a nest the likelihood of success increased by approximately 26%. At successful nests, Wysage_5.0 averaged 9.8 ± 0.1% versus 9.4 ± 0.2% at unsuccessful nests. At the patch scale, topographic wetness index (TWI) was negatively related to nest success. As TWI increased by 1 unit within a 0.282-km radius of a nest the likelihood of nest loss increased by 28%. TWI_0.25 averaged 5.5 ± 0.1 versus 5.8 ± 0.2 at successful versus unsuccessful nests, respectively. None of the anthropogenic variables in the anthropogenic model subset were better than the null model ($\Delta AIC_{SUR} \geq 2$). The final nest survival model

provided a good fit to the data, $\chi^2_3 = 8.72$, $P < 0.033$ and with a C index value of 0.79, the discrimination ability of the model was acceptable.

Nest survival was similar from year to year, with a 43.4% ± 5.4% K-M nest survival estimate over a 28-day incubation period. Predictor variables Shrbhgtsd_1.0, TWI_0.25, and Dstbarea^2_1.0 formed the final nest survival model that was combined with the 28-day nest survival estimate to produce the nest SPF. I mapped the SPF predicting nest survival onto the ARPA landscape to spatially display habitat-specific survival probabilities, where 1 was the highest probability of survival predicted from the SPF and 0 the lowest (Fig. 2.8).

Brood survival.—Variables included in the brood survival models represent average accumulative exposure over the duration preceding a mortality event or to 40 days if the brood survived. Brood survival to 40 days was correlated to both environmental and anthropogenic variables at the 1-km^2 scale (Table 2.11). The accumulative environmental variables relating to daily brood survival included the percent herbaceous cover (Herb) and Shrbhgtsd. Herbaceous cover within a 0.564-km radius of successive brood locations was negatively related to daily brood survival. With a 1% increase in herbaceous cover the odds of 40-day brood survival decreased by approximately 11%. For broods that survived, Herb_1.0 averaged 10.2 ± 0.4% and for broods that did not survive, Herb_1.0 averaged 15.2 ± 0.7%. Average accumulative Shrubhgtsd_1.0 was positively correlated with daily brood survival. Therefore, an increase from 0 to 5 cm of Shrubhgtsd_1.0 over successive brood locations corresponded with approximately an 80% increase in the probability of daily survival (Fig. 2.7). At 40-day brood survival locations, Shrubhgtsd_1.0 averaged 8.2 ± 0.2 cm compared to 6.8 ± 0.2 cm at locations preceding brood loss. The combination of the final anthropogenic model and final environmental model moderately improved model fit ($w_i = 0.52$; Table 2.9). The top

anthropogenic model included the quadratic term for total surface disturbance area at the 1-km^2 scale (Dstbarea^2_1.0). The quadratic term suggests that accumulative exposure to Dstbarea^2_1.0 initially has little effect on 40-day brood survival, but at a threshold of approximately 4% surface disturbance, the risk of daily brood loss begins to increases dramatically with increasing disturbance (Fig. 2.9). For example, this relationship indicates that an increase in surface disturbance from 6% to 7% equates to approximately a 29% increase in the probability of daily brood loss. Broods that survived were using habitats with a mean of approximately 0.6 ± 0.1% surface disturbance compared to approximately 0.7 ± 0.3% surface disturbance for broods that did not survive. The final brood survival model provided good fit to the data, $\chi^2_4 = 16.26$, $P < 0.003$. However, the *C* index value of 0.68 indicated that the discrimination ability of the model was poor although it was close to the acceptable range of ≥0.70.

The K-M brood survival estimated to 40 days post-hatch was 76.2% ± 8.0%. I combined the final brood survival model consisting of the variables Herb_1.0, Shrubhgtsd_1.0, and Dstbarea^2_1.0 with the 40-day brood survival estimate to form the brood SPF. The SPF predicting brood survival to the end of this time period was mapped onto the ARPA landscape to spatially display habitat specific survival probabilities (Fig. 2.10).

Female survival.—The K-M female summer survival estimate to 110 days was 93.0% ± 2.6% (2008–2009) and in winter was 77.9% ± 5.0% (t = 242 days; 2007–2010). Environmental variables that were predictive of sage-grouse female summer survival (t = 110) included Shrbhgtsd_1.0 and VRM_5.0. Like brood survival, variables represent average accumulative exposure over the duration preceding a mortality event or to 110 days if the female survived. The variability in shrub height within a 0.564-km radius of successive female locations was positively correlated with female survival. In fact, an increase from 0 to 10 cm in the standard

deviation of shrub height resulted in an approximately 92% increase in the probability of daily female survival (Fig. 2.7). At locations used by females who survived, Shrubhgtsd_1.0 averaged 7.7 ± 0.1 cm compared to 6.9 ± 0.2 cm at locations proceeding female death. As terrain roughness (VRM_5.0) increased female risk also increased. A 1000 unit increase in VRM_5.0 resulted in a 43% decrease in female daily survival risk. At successive locations used by females that survived, VRM_5.0 averaged $7.3 \times 10^{-4} \pm 1.8 \times 10^{-5}$ units versus $7.1 \times 10^{-4} \pm 6.0 \times 10^{-5}$ units at locations used by females who died.

Model support increased somewhat with a combined model including the final environmental model and the final anthropogenic model (w_i = 0.58; Table 2.10). The final anthropogenic model included the distance to nearest anthropogenic edge (Edgedist). Edgedist suggested that as the distance from anthropogenic edge increased the probability of 110-day female survival decreased. Thus, daily survival was higher for females using habitats closer to anthropogenic infrastructure such as well pads and improved roads. Over successive locations, predicted daily female survival within 1 km of anthropogenic edge was approximately double that of daily female survival at a distance of 2 km from anthropogenic edge. Edgedist for females that survived to 110 days versus females that did not survive was 1.04 ± 0.03 km and 1.7 ± 0.1 km, respectively. The final female survival model provided a good fit to the data, χ^2_3 = 12.80, $P < 0.005$ and the C index value of 0.74 indicated acceptable model discrimination ability.

The variables Shrbhgtsd_1.0, VRM_5.0, and Edgedist formed the final female summer survival model. This model was combined with the female summer survival estimate to form the female SPF predicting survival to t = 110 days. It was then mapped onto the ARPA landscape to spatially display habitat-specific survival probabilities (Fig. 2.10).

I rescaled the combined female summer occurrence layer to spatially display probabilities of female summer occurrence (Fig. 2.6). The λ map is displayed as a continuum from the highest predicted λ value (λ = 1.22) to the lowest (λ = 0.34; Fig. 2.12). The habitat quality map derived from female summer occurrence and λ represents a continuous prediction of habitat quality and suggests that about 50% of the available habitat is moderate to high quality (Fig. 2.13). The spatial quantification of source and sink habitats on the ARPA landscape indicated that of the sage-grouse habitat within the ARPA, the source-sink map predicted 40% as selected source, 42% as non-selected source, 4% as selected sink, and 14% as non-selected sink (Fig. 2.14).

DISCUSSION

My analysis provides critical information for persistence of greater sage-grouse within a developing energy field (ARPA). In my analyses I used *a priori* information (Homer et al. 1993, Wisdom et al. 2002, Aldridge and Boyce 2007, Aldridge and Boyce 2008, Doherty et al. 2008, Doherty et al. 2010) and theorized ecological relationships to inform my GIS variables. I incorporated this suite of variables in modeling to explore and identify the most important variables predicting female sage-grouse occurrence and fitness over the summer. I used my final ecological models to spatially display female sage-grouse habitat quality during the breeding season within the ARPA to inform habitat management and conservation in this developing CBNG field.

Anthropogenic variables related to CBNG development were ubiquitous in all of the final occurrence models, suggesting that anthropogenic features are negatively influencing habitat selection through all summer life-stages of female sage-grouse. Anthropogenic variables do not seem to be broadly influencing fitness throughout the female summer life-stages. That is, for

nest and female survival models the variables most correlated with reduced fitness were environmental variables such as the variability in shrub heights. My findings do indicate that total surface disturbance ≥4% results in reduced brood survival. However, my occurrence modeling suggests that, because these highly disturbed areas were primarily being avoided by brooding females the potential fitness consequences are most often not realized. Predictor variables incorporating multiple spatial scales proved predictive in almost all of my occurrence and fitness models. With the exception for early non-brooding females, sagebrush canopy cover at different scales was represented in each of the final occurrence models. Finally, I found that habitat quality was not homogenous across the ARPA landscape, but spatially variable among habitat patches.

Ecologists have long recognized the importance of scale in studies of ecological pattern and process (Johnson 1980, Morris 1987, Wiens 1989, Meyer et al. 2002). My results elucidate the importance of considering different, but biologically relevant scales or "lenses" in which to view ecosystems (Diez and Giladi 2011) for both sage-grouse occurrence and fitness. While assessing landscape-scale sage-grouse nest selection, Doherty et al. (2010) demonstrated multiscale habitat associations. Likewise, in my final nest RSF, 2 patch-scale variables (Bsage_0.25 and Litter_0.25), 1 smaller landscape-scale variable (Vwell_1.0), and 1 larger landscape-scale variable (NDVIsd_5.0) were predictive of nest selection. However, if only a single scale was considered in my research some of these predictor variables would have been dismissed as uninformative. For example, Vwell at the patch-scale had an AIC_c score (AIC_c = 261.089) that was no better than the null model (AIC_c = 261.045). Yet, at the 1-km^2 landscape-scale it had good support individually (AIC_c = 257.032) and greatly improved the RSF model (w_i = 0.77).

Previous sage-grouse research on habitat-specific fitness considered only a single landscape-scale (1-km^2; Aldridge and Boyce 2007). However, research on other avian species has demonstrated variations in fitness at different scales especially in human modified landscapes (Chalfoun and Martin 2007, Robinson et al. 1995, Robinson and Hoover 2011). In concurrence with these findings, I found that sage-grouse fitness parameters were scale-dependent. For example, my nest SPF model contained 3 variables at 3 spatial scales including topographic wetness index (TWI) at the patch-scale (0.25-km^2), heterogeneity in shrub height (Shrbhgtsd) at the smaller landscape-scale (1-km^2), and the percent Wyoming big sagebrush canopy cover (Wysage) at the largest landscape-scale (5-km^2).

Similar to other landscape-scale research (Aldridge and Boyce 2007, Doherty et al. 2010) as well as local-scale research (Connelly et al. 2000, Braun et al. 2005, Holloran et al. 2005, Hagen et al. 2007, Doherty et al. 2010), nest occurrence was strongly correlated with big sagebrush canopy cover with the odds of nest occurrence increasing proportionately with increasing canopy cover. Sagebrush canopy cover, albeit in different forms and at different scales, was present in my RSF models throughout every summer female life-stage with the exception of the early non-brooding RSF. Furthermore, it is noted that areas with high cover of tall sagebrush are important to sage-grouse in the ARPA during winter (J.L. Beck, unpublished data), suggesting the need to conserve these areas for sage-grouse conservation in the ARPA.

During the early and late brood-rearing periods the quadratic form of sagebrush cover (not specific to *Artemisia* taxa) at the 1-km^2 scale was predictive of selection. Thus, brooding female sage-grouse appear to be selecting habitats with moderate sagebrush cover, but avoiding areas with the highest cover. Moderate sagebrush stands likely provide refugia from predators while also providing interstitial space for growth of forb resources that are essential to brood

development (Bergerud 1988, Johnson and Boyce 1990, Holloran and Anderson 2004, Connelly et al. 2011, Hagen 2011). Further support for this finding comes from Aldridge and Boyce (2007) who also found moderate sagebrush cover to be important to brooding females at the same landscape-scale. Female sage-grouse during early and late brood-rearing periods were selecting habitats with a heterogeneous distribution of herbaceous cover. Thus habitats with forb patches intermixed with moderate sagebrush cover seem to be preferred by brooding females. This supports the concept that habitat selection during the breeding season is driven by the need to meet biological demands while also having adequate concealment from predators (Hagen 2011). At the patch-scale (0.25-km^2), litter was also positively related to nest habitat selection. To my knowledge no other landscape-scale sage-grouse research has identified this relationship. It must be noted that the litter variable not only included ground plant and animal organic matter, but also dead standing woody vegetation (Homer et al. 2012) that likely provided additional vertical structural diversity and cover. At the local-scale (within 5 to 15 m), Sveum et al. (1998) and Kirol et al. (2012) found that the likelihood of nest selection increased with greater litter and Kaczor (2008) found that successful sage-grouse nests in South Dakota had a higher percentage of litter surrounding nests than unsuccessful nests. Furthermore, local-scale research on other gallinaceous species such as Mountain Quail (*Oreortyx pictus*) also suggests an association between nest site selection and litter (Reese et al. 2005).

Even though there was some habitat overlap, my results show that during summer females without broods were not selecting the same habitats as females with broods (Fig. 2.2–2.5). Unlike late brood-rearing, the distance to forest edge was supported in the late non-brooding model. The relationship to forest edge was unexpected, in that late non-brooding females were more likely to occur closer to forest edge. On the contrary, during winter, Doherty

et al. (2008) found that female sage-grouse flocks were avoiding coniferous habitats. The coniferous habitats in the ARPA are mainly distributed along the upper elevation ridgelines and along the eastern edge. Thus, late non-brooding females seemed to be selecting the foothill habitats at the base of these forested ridgelines during early and late summer. This selection may be related to a more productive understory associated with these areas.

Anthropogenic predictor variables improved model support in all of the final occurrence models specific to each female summer life-stage. Visual well density was negatively correlated with female sage-grouse occurrence during nesting and early brood-rearing at the 1-km^2 scale and early non-brooding and late non-brooding at the 5-km^2. For nest occurrence, the addition of 1 visible well within 0.564 km of a nest decreased the probability of occurrence by approximately 35%. Researchers in other portions of the sage-grouse range also being influenced by oil and gas development have previously identified relationships between well or visible well densities and occurrence during different life-stages (Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008). Aldridge and Boyce (2007) in Canada found that whereas broods were still occurring in habitats with oil and gas development, habitat avoidance occurred as the number of visible wells increased within a 1-km^2 area. The quadratic term for total disturbance area was an important predictor in the late brood-rearing model. This quadratic relationship suggests that moderate disturbance was tolerated by late brood-rearing grouse, but as disturbance increased to approximately 2% a threshold of tolerance was reached and avoidance began to occur (Fig. 2.4).

My survival analyses results illustrate habitat-specific variations in survival or risk across the ARPA landscape. Supported by local-scale research (Connelly et al. 1991, Holloran et al. 2005, Connelly et al. 2011), I found that sage-grouse nest success had a positive relationship to

sagebrush canopy cover. Specifically, I found that as Wyoming big sagebrush canopy cover within a 1.260-km radius (5-km^2) increased so did the probability of nest survival. Sagebrush communities in my study area were dominated by nearly equal amounts of Wyoming big sagebrush and mountain big sagebrush (BLM 2006, Rodemaker and Driese 2006). Because the relationship was specific to the Wyoming big sagebrush subspecies (i.e., the variable Sage_5.0 was not as well supported) this result suggests that not only is sagebrush cover within a large area important to nest survival, but nests were more likely to survive in Wyoming big sagebrush versus mountain big sagebrush stands. Similar to Aldridge and Boyce (2007), I did not find any significant correlations between nest survival and anthropogenic development.

The variability in shrub heights within a 1-km^2 area was predictive of nest, brood, and adult female survival throughout the summer. Because a strong correlation between Shrubhgtsd_1.0 and survival was omnipresent in all of my survival models it appears that stands with homogenous vertical cover of sagebrush and other shrub species were riskier habitats for females in every summer life-stage. I am unaware of any others who have specifically assessed variability in shrub heights and survival at the landscape-scale, although Aldridge and Boyce (2007) found that nest survival greatly improved in habitats containing a heterogeneous mix of sagebrush cover.

Anthropogenic predictor variables informed my brood survival and adult female survival models, but the mechanisms were quite different. I found that brood survival began to decrease when a threshold of about 4% surface disturbance within a 0.564-km radius of brood-rearing habitat was reached and brood-rearing habitat becomes considerably riskier at approximately 6% surface disturbance (Fig. 2.9), suggesting that moderate levels of surface disturbance in habitats being used by brooding females appeared to have little influence on brood survival. Yet, once a

threshold of disturbance was reached, the risk to brood survival started to increase dramatically (Fig. 2.8 and 2.9). Aldridge and Brigham (2007) found that daily chick survival (56-days) decreased with greater well densities also within a 0.564-km radius. Similar relationships have been found in other species, such as the grizzly bear (*Ursus arctos horribilis*), where researchers found that an increase in survival risk was strongly correlated with anthropogenic habitats (Johnson et al. 2004).

Conversely, I found that adult female survival decreased with a greater distance from anthropogenic edge. That is, my results indicate that female survival was higher in many of the same habitats where CBNG development was occurring (Fig. 2.10). Thus accumulative exposure to CBNG modified habitats throughout the summer may not have been detrimental to adult female survival. I believe there are two probable explanations for this relationship. First, CBNG development may have disrupted predator-prey behavior because common sage-grouse predators may have avoided anthropogenic edge thus reducing risks to adults. In some cases, research on avian species has shown that human-altered landscapes can provide a degree of refugia for prey as a consequence of predator avoidance of those areas (Tewksbury et al. 1998, Francis et al. 2009). Second, the distance to anthropogenic edge may be a proxy for less rugged terrain where female sage-grouse experienced reduced risk. Support for this explanation comes from a second environmental variable I found predictive of female summer adult survival. I found that the level of terrain roughness at my largest landscape scale (VRM_5.0) was negatively related to adult female summer survival. Thus, habitats with greater amounts of topographic relief at my largest landscape scale were riskier habitats to female sage-grouse during summer. In the ARPA this would include several prominent drainage basins and ridgelines that may be providing perching and nesting substrates for aerial sage-grouse predators

such as golden eagles (*Aquila chrysaetos*). Habitats with CBNG development within the ARPA most often occur in areas that are relatively flat. Therefore, even though Edgedist and VRM_5.0 were not directly correlated they may be predicting a similar mechanism. This would suggest that adult female summer survival is independent of CBNG development within the ARPA. Regardless of the mechanisms I found no evidence of reduced adult female summer survival at the level of CBNG development that occurred during my study.

The λ model is deliberately sensitive to changes in adult female "breeders" survivorship (M. J. Holloran, Senior Ecologist, Wyoming Wildlife Consultants LLC, personal communication, 2011) because in long-lived birds like sage-grouse, λ is often more sensitive to breeder survival than any other demographic rate (McDonald and Caswell 1993). Furthermore, population viability analysis for a sage-grouse population in North Park, Colorado indicated that adult female and juvenile survival were the most significant demographic rates followed by adult and juvenile fecundity (Johnson and Braun 1999). The λ map reflects the significance of female survival as many of the habitats that have $\lambda < 1$ are also habitats with low predicted female summer survival. My λ model predicts the vast majority of the sage-grouse habitat within the ARPA has the potential to contribute to a stable or increasing sage-grouse population ($\lambda > 1$). The λ model and corresponding map suggest that CBNG development was not increasing the amount of habitat with $\lambda < 1$ unless surface disturbance exceeded approximately 4% within a 1-km^2 area area at which the lower predicted brood survival caused λ to fall below 1. Furthermore, my results provide little evidence that selected sinks or ecological traps are resulting from anthropogenic disturbance within the ARPA, as has been found with other avian species (Misenhelter and Rotenberry 2000, Pearson and Fraterrigo 2011) and mammalian species (Knight et al. 1988) in human modified landscapes. It appears that possible ecological traps

were not occurring because brooding female sage-grouse appeared to be avoiding these areas; thus, potential fitness consequences are not realized.

It is important to note that the predicted λ values and corresponding maps I provide have limitations. One limitation is that mechanisms I did not measure directly such as sage-grouse immigration or emigration, predator intensity, and climatic differences are not considered in the λ model. However, many of the variables I assessed associated with cover are proxies for predation risk because they provide concealment from aerial and ground predators (Hagen 2011). A second limitation is that the model may over predict λ in some cases when habitat-specific conditions cause the corresponding SPF to predict 100% survival for one or all of the variable-adjusted demographics (e.g., nest, brood, or adult female summer survival). Because of these limitations the source-sink threashold ($\lambda < 1$) should be considered accordingly when assessing habitat quality. However, I believe I largely corrected for this by incorporating rates from the sage-grouse literature representing the lower range in these demographic responses (Schroeder et al. 1999, Connelly et al. 2011) into the λ model. Because my habitat quality map is independent of the λ threshold of 1 (e.g., λ is a constant value from lowest to highest) it provides additional information on the importance of specific habitat patches to the ARPA sage-grouse population.

My occurrence models for each life-stage and subsequent female summer occurrence map indicate that female sage-grouse are avoiding potential source habitats (e.g., non-selected source) mainly due to visual wells. In fact, my models predict that almost half of the source habitat is falling into the non-selected source category. Therefore, my results suggest a large percentage of source habitats are contributing little to recruitment because of being largely avoided due to CBNG infrastructure.

My analysis was designed to spatially predict habitat quality on the basis of the best-supported landscape variables predicting sage-grouse occurrence and corresponding fitness outcomes. My results demonstrate that occurrence and fitness are influenced by environmental and anthropogenic habitats at multiple spatial scales. My source-sink map suggests that the ARPA currently has abundant source habitat. Yet, my results provide strong evidence that source-sink dynamics within the ARPA landscape may be shifting as a result of CBNG development. However, the apparent shift is largely being driven by avoidance or displacement and not fitness consequences, in that this shift is resulting in selected source habitats becoming non-selected source habitats. In conclusion, the ecological conditions that are of greatest concern for sage-grouse population persistence in the ARPA may be avoidance of otherwise productive habitats largely resulting from anthropogenic changes being driven by CBNG development.

MANAGEMENT IMPLICATIONS

Because greater sage-grouse are imperiled in much of their current range (United States Fish and Wildlife Service [USFWS] 2010), there is a critical need for better management practices where sage-grouse and anthropogenic development overlap. Current sage-grouse mitigation measures employed by the BLM focus on buffers surrounding sage-grouse leks and generally include a 0.4 to 1.6 km no occupancy buffer, determined on a case-by-case basis, and a 3.2 km seasonal no disturbance timing stipulation (BLM 2007). However, the focus on lek buffers could result in critical high-quality habitats being left unprotected and management resources directed to protecting low-quality habitats. In addition, the buffer approach would likely be ineffective at protecting large intact source habitats necessary for population persistence.

My research suggests that occurrence and fitness are being driven by habitat characteristics at large spatial scales. Thus, to maintain sage-grouse populations, management should also consider larger scale mitigation measures. As CBNG development continues in the ARPA and elsewhere, a critical amount of high-quality habitat must be maintained to ensure a viable sage-grouse population in the future. Because local population dynamics depend on a balance between mortality and fecundity as well as demographic subsidies from adjacent sources (Pearson and Fraterrigo 2011), selected source habitats, if set aside, provide a surplus of dispersers that stand ready to recolonize non-selected source habitat after reclamation takes place. My models suggest the most productive habitat expanses, contributing to sage-grouse population persistence within the ARPA, include much of the habitat north of Muddy Creek, the area west of Dotty Mountain Compressor Road and south of Muddy Creek, the Garden Gulch area north of Cow Butte Road, The Willows mainly east of Willows Road, as well as areas south of Muddy Mountain and east and west of McCarty Canyon Road (Fig. 2.13 and 2.14).

Anthropogenic development in high occurrence brood-rearing habitats (Fig. 2.2 and 2.4) should ensure that surface disturbance does not exceed approximately 4%. Also, visibility from surrounding sagebrush habitats, especially if they are selected source habitats, should be considered during well and infrastructure placement. Directional-drilling technology offers new methods to reduce surface disturbance and the visual footprint on energy development landscapes. I recommend continued monitoring of key sage-grouse habitat selection and fitness parameters including nesting and brood-rearing selection and nest, brood, and adult female survival to test for possible temporal changes in resource availability related to year to year climatic differences as well as well field expansion that may affect the performance of the ecological models that I provide.

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Table 2.1. Spatial predictor variables used for sage-grouse nest, brood, female occurrence and survival modeling in south-central Wyoming, USA, 2008 and 2009. Data are 30-m resolution and spatial scales are circular unless indicated otherwise.

Model category/ predictor variable	**Spatial scale (km^2)**	**Description**
Environmental		
Baresoil	0.25, 1.0, 5.0	Mean bare ground (%; Homer et al. 2012) calculated using a moving window
Bsage[b]	0.25, 1.0, 5.0	Mean big sagebrush (*Artemisia tridentata*) cover (%; Homer et al. 2012) calculated using a moving window
Bsagesd	0.25, 1.0, 5.0	Standard deviation big sagebrush (*Artemisia tridentata*) cover (%; Homer et al. 2012) calculated using a moving window
Forestdist[b]		Distance (km) to nearest conifer stand from NW ReGap (Lennartz 2007) and verified using NAIP[c] imagery (2009)
Herb[b]	0.25, 1.0, 5.0	Mean herbaceous cover (%; Homer et al. 2012) calculated using a moving window
Herbsd	0.25, 1.0, 5.0	Standard deviation herbaceous cover (%; Homer et al. 2012) calculated using a moving window
Litter	0.25, 1.0, 5.0	Mean litter (%; Homer et al. 2012) calculated using a moving window
Mesic[a]	0.25, 1.0, 5.0	Proportion of area (%) that is mesic habitat derived from converting NAIP[c] imagery (2009) to NDVI[d] and ground-truthed to determine value break (categorical [0,1])
Mesicdist[b]		Distance (km) to nearest mesic area derived from converting NAIP[c] imagery (2009) to NDVI[d] and ground-truthed to determine cell value break (categorical [0,1])
NDVI	0.25, 1.0, 5.0	Mean normalized differential vegetation index (NDVI) values derived from NAIP[c] imagery calculated using a moving window

Model category/ predictor variable	Spatial scale (km^2)	Description
NDVIsd	0.25, 1.0, 5.0	Standard deviation of normalized differential vegetation index (NDVI) values calculated using a moving window
Sage[b]	0.25, 1.0, 5.0	Mean sagebrush (All *Artemisia* spp.) cover (%; Homer et al. 2012) calculated using a moving window
Sagesd	0.25, 1.0, 5.0	Standard deviation sagebrush (all *Artemisia* spp.) cover (%; Homer et al. 2012) calculated using a moving window
Shrbhgt	0.25, 1.0, 5.0	Mean shrub height (cm; Homer et al. 2012) calculated using a moving window
Shrbhgtsd	0.25, 1.0, 5.0	Standard deviation shrub height (cm; Homer et al. 2012) calculated using a moving window
Slope[a]	0.25, 1.0, 5.0	Mean slope (%) calculated using a moving window
TWI[a]	0.25, 1.0, 5.0	Mean topographic wetness index (TWI; high values = increased soil moisture; Theobald 2007) calculated using a moving window
VRM[ae]	0.25, 1.0, 5.0	Mean topographic roughness (vector roughness measure [VRM; Sappington et al. 2007]) calculated using a moving window[a]
Wysage[b]	0.25, 1.0, 5.0	Mean Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) cover (%; Homer et al. 2012) calculated using a moving window
Wysagesd	0.25, 1.0, 5.0	Standard deviation Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) cover (%; Homer et al. 2012) calculated using a moving window
Anthropogenic		
Dstbarea[ab]	0.25, 1.0, 5.0	Surface disturbance cell count (bare ground resulting from vegetation removal)─combination of energy infrastructure (improved gravel roads[g], energy well sites[f], compressor sites, and human dwellings digitized or confirmed using NAIP[c] imagery

Model category/ predictor variable	Spatial scale (km^2)	Description
Edgedist		Distance (km) to nearest anthropogenic edge—a combination of energy infrastructure (improved gravel roads[g], energy well sites[f], compressor sites, and human dwellings digitized or confirmed using NAIP[c] imagery
Fence	0.25, 1.0, 5.0	Total linear distance (km) of fence (mainly grazing allotment fences) within analysis region
Fencedist[b]		Distance (km) to nearest fence (mainly barbwire grazing allotment fences)
Haulrd	0.25, 1.0, 5.0	Total linear distance (km) of haul road[g] (improved gravel road) within analysis region–verified using NAIP[c] imagery
Hauldist[b]		Distance (km) to nearest haul road[g] (improved gravel road)—time-stamped and verified using NAIP[c] imagery
Two-track	0.25, 1.0, 5.0	Total linear distance (km) of unimproved road (two-track road) within analysis region
Two-trackdist[b]		Distance (km) to nearest unimproved road (two-track)
Vwell	0.25, 1.0, 5.0	Count of visible energy wells[f] within analysis region–verified using NAIP[c] imagery
Well	0.25, 1.0, 5.0	Count of energy wells[f] within analysis region–verified using NAIP[c] imagery
Welldist[b]		Distance (km) to nearest energy well site[f]—verified using NAIP[c] imagery

[a]10-m resolution.
[b]Quadratic transformations assessed.
[c]USDA national agriculture imagery program (USDA 2010).
[d]Normalized differential vegetation index.
[e]Square analysis regions.
[f]Time-stamped on the basis of spud dates and batched into monthly increments thus enabling us to depict temporal additions to infrastructure to prevent including infrastructure in the analysis until it actually exists on the ground.

[g]When constructed in concurrence with a energy well site–time-stamped on the basis of corresponding well spud date and batched into monthly increments thus enabling us to depict temporal additions to infrastructure to prevent including infrastructure in the analysis until it actually exists on the ground.

Table 2.2. Quantification of predicted source and sink habitats on the ARPA landscape, south-central Wyoming, USA.

Occurrence	**Fitness**	**Habitat categories**
↑	$\lambda \geq 1$	Selected source
↓	$\lambda \geq 1$	Non-selected source
↑	$\lambda < 1$	Selected sink
↓	$\lambda < 1$	Non-selected sink
NH	NH	Non-habitat

↑ Summer female occurrence above mean probability.
↓ Summer female occurrence below mean probability.
≥1 Stable or increasing population.
<1 Decreasing population.
NH Non-habitat areas.

Table 2.3. Model category combinations (environmental and anthropogenic) considered in my sequential modeling approach predicting nesting sage-grouse occurrence in south-central Wyoming, USA, 2008 and 2009.

Model (predictor variable_spatial scale [km^2])[a]	**LL**[b]	***K***[b]	**AIC$_c$**[b]	**ΔAIC$_c$**[b]	***w$_i$***[b]
Environmental + Anthropogenic	–113.62	5	235.47	0.00	0.77
Environmental (Bsage_0.25, Litter_0.25, NDVIsd_5.0)	–115.85	4	237.83	2.36	0.24
Anthropogenic (Vwell_1.0)	–127.51	2	257.03	21.57	0.00
Null	–130.52	1	261.05	25.58	0.00

[a]Model categories (subsets) and associated predictor variables assessed individually and combined in my sequential modeling approach. Refer to Table 2.1 for predictor variable descriptions.
[b]Log-likelihood (LL), number of parameters (K), Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) score, change in AIC$_c$ score from top model (ΔAIC$_c$), and Akaike weights (w_i).

Table 2.4. Model category combinations (environmental and anthropogenic) considered in my sequential modeling approach predicting female sage-grouse early brood-rearing occurrence in south-central Wyoming, USA, 2008 and 2009.

Model (predictor variable_spatial scale [km^2])[a]	**LL**[b]	***K***[b]	**AIC$_c$**[b]	**ΔAIC$_c$**[b]	**w_i**[b]
Environmental + Anthropogenic	–80.79	7	176.44	0.00	0.99
Environmental (Herbsd_1.0, Sage^2_1.0)	–87.74	4	183.78	9.56	0.01
Anthropogenic (Two-track_5.0, Two-trackdist, Vwell_1.0)	–90.83	4	187.84	13.62	0.00
Null	–95.44	1	190.87	16.66	0.00

[a]Model categories (subsets) and associated predictor variables assessed individually and combined in my sequential modeling approach. Refer to Table 2.1 for predictor variable descriptions.
[b]Log-likelihood (LL), number of parameters (*K*), Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) score, change in AIC$_c$ score from top model (ΔAIC$_c$), and Akaike weights (w_i).

Table 2.5. Model category combinations (environmental and anthropogenic) considered in my sequential modeling approach predicting non-brooding female sage-grouse occurrence during the early brood-rearing period in south-central Wyoming, USA, 2008 and 2009.

Model (predictor variables_spatial scale [km^2])[a]	**LL**[b]	***K***[b]	**AIC$_c$**[b]	**ΔAIC$_c$**[b]	***w$_i$***[b]
Environmental + Anthropogenic	–147.12	8	310.79	0.00	1.00[c]
Environmental (Litter_0.25, NDVIsd_1.0, VRM_1.0)	–160.76	5	331.74	20.96	0.00
Anthropogenic (Two-trackdist^2, Vwell_5.0)	–166.79	4	341.73	30.94	0.00
Null	–185.84	1	373.70	62.91	0.00

[a]Model categories (subsets) and associated predictor variables assessed individually and combined in my sequential modeling approach. Refer to Table 2.1 for predictor variable descriptions.
[b]Log-likelihood (LL), number of parameters (K), Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) score, change in AIC$_c$ score from top model (ΔAIC$_c$), and Akaike weights (w_i).
[c]The true value is w_i = 0.999972.

Table 2.6. Model category combinations (environmental and anthropogenic) considered in my sequential modeling approach predicting female late brood-rearing occurrence in south-central Wyoming, USA, 2008 and 2009.

Model (predictor variables_spatial scale [km^2])[a]	**LL**[b]	***K***[b]	**AIC$_c$**[b]	**ΔAIC$_c$**[b]	***w$_i$***[b]
Environmental + Anthropogenic	–84.16	8	185.42	0.00	0.54
Environmental (Herbsd_5.0, Sage^2_1.0)	–88.74	4	185.79	0.36	0.45
Anthropogenic (Dstbarea^2, Hauldist, Two-trackdist)	–91.89	5	194.23	8.81	0.01
Null	–96.84	1	195.71	10.29	0.00

[a]Model categories (subsets) and associated predictor variables assessed individually and combined in my sequential modeling approach. Refer to Table 2.1 for predictor variable descriptions.
[b]Log-likelihood (LL), number of parameters (*K*), Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) score, change in AIC$_c$ score from top model (ΔAIC$_c$), and Akaike weights (w_i).

Table 2.7. Model category combinations (environmental and anthropogenic) considered in my sequential modeling approach predicting non-brooding female occurrence during the late brood-rearing period in south-central Wyoming, USA, 2008 and 2009.

Model (predictor variable_spatial scale [km^2])[a]	**LL**[b]	***K***[b]	**AIC$_c$**[b]	**ΔAIC$_c$**[b]	***w$_i$***[b]
Environmental + Anthropogenic	–207.07	6	426.40	0.00	0.72
Environmental (Forestdist, Sage_0.25)	–210.10	4	428.33	1.93	0.28
Anthropogenic (Two-trackdist, Vwell_5.0)	–215.97	3	438.01	11.61	0.00
Null	–219.62	1	441.25	14.85	0.00

[a]Model categories (subsets) and associated predictor variables assessed individually and combined in my sequential modeling approach. Refer to Table 2.1 for predictor variable descriptions.
[b]Log-likelihood (LL), number of parameters (K), Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) score, change in AIC$_c$ score from top model (ΔAIC$_c$), and Akaike weights (w_i).

Table 2.8. Final resource selection function models and associated spatial variables predicting female sage-grouse nesting, early brood-rearing, early non-brooding, late brood-rearing, and late non-brooding occurrence in south-central Wyoming, USA, 2008 and 2009. Parameter coefficients, 95% confidence intervals, and odds ratios from multi-model inference.

	Spatial scale (km^2)	**Coefficient**	**95% CI**		***P*-value**[a]	**Odds ratio**
			Lower	**Upper**		
Nest RSF						
Environmental model						
Bsage	0.25	0.191	0.131	0.251	0.002	1.210
Litter	0.25	0.063	0.022	0.104	0.001	1.065
NDVIsd	5.0	–21.850	–27.948	–15.751	0.01	0.804[e]
Anthropogenic model						
Vwell	1.0	–0.618	–1.422	–0.039	0.04	0.539
Early brooding RSF						
Environmental model						
Herbsd	1.0	–0.372	–0.497	–0.247	0.008	0.689
Sage[2b]	1.0	–0.056	–0.078	–0.033	0.02	0.946
Anthropogenic model						
Two-track	5.0	0.137	0.078	0.197	0.05	1.147
Two-trackdist (km)		–2.613	–4.405	–1.178	0.05	0.073
Vwell	1.0	–0.745	–1.213	–0.277	0.13	0.475
Early non-brooding RSF						
Environmental model						
Litter	0.25	0.073	0.043	0.103	<0.001	1.076
NDVIsd	1.0	–14.570	–21.030	–8.109	<0.001	0.470[d]

	Spatial scale (km^2)	Coefficient	95% CI		*P*-value[a]	Odds ratio
			Lower	Upper		
VRM	1.0	–571.902	–36.810	–06.994	<0.001	0.423[e]
Anthropogenic model						
Two-trackdist[2b] (km)		5.584	3.148	8.020	0.12	1.673[c]
Vwell	5.0	–1.136	–1.593	–0.679	0.01	0.321
Late brooding RSF						
Environmental model						
Herbsd	5.0	–0.130	–0.240	–0.021	0.04	0.878
Sage[2b]	1.0	–0.086	–0.123	–0.049	0.02	0.918
Anthropogenic model						
Dstbarea[2]	5.0	–0.0001	–0.0002	0.0000	0.11	0.905[f]
Hauldist (km)		–0.333	–0.506	–0.161	0.12	0.717
Two_trackdist (km)		–2.445	–3.581	–1.302	0.10	0.087
Late non-brooding RSF						
Environmental model						
Forestdist (km)		–0.231	–0.291	–0.171	0.002	0.959
Sage	0.25	0.187	0.157	0.216	0.001	1.205
Anthropogenic model						
Two-trackdist (km)		1.072	0.573	1.571	0.11	2.922
Vwell	5.0	–0.844	–1.12	–0.571	0.01	0.430

[a]*P*-values from single variable models except for quadratic variables were the *P*-values from the combined 2 variable model.
[b]Quadratic form (variable + varable[2]).
[c]For interpretation, odds ratio estimated for a 10 unit change in variable.
[d]For interpretation, odds ratio estimated for a 100 unit change in variable.
[e]For interpretation, odds ratio estimated for a 1000 unit change in variable.

Table 2.9. Model category combinations (environmental and anthropogenic) considered in my sequential modeling approach predicting brood survival to 40 days in south-central Wyoming, USA, 2008 and 2009.

Model (predictor variable_spatial scale [km^2])[a]	**LL**[b]	***K***[b]	**AIC$_{SUR}$**[b]	**ΔAIC$_{SUR}$**[b]	w_i[b]
Environmental + Anthropogenic	–27.52	4	63.42	0.00	0.52
Environmental (Herb_1.0, Shrbhgtsd_1.0)	–29.81	2	63.81	0.39	0.43
Anthropogenic (Dstbarea^2_1.0)	–32.24	2	68.66	5.24	0.04
Null	–35.94	0	71.36	7.94	0.01

[a]Model categories (subsets) and associated predictor variables assessed individually and combined in my sequential modeling approach. Refer to Table 2.1 for predictor variable descriptions.
[b]Log-likelihood (LL), number of parameters (*K*), Akaike's Information Criterion adapted for survival models (AIC$_{SUR}$) score, change in AIC$_{SUR}$ score from top model (ΔAIC$_{SUR}$), and Akaike weights (w_i).

Table 2.10. Model category combinations (environmental and anthropogenic) considered in my sequential modeling approach predicting female summer survival to 110 days in south-central Wyoming, USA, 2008 and 2009.

Model (predictor variable_spatial scale [km^2])[a]	**LL**[b]	***K***[b]	**AIC$_{SUR}$**[b]	**ΔAIC$_{SUR}$**[b]	w_i[b]
Environmental + Anthropogenic	–71.80	3	149.67	0.00	0.58
Anthropogenic (Distedge)	–73.40	1	148.82	0.74	0.40
Environmental (Shrbhgtsd_1.0, VRM_5.0)	–75.76	2	155.17	7.09	0.02
Null	–78.57	0	157.15	9.07	0.00

[a]Model categories (subsets) and associated predictor variables assessed individually and combined in my sequential modeling approach. Refer to Table 2.1 for predictor variable descriptions.
[b]Log-likelihood (LL), number of parameters (*K*), Akaike's Information Criterion adapted for survival models (AIC$_{SUR}$) score, change in AIC$_{SUR}$ score from top model (ΔAIC$_{SUR}$), and Akaike weights (w_i).

Table 2.11. Final models and associated spatial variables predictive of survival for nest, brood, and adult female in south-central Wyoming, USA, 2008 and 2009. Parameter coefficients, 95% confidence intervals, and risk ratios from multi-model inference.

Models	**Spatial scale (km^2)**	**Coefficient**	**95% CI**		***P*-value**[b]	**Risk ratio**
			Lower	**Upper**		
Nest survival						
Environmental model						
Shrbhgtsd	1.0	–0.099	–0.169	–0.029	0.09	0.906
TWI	0.25	0.247	0.097	0.396	0.11	1.280
Wysage	5.0	–0.295	–0.430	–0.159	0.02	0.745
Brood survival[a]						
Environmental model						
Herb	1.0	0.105	0.051	0.160	0.02	1.111
Shrbhgtsd	1.0	–0.500	–0.710	–0.291	0.18	0.606
Anthropogenic model						
Dstbarea^{2}[c]	1.0	0.002	0.001	0.003	0.06	1.002
Female summer survival[a]						
Environmental model						
Shrbhgtsd	1.0	–0.167	–0.263	–0.041	0.09	0.850
VRM[d]	5.0	0.356	–0.092	0.803	0.07	1.430
Anthropogenic model						
Edgedist (km)		0.717	0.504	0.930	0.001	2.050

[a]Contains time-dependent variables that represent average accumulative exposure to the corresponding habitat characteristics over the entire survival time and specific to each individual.
[b]*P*-values from single variable models except for quadratic variables were the *P*-values come from the combined 2 variable model.
[c]Quadratic form (variable + varable^{2}).
[d]Statistics for a 1000 unit change in variable.

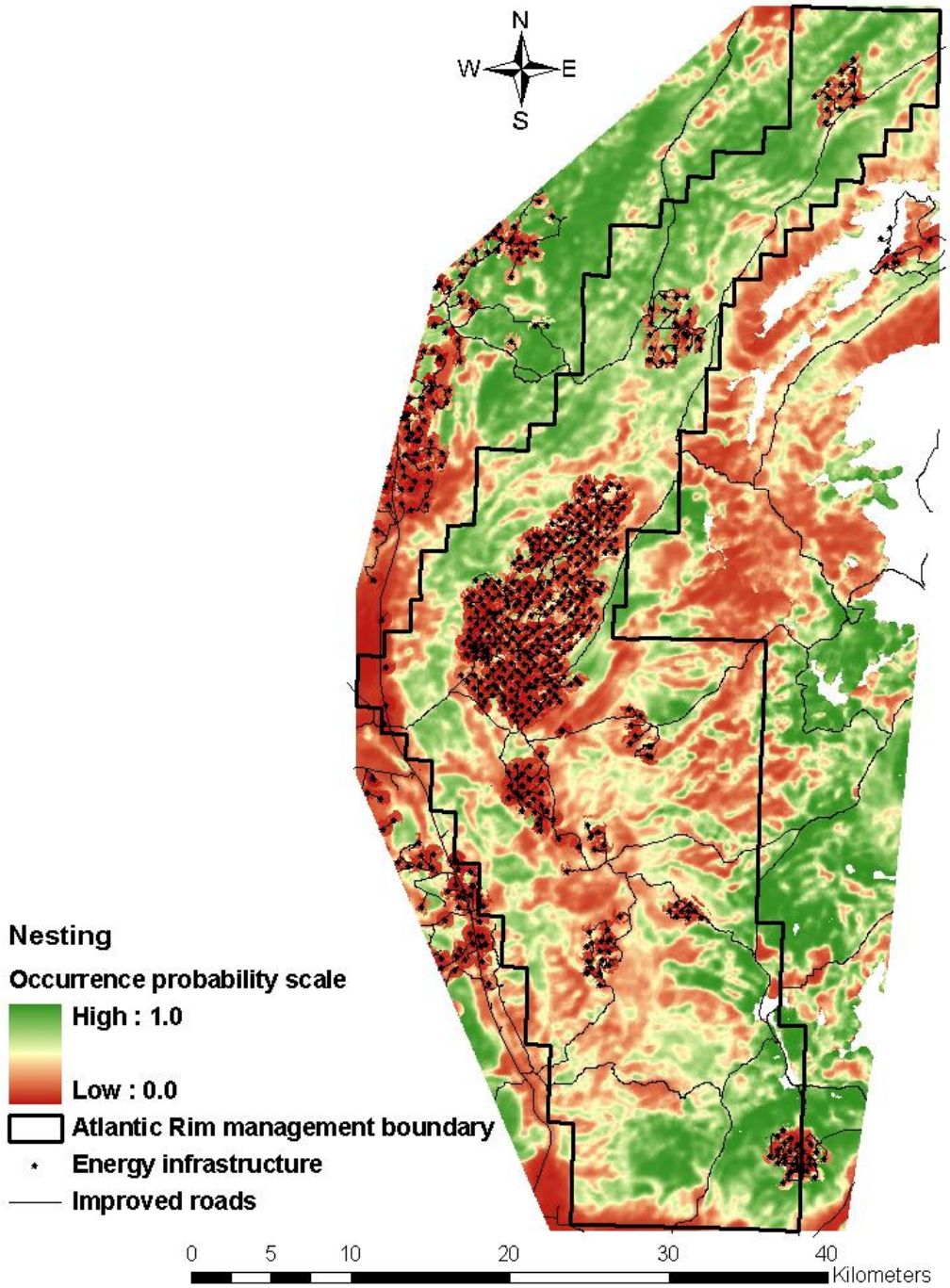

Figure 2.1. Predicted probability of nesting sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

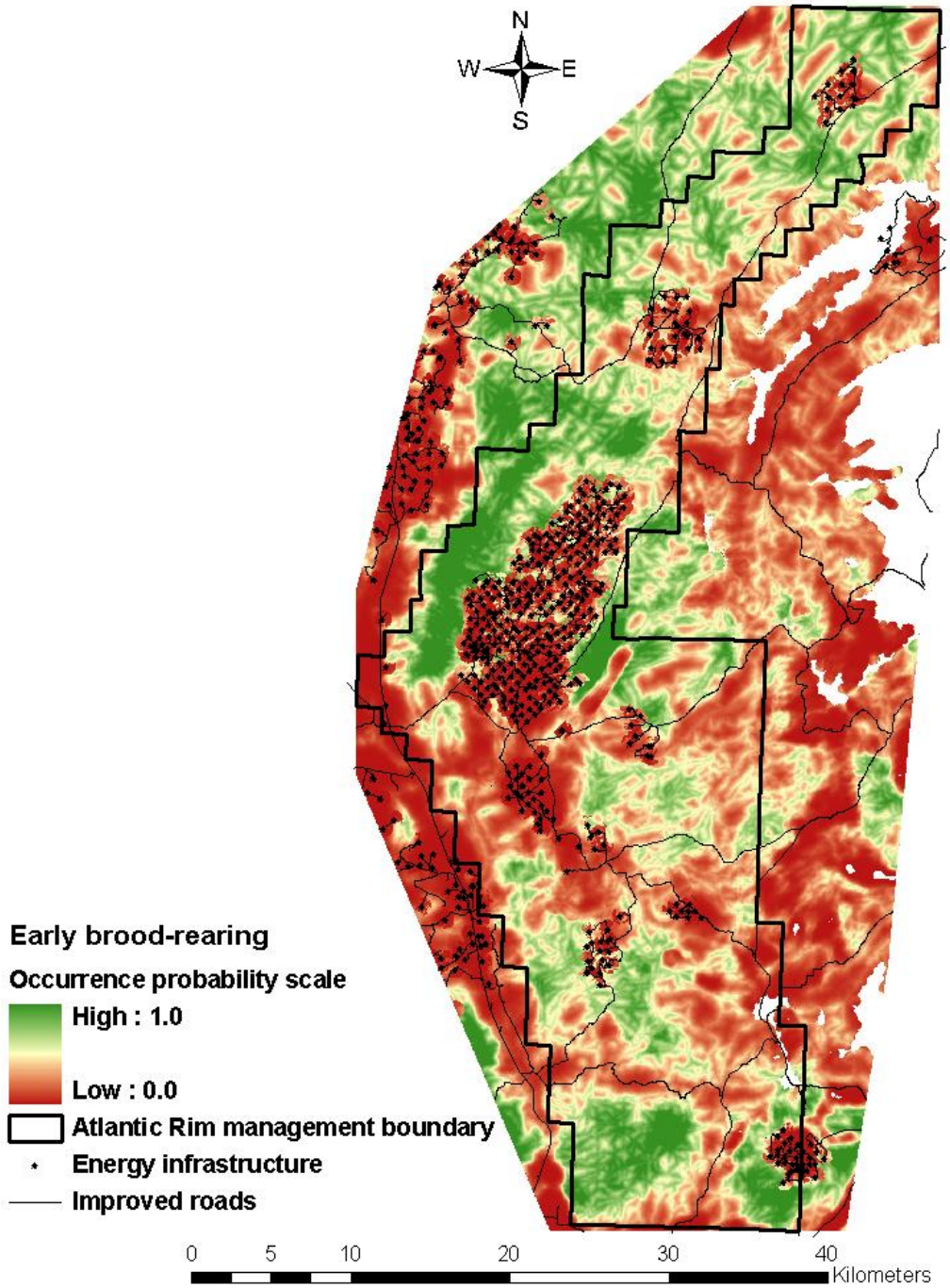

Figure 2.2. Predicted probability of early brood-rearing sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

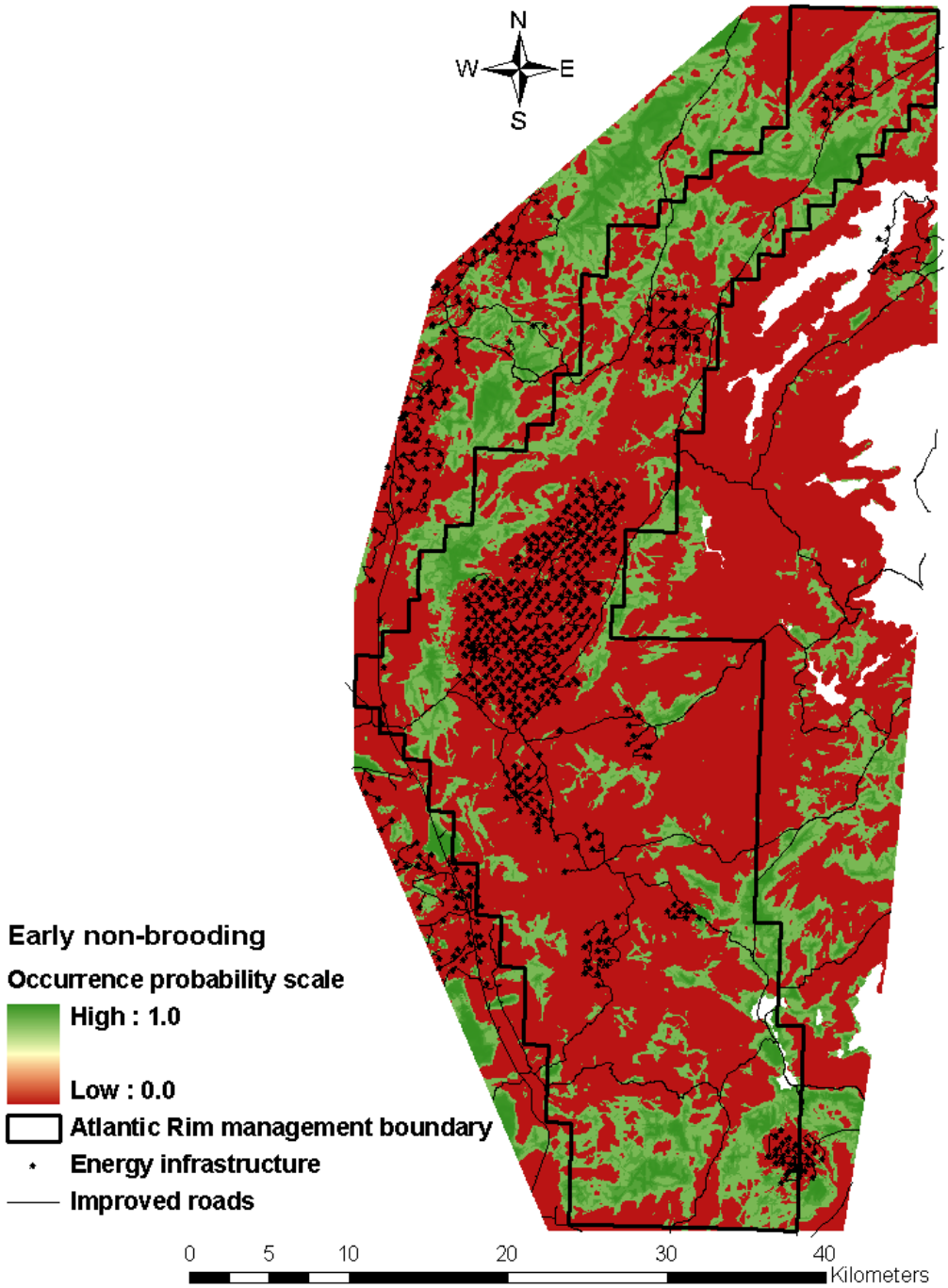

Figure 2.3. Predicted probability of early non-brooding sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

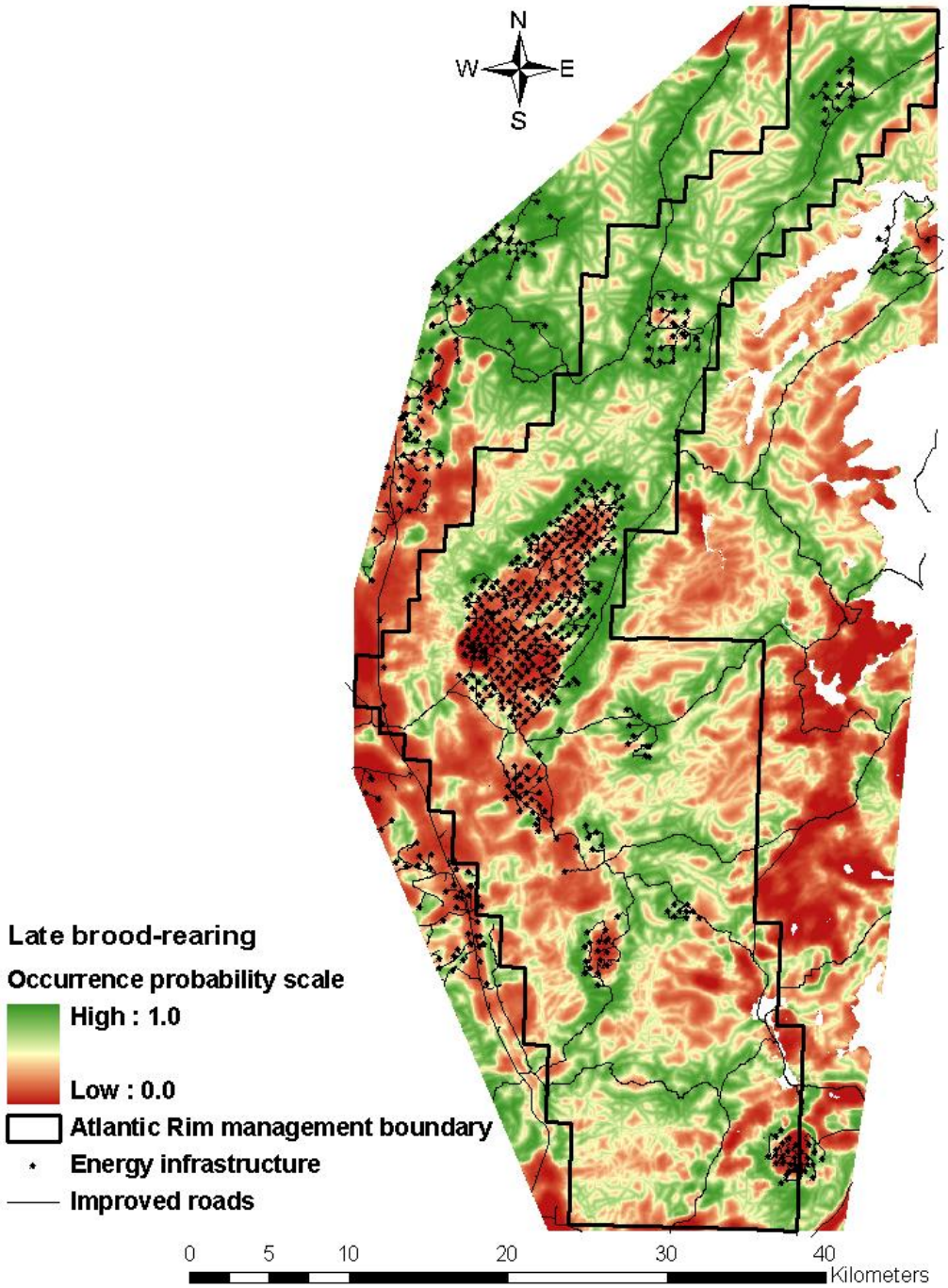

Figure 2.4. Predicted probability of late brood-rearing sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

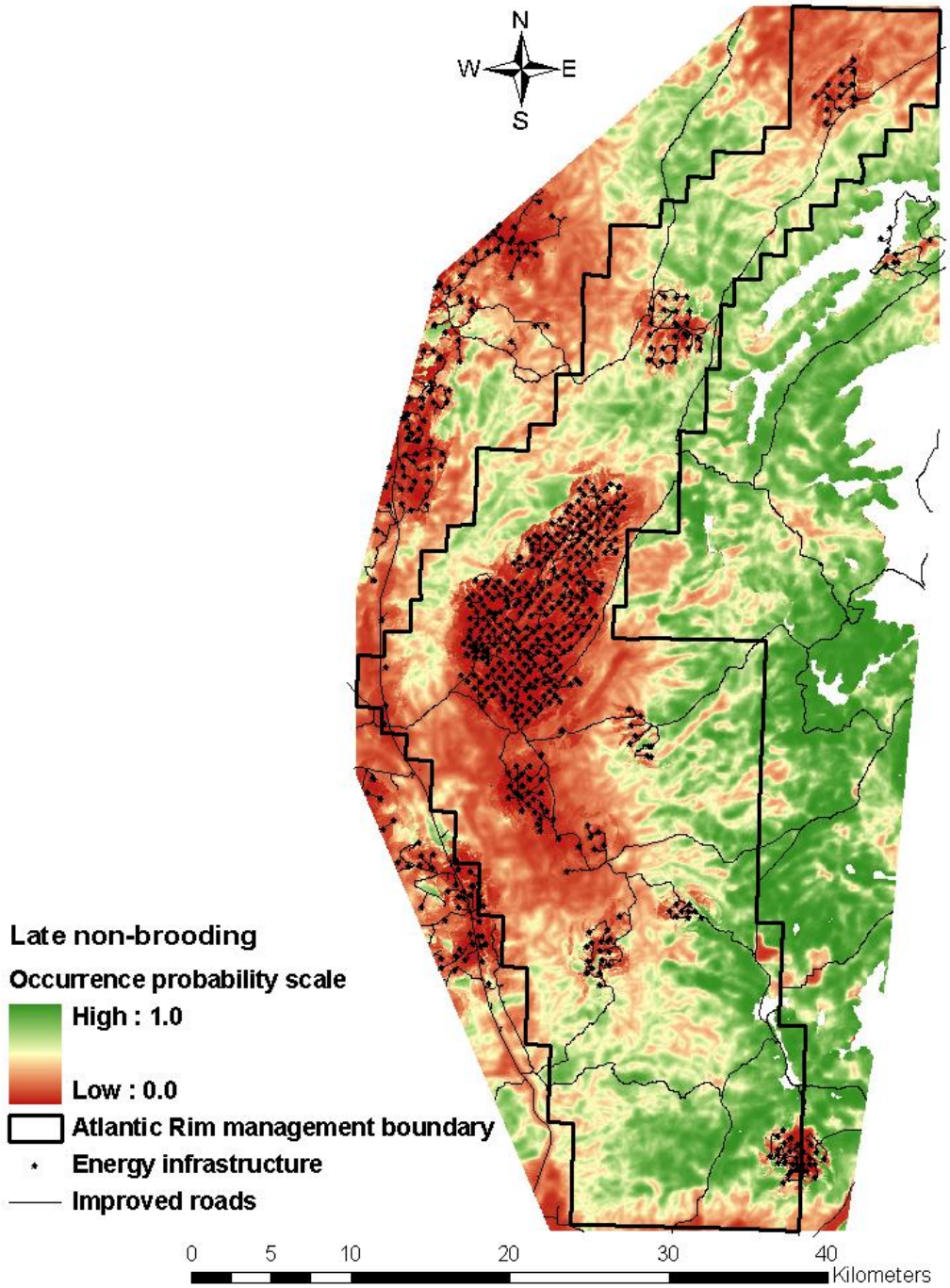

Figure 2.5. Predicted probability of late non-brooding sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

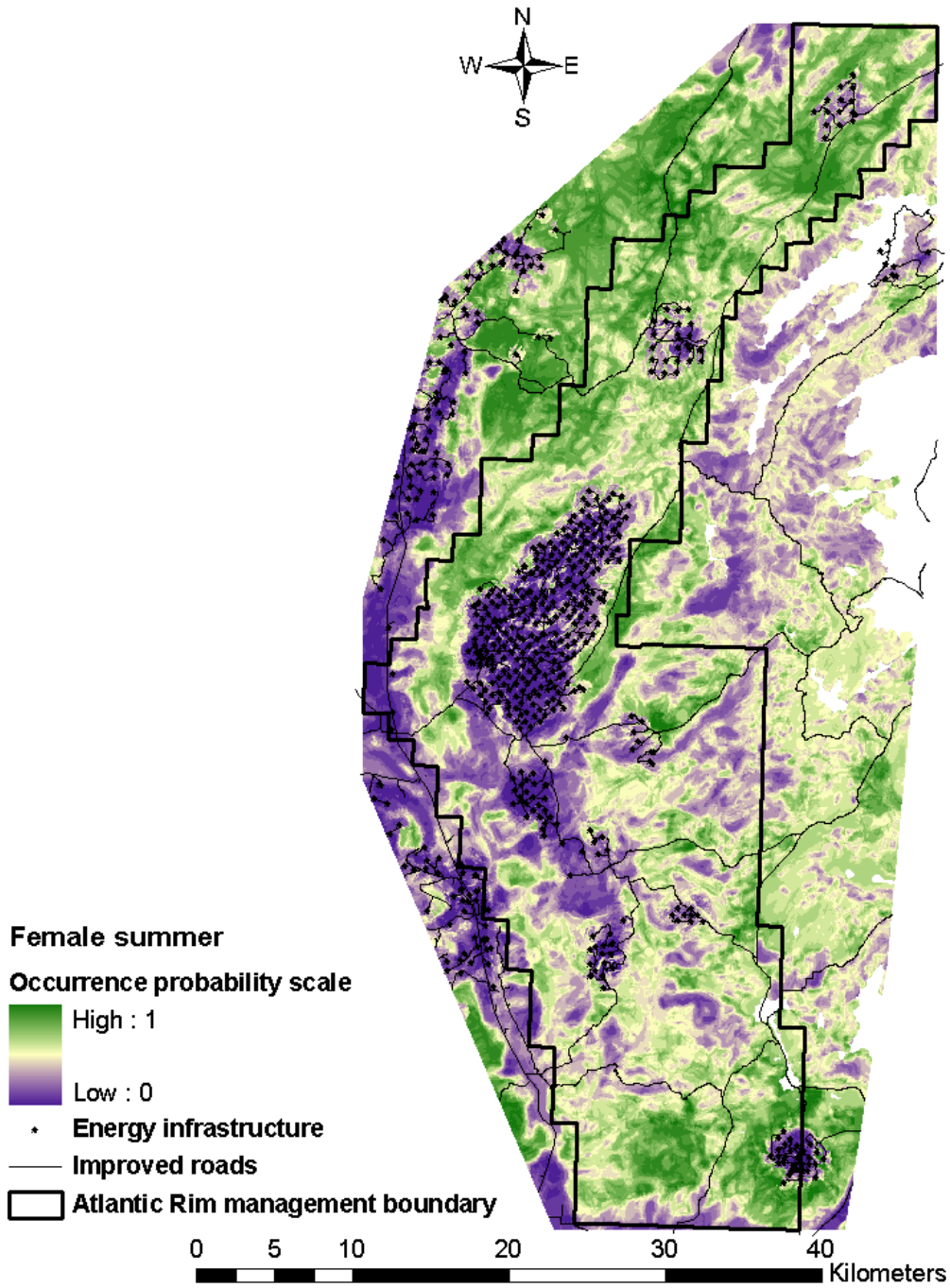

Figure 2.6. Predicted probability of female sage-grouse occurrence throughout the summer in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of selection by females with 1 (green) being the highest and 0 (purple) being the lowest probability.

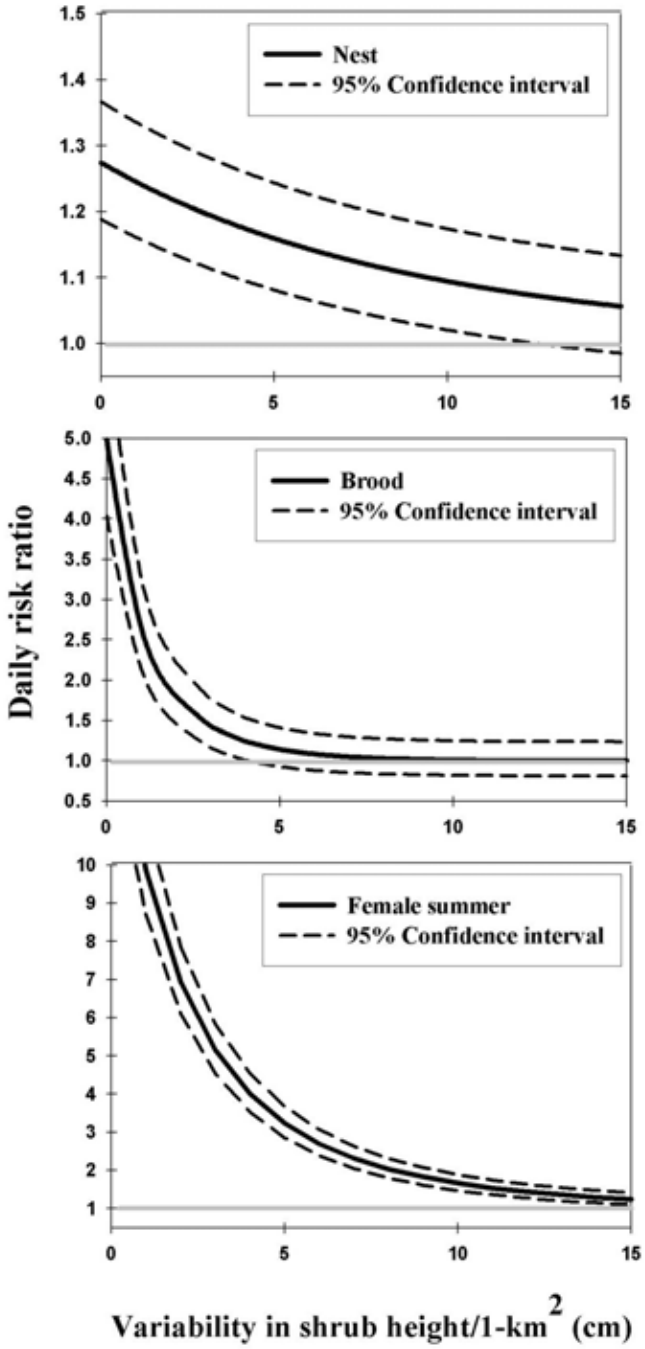

Figure 2.7. Shrub height variability and daily survival risk for nest, brood, and adult female summer daily survival at the 1-km^2 scale, south-central, Wyoming, USA, 2008 and 2009.

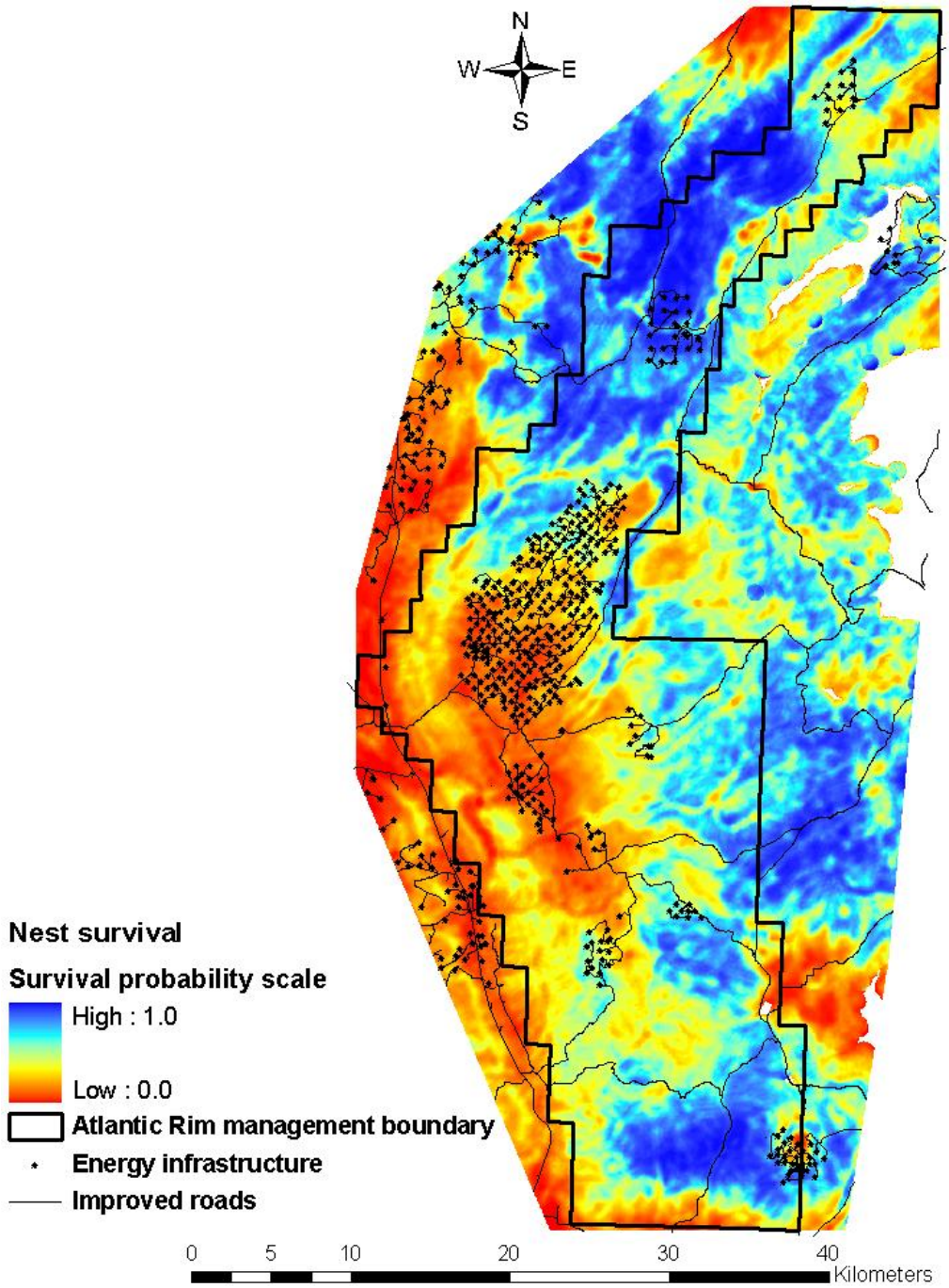

Figure 2.8. Predicted probability of sage-grouse nest survival to 28 days. Mapped as a survival probability function in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of 40-day brood survival with 1 (blue) being the highest and 0 (red) being the lowest probability.

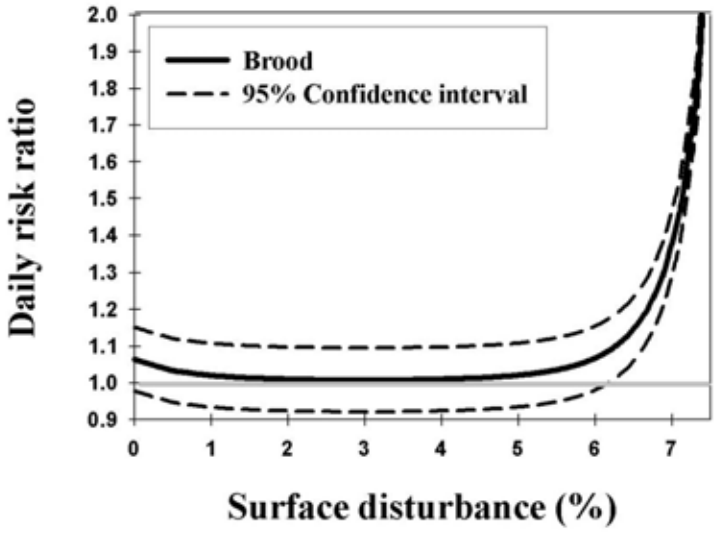

Figure 2.9. Risk of daily brood loss over successive brood locations as a function of the percent of surface disturbance area at the 1-km^2 scale, south-central, Wyoming, USA, 2008 and 2009.

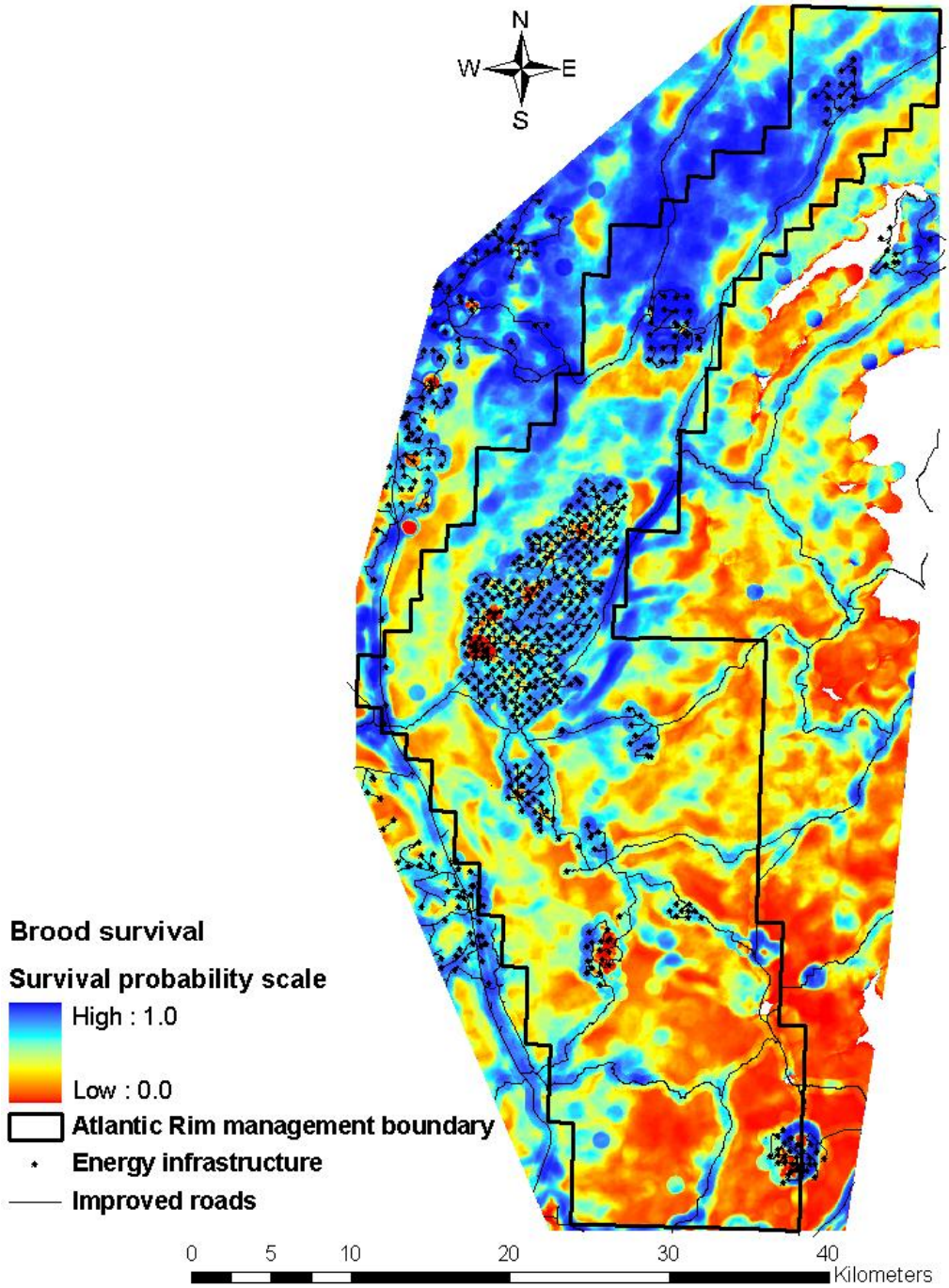

Figure 2.10. Predicted probability of sage-grouse brood survival to 40 days. Mapped as a survival probability function in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of 40-day brood survival with 1 (blue) being the highest and 0 (red) being the lowest probability.

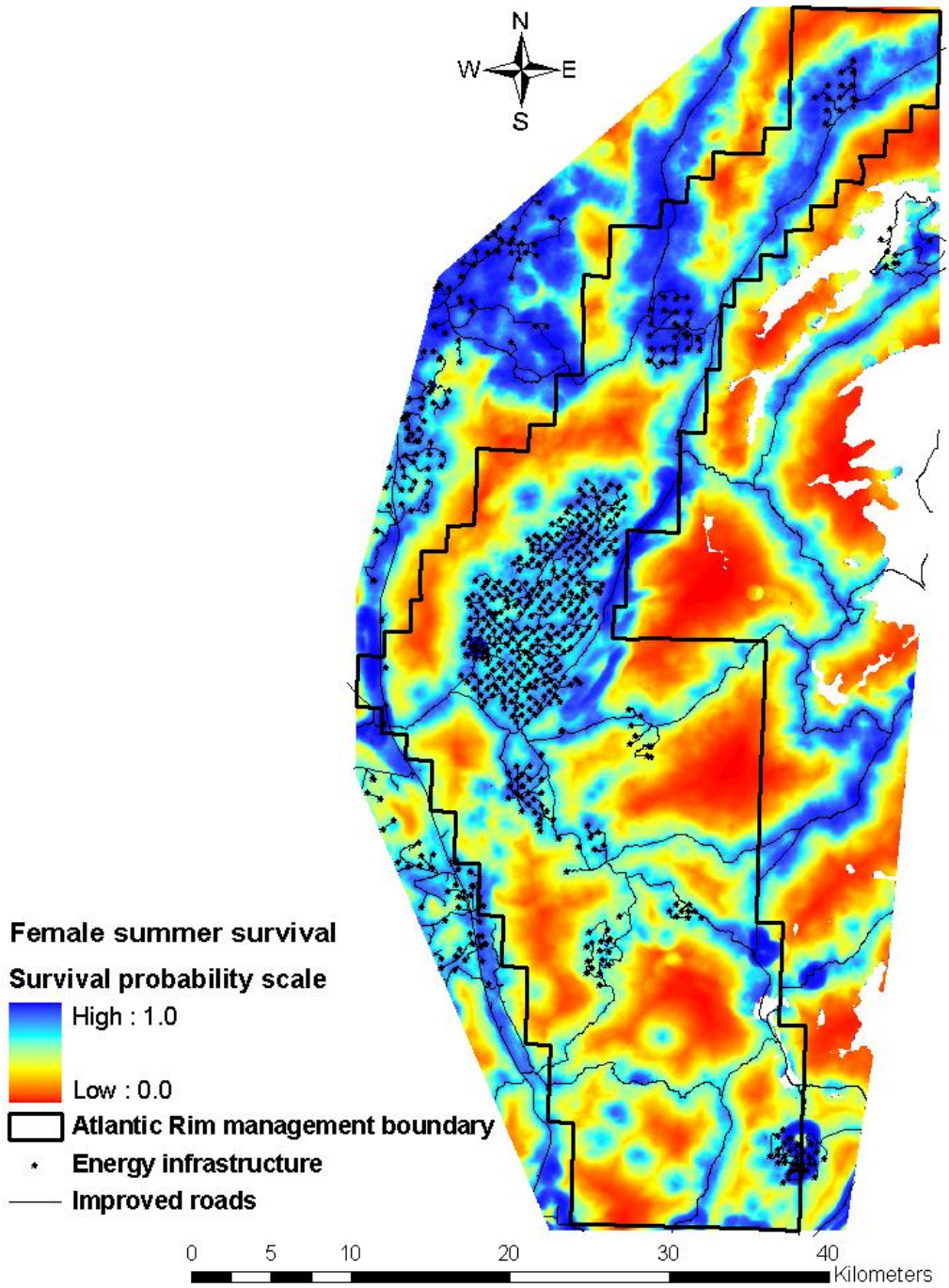

Figure 2.11. Predicted probability of sage-grouse summer female survival to 110 days. Mapped as a survival probability function in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of 110-day brood survival with 1 (blue) being the highest and 0 (red) being the lowest probability.

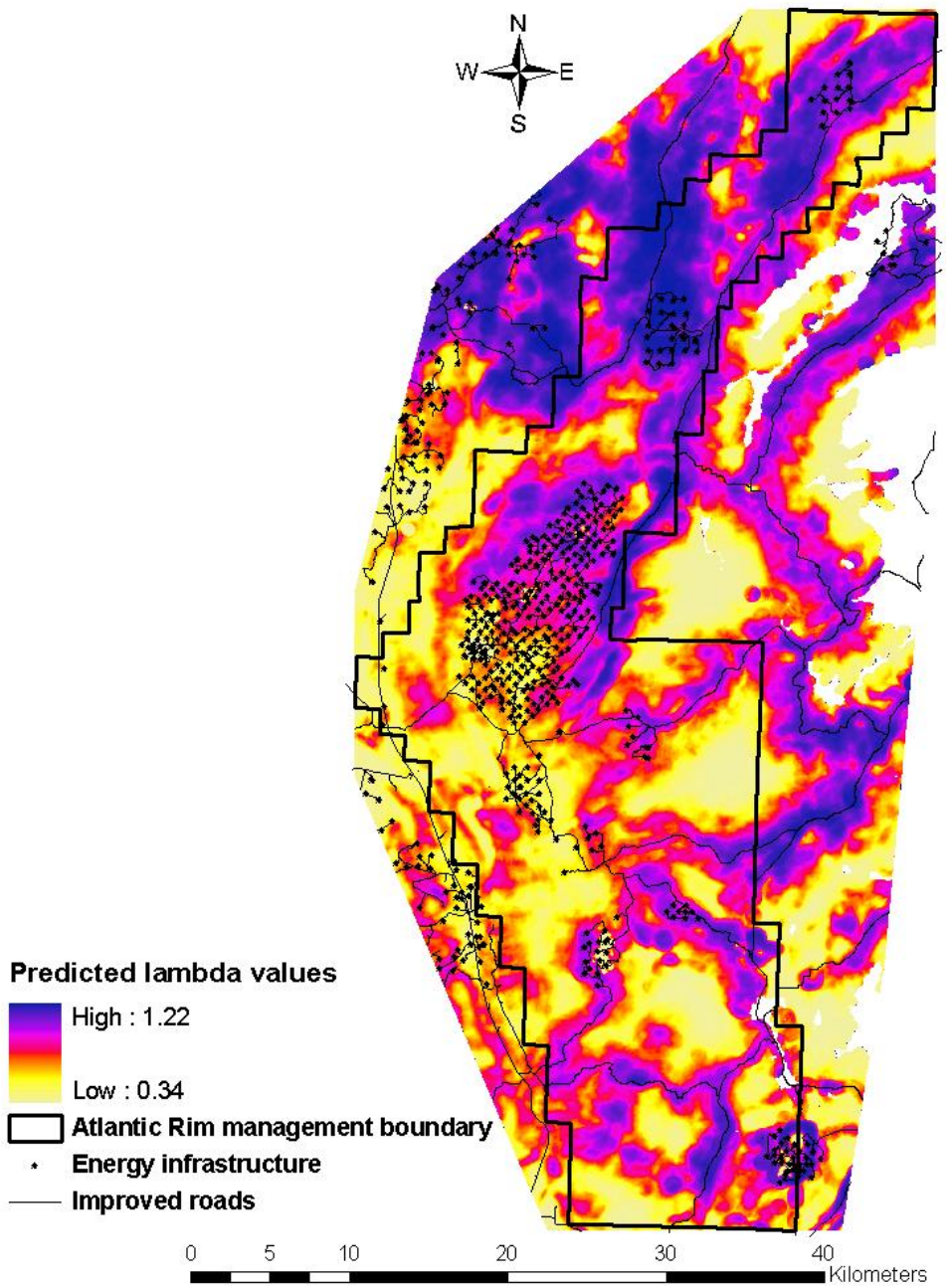

Figure 2.12. Predicted sage-grouse population growth rate (λ) based on variable adjusted survival probability functions specific to nest, brood, and summer female (brooding or non-brooding) survival in south-central, Wyoming, USA, 2008 and 2009, as well as fixed demographic rates. The map displays a continuum from the highest predicted λ value (dark blue) to the lowest (light yellow).

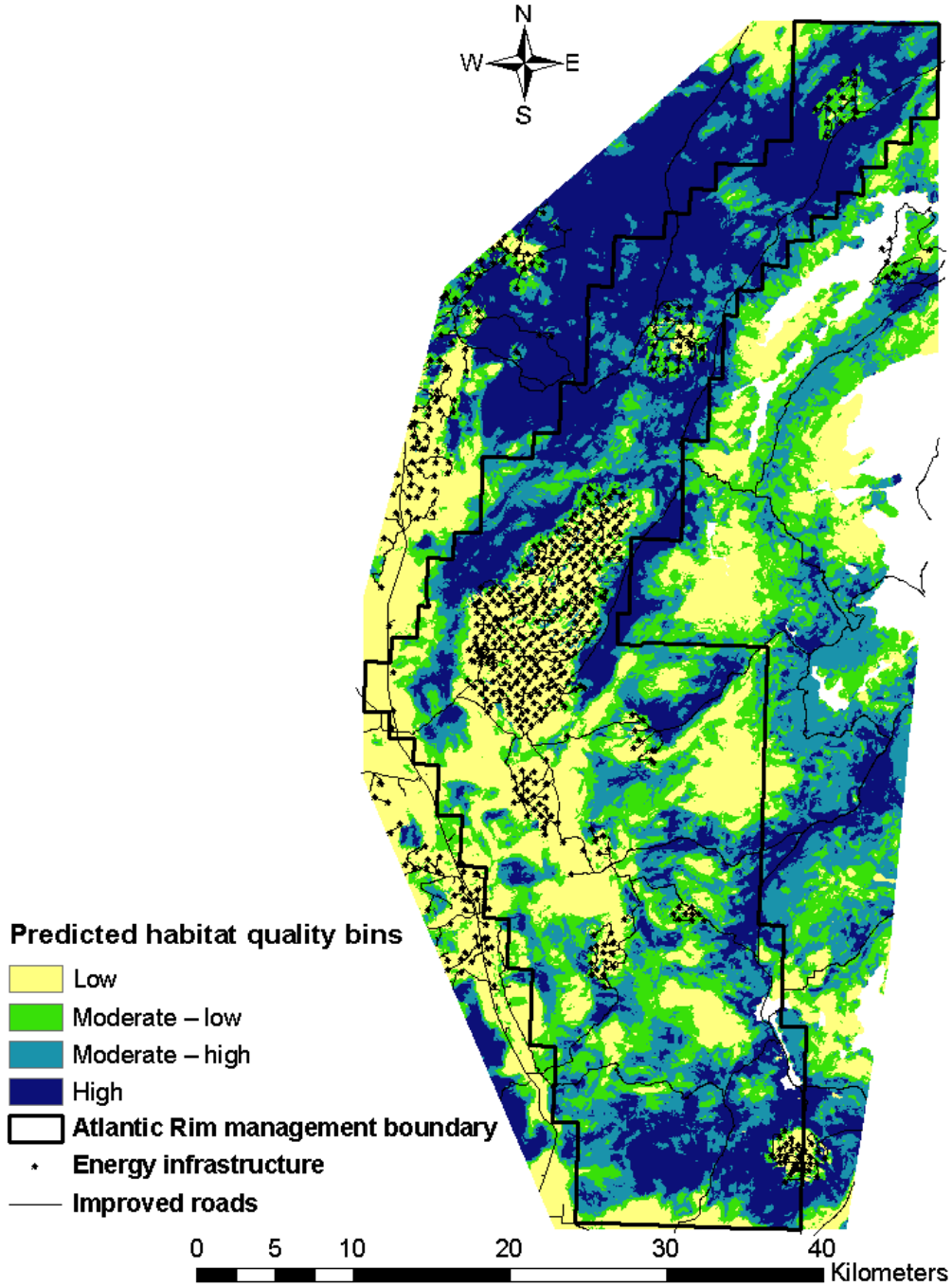

Figure 2.13. Predicted habitat quality (female summer occurrence + λ prediction) for sage-grouse during the reproductive season in south-central, Wyoming, USA, 2008 and 2009. The map displays habitat quality bins derived from the distribution of female summer occurrence and λ predictions divided into quartiles containing 25 percentile values.

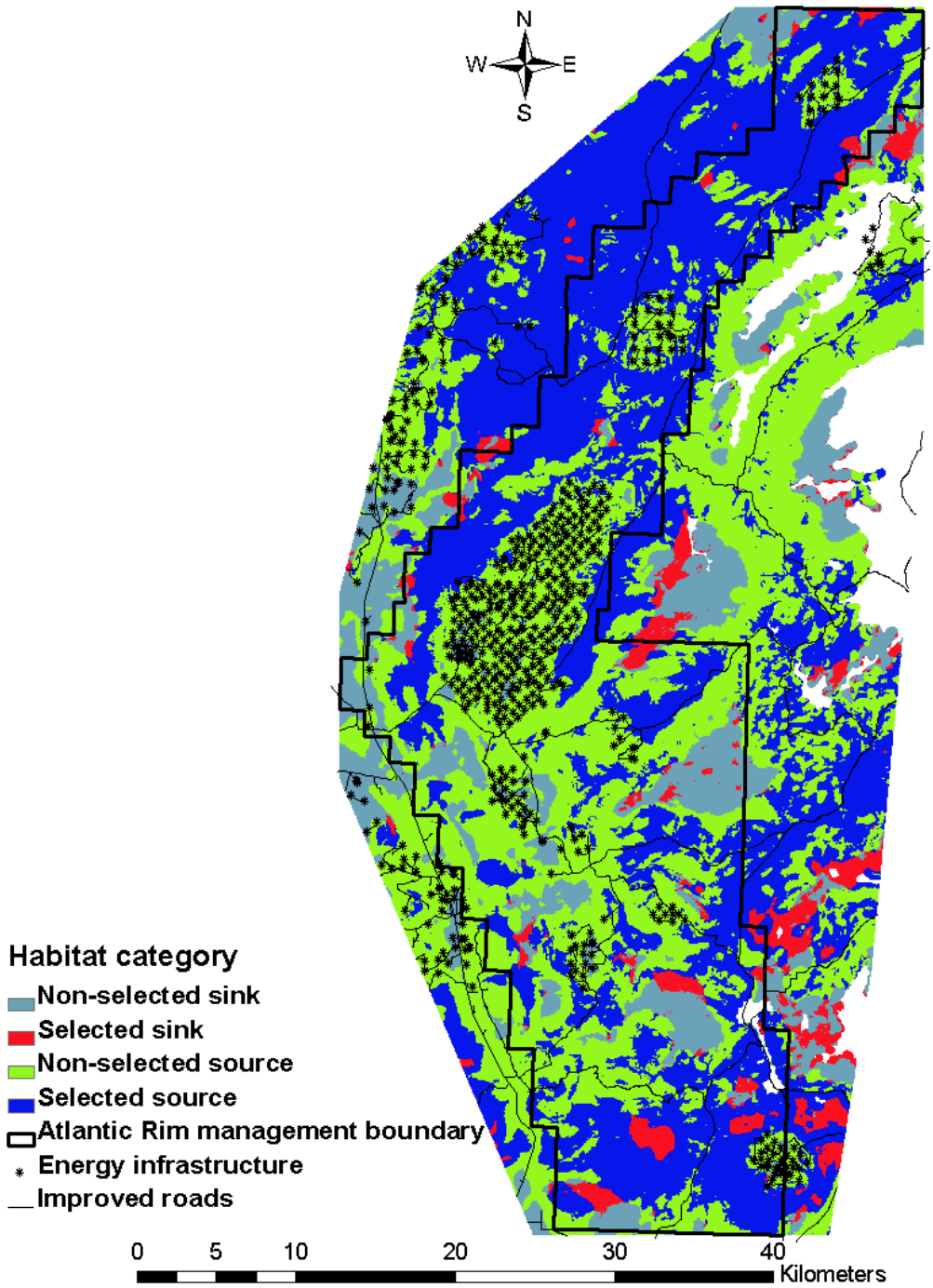

Figure 2.14. Predicted sink and source habitats for sage-grouse in south-central, Wyoming, USA, 2008 and 2009. The habitat categories are based on the λ threshold of 1 and a binary measure of occurrence probability with the break at the mean value between high and low probability. The quantification of source-sink categories is described in Table 2.2.

CHAPTER 3

USING A REFERENCE AREA TO VALIDATE GREATER SAGE-GROUSE NEST OCCURRENCE AND SURVIVAL MODELS AND COMPARE IMPACTED AND NON-IMPACTED LANDSCAPES

In the format for manuscripts submitted to the *Journal of Wildlife Management*

ABSTRACT

Wildlife-habitat models that are used to make predictions that occur over time and space need to be rigorously validated against data that are not used to train models. The inability of most studies to incorporate a reference for comparison such as a non-impacted area or a spatial control leads to ambiguity regarding possible environmental consequences of an anthropogenic activity; that is conditions had that activity never occurred (Osenberg and Schmitt 2003). Using radio-marked greater sage-grouse (*Centrocercus urophasianus*) in south-central, Wyoming (2008 and 2009), my first study objective was to use an off-site reference area (Stewart Creek [SC]) to assess the robustness of my sage-grouse nest occurrence and survival models developed for the Atlantic Rim Project Area (ARPA). My second objective was to evaluate the utility of the SC reference area as a spatial control (control-impact design) to investigate possible effects of habitat loss and fragmentation resulting from coalbed natural gas (CBNG) development occurring in the ARPA, but not in SC, on greater sage-grouse nest selection and survival patterns. My nest occurrence model, in the form of a resource selection function (RSF), strongly predicted nest occurrence in the non-impacted reference area with the CBNG component of the model left unestimated. A Spearman's correlation based on ranked output from a 5-fold cross validation procedure demonstrated good predictive ability ($r_s = 0.87$, $P < 0.01$, $n = 10$) when it

was applied to SC. Further, 73% of the nests in the SC sample were within the nest RSF occurrence areas with high and moderate-high relative probabilities of selection. My habitat-specific nest survival model, derived from Cox's proportional hazards modeling and in the form of a risk function, demonstrated that unsuccessful nests in SC had greater exposure to habitat predicted by the model as riskier. Specifically, unsuccessful nests were exposed to statistically greater (t_{14} = 2.28, P = 0.02) daily relative risk values when compared to successful nests using a one-tailed t-test. When I considered SC as a spatial control and used the Kaplan-Meier (K–M) product-limit estimator and log-rank test to assess statistical differences, I found nest success was higher (χ^2_1 = 3.67, P = 0.05) in SC ($\hat{S}$ = 64.5% ± 8.6%) compared to the ARPA ($\hat{S}$ = 43.4% ± 5.4). However, the ARPA nest survival model adjusted to a non-impacted setting using SC nest survival data did not explain the differences in nest success. My approach to replace time (pre-development data) with space (using SC as a spatial control) by modeling the ARPA RSF against the SC nest occurrence data (i.e., nest selection in the absence of CBNG development) and then spatially shifting the adjusted model back to the ARPA functioned poorly in practice. This elucidates an important consideration in choosing a spatial control related to the variability in habitat conditions between the impacted and non-impacted areas. This model validation process and other research (see Chapter 4) demonstrated that the ARPA and SC had similar habitats. However, this approach was ineffective because of differences in the degree of habitat variability between areas─specifically greater variability in the variables that formed the ARPA specific nest occurrence models. When I adjusted the model to SC and spatially shifted it back to the ARPA, I was extrapolating outside of the habitat data range used to adjust the model and predictions outside of the range of predictor variable values can, as demonstrated here, produce grossly incorrect predictions. Consequently, the reference area was not a robust control in which

to assess nest habitat selection changes resulting from CBNG development. Yet, the non-impacted reference area (SC) proved valuable for both nest survival and occurrence model validation and as a comparison of nest success rates to an impacted area (ARPA).

INTRODUCTION

Wildlife-habitat models, and specifically those created for prediction over time and space, need to be rigorously tested or validated (Boyce et al. 2002, Johnson et al. 2006, Morris et al. 2006) because most wildlife-habitat models formed to predict species occurrence or fitness are dictated by the environmental conditions at a specific time and place used to generate the model (Morris et al. 2006). Model validation using out-of-sample and off-site data, data that were not used to train the model, provides further assurance of model reliability and its relevance in new areas (Boyce et al. 2002, Howlin et al. 2003, Johnson et al. 2006). A key question associated with model validation using data from another study area is how well can a model predict in other places or other times (Boyce et al. 2002)? However, habitat-specific models are often unreliable in new areas because environmental and demographic conditions may vary significantly among locations (Morris et al. 2006).

Resource selection functions (RSFs) are used to quantify the habitat characteristics of the physical environment influencing an animal's selection process. When coupled with Geographic Information Systems (GIS), RSFs can be used to spatially display the relative probability of occurrence (Boyce et al. 2002, Manly et al. 2002). Perhaps the most important aspect of an RSF is to predict resource selection for a population into the future or to make predictions in a new area that is ecologically similar to the area used to estimate the RSF (Boyce et al. 2002).

Survival or risk models, although less commonly used than RSFs, enable one to predict fitness consequences of habitat use and, if robust, may be used to predict survival outcomes in

different places and times. Specifically, Cox's proportional hazards regression model (hereafter Cox model [Cox 1972]) allows researchers to link habitat-specific conditions to daily survival or risk and map these in GIS (Johnson et al. 2004, Aldridge and Boyce 2007). Thus, survival models can be used to provide critical information on habitat-specific fitness outcomes (Chapter 2, Johnson et al. 2004, Aldridge and Boyce 2007, Aldridge and Boyce 2008) to more accurately quantify and predict habitat quality─the ability of the environment to provide conditions suitable for population persistence (Hall et al. 1997). Therefore, it reasons that rigorous validation of survival models is of equal importance to that of RSFs.

Research on greater sage-grouse (*Centrocercus urophasianus;* hereafter sage-grouse) and other sagebrush (*Artemisia* spp.) obligates has shown displacement from previously occupied habitats because of avoidance behavior related to oil and gas development (Holloran 2005, Doherty et al. 2008, Sawyer et al. 2006, Walker et al. 2007, Carpenter et al. 2010, Holloran et al. 2010, Gilbert and Chalfoun 2011, Naugle et al. 2011). Sage-grouse population fitness, as with most avian species, is largely influenced by nest fate (Bergerud 1988, Crawford et al. 2004, Shaffer 2004). Previous research on sage-grouse nest selection and survival suggests impacts of oil and gas development include later hatching dates (Kaiser 2006), lower nest initiation rates (Lyon and Anderson 2003), as well as increased avian predation of nests (Holloran 2005). Furthermore, research in the Atlantic Rim project area (ARPA) suggests that at large spatial scales nesting female sage-grouse are avoiding areas in direct relation to the number of visible wells; thus, as visible wells increase within a 1.0-km^2 area the likelihood of nest occurrence decreases (see Chapter 2). Yet, my nest survival analysis for the ARPA did not detect any direct relationships between energy development and sage-grouse nest fate (see Chapter 2).

The research presented here includes the ARPA, which was to be developed for coalbed natural gas (CBNG) reserves, and an adjacent non-impacted reference area (Stewart Creek [SC]) both occurring in south-central, Wyoming, USA. The BLM Record of Decision for the Atlantic Rim Natural Gas Field was completed in 2007 and describes the potential development of 2,000 natural gas wells, in addition to 116 previously established exploration wells (BLM 2007). At the conclusion of my field research in August 2009, approximately 600 natural gas wells were established in the ARPA with the majority of development being highly concentrated in the center of the study area. The SC reference area was approximately 15 km north of the ARPA and contained largely intact big sagebrush (*A. tridentata* spp.) habitat with minimal anthropogenic disturbance and no CBNG development.

Documenting an anthropogenic impact that has already occurred yields limited inference unless we have a means of comparison; that is a measure of conditions had that activity never occurred (Osenberg and Schmitt 2003). The inability of most studies to incorporate a reference for comparison such as pre-impact conditions (temporal control) or a spatial control leads to ambiguity regarding possible environmental consequences of an anthropogenic activity. Spatial and temporal inferences can be drawn from ecological impact studies that include either pre-treatment data and/or a control area (Green 1979). Because I do not have pre-development data in the ARPA, I am limited to inferences based on spatial pattern alone (control-impact design; Green 1979, Osenberg and Schmitt 2003), which I explore in this chapter by using an adjacent non-impacted reference area (SC).

My objectives were 3-fold. First, I used the SC reference area to test the robustness of my ARPA nest occurrence and survival models with out-of-sample data and determined if the models were applicable to an area with a distinct sage-grouse population. This also provided a

measure of habitat likeness between the areas. Second, I compared nest success rates over the same temporal period between the ARPA and the adjacent non-impacted area (SC). Finally, I explored the utility of the SC reference area as a control by replacing time (i.e., pre-development data) with space (non-impacted area [SC]) to assess potential CBNG impacts on sage-grouse nest selection patterns in the ARPA.

Specifically, I attempted to evaluate potential connections between CBNG development and spatial extents and patterns of sage-grouse nest selection in the ARPA by comparing these to the same measures in the non-impacted reference area over the same temporal period. I did not assess differences in nest survival models because I found no direct correlations between CBNG related features and nest survival at the landscape scale in the ARPA (see Chapter 2). However, I compared nest survival demographics between the two areas over the same temporal period. Because this analysis builds upon my sage-grouse nest occurrence and survival modeling in the ARPA, I provide a brief explanation of my modeling procedure, final models, and the spatial predictions of nest occurrence and survival in the ARPA (Chapter 2).

STUDY AREA

The SC was selected as the ARPA reference area for the following reasons: 1) it had minimal anthropogenic features and no CBNG development, 2) it was located immediately north, approximately 15 km, of the ARPA and as a result was expected to have similar environmental conditions, 3) vegetation communities were similar between the ARPA and SC, 4) land ownership (federal, state, and private) and parcel distribution within the SC was similar to the ARPA, 5) the SC and ARPA both provided forage for seasonal livestock grazing, 6) sage-grouse in both areas do not appear to intermix (J.L. Beck, unpublished data), which eliminates the confounding of habitat and demographic responses for mixed populations, and 7) like the ARPA

the SC has an established sage-grouse population (South Central Sage-grouse Local Working Group [LWG] 2007). The majority of land in the ARPA and SC is federally owned and administered by the Bureau of Land Management (BLM). The ARPA and SC areas are dominated by Wyoming big sagebrush (*A. t. wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) communities and provide year-round habitat for sage-grouse (South Central Sage-grouse LWG 2007, BLM 2000*a*).

The ARPA lies in southern Carbon County, Wyoming and encompasses 1,093 km² in Townships 13 through 20 North and Ranges 89 through 92 West. The ARPA lies east of Wyoming Highway 789 between Rawlins and Baggs and includes 64.3% (701.9 km²) federal, 5.2% (57.0 km²) state, and 30.5% (334.1 km²) private lands. Major land uses in the ARPA included energy extraction, and livestock grazing. The ARPA included all or parts of 21 livestock allotments totaling 1,507 km² (BLM 2006*a*). The BLM managed the federal lands as well as 22.6 km² of federal mineral estate underlying private land within the study area (BLM 2007). Well field development for the ARPA includes the drilling of 1,800 CBNG wells and 200 deep natural gas wells (BLM 2007). Various drilling and production related facilities (e.g., roads, pipelines, water wells, disposal wells, compressor stations, and gas processing facilities) were also being constructed within the ARPA (BLM 2007). Development and drilling began in 2007 and is expected to continue for approximately 20 years, with the project life predicted to range from 30 to 50 years (BLM 2007).

Livestock grazing is the main land use within SC. Stewart Creek contained 5 allotments encompassing the entire area and totaling 821 km² (BLM 2006*b*). The SC is approximately 32.2 to 64.4 km north and west of Rawlins and encompassed approximately 820 km² of federal (70.0

%), state (5 %), and private (25 %) lands in Sweetwater and Fremont counties, Wyoming. The SC included Townships 23 to 25 North and Ranges 90 to 92 West.

The ARPA and SC are within the semi-desert grass-shrub zone in the Cool Central Desertic Basin and Plateaus major land resource area (Natural Resources Conservation Service [NRCS] 2006). The semi-desert grass-shrub zone in this region is characterized by a vast sagebrush steppe with average annual precipitation ranging between 18.0 to 30.5 cm (NRCS 2006). The region encompassing my study areas typically has cool temperatures with average daily temperatures ranging between a low of –16 degrees (°) C and a high of 0.5°C in midwinter and between 13°C and 24°C in midsummer (BLM 2006*a*,*b*). Temperature extremes range from –46°C to 38°C and the frost-free period generally occurs from mid-May to mid-September. Precipitation is evenly distributed throughout the year with minor peaks in May, July, and October. The months with highest snow accumulation are December and January with an average of 98.6 cm of snow falling during the year (BLM 2006*a*, BLM 2006*b*).

Mountain and Wyoming big sagebrush were the dominant vegetation types in the ARPA and SC (BLM 2006*a*, BLM 2006*b*). The mountain big sagebrush cover type was mainly distributed along the foothills at higher elevations within the study areas. Bitterbrush, chokecherry (*Prunus virginiana*), alderleaf mountain mahogany (*Cercocarpos montanus*), Douglas rabbitbrush (*C. viscidiflorus*), rubber rabbitbrush (*E. nauseosus*), Saskatoon serviceberry (*Amelanchier alnifolia*), and mountain snowberry (*Symphoricarpos oreophilus*) were other common shrubs within this cover type. A variety of forb and grass species composed the understory within the mountain big sagebrush cover type. Common forbs included arrowleaf balsamroot (*Balsamorhiza sagittata*), beardtongue (*Penstemon* spp.), bluebells (*Mertensia* spp.), buttercup (*Ranunculus spp*.), false dandelion (*Agoseris glauca*), geranium (*Geranium*

richardsonii), groundsel (*Senecio* spp.), Indian paintbrush (*Castilleja* spp.), locoweed (*Astragalus* spp.), phlox (*Phlox multiflora*), sego lily (*Calochortus nuttallianum*), silky lupine (*Lupinus sericeus*), sulfur buckwheat (*Eriogonum umbellatum*), and wild onion (*Allium* spp.; BLM 2006). Common grasses associated with mountain big sagebrush communities included bluebunch wheatgrass (*Pseudoroegneria spicata*), bottlebrush squirreltail (*Elymus elymoides*), green needlegrass (*Nassella viridula*), Idaho fescue (*Festuca idahoensis*), little bluegrass (*Poa secunda*), mutton bluegrass (*Poa fendleriana*), needle-and-thread (*Hesperostipa comata*), oniongrass (*Melica bulbosa*), prairie junegrass (*Koeleria cristata*), spike fescue (*Leucopoa kingii*), and thickspike wheatgrass (*Elymus macrourus;* BLM 2006*a*, *b*).

Wyoming big sagebrush dominated the lower elevations within the ARPA and SC. Other shrub species associated with this cover type included broom snakeweed (*Gutierrezia sarothrae*), cotton horsebrush (*Tetradymia canescens*), Douglas rabbitbrush, rubber rabbitbrush, and winterfat (*Krascheninnikovia lanata*). Major forbs comprising the understory included beardtongue, hollyleaf clover (*Trifolium gymnocarpum*), Hood's phlox (*Phlox hoodii*), hooker sandwort (*Arenaria hookeri*), locoweeds, goldenweed (*Happlopappus* spp.), low buckwheat (*Eriogonum ovalifolium*), spring parsley (*Cymopterus acaulis*), and wild onion. Common grasses in Wyoming big sagebrush communities included bottlebrush squirreltail, Indian ricegrass (*Achnatherum hymenoides*), little bluegrass, needle-and-thread, thickspike wheatgrass, threadleaf sedge (*Carex filifoli*), and western wheatgrass (*Pascopyrum smithii*; BLM 2006*a*, *b*).

METHODS

Radio-marking and Monitoring Sage-Grouse

I captured female sage-grouse from mid-March through late April 2008 and 2009 on or near 14 leks in the ARPA and 5 leks in the SC using established spot-lighting and hoop-netting protocols

(Giesen et al. 1982, Wakkinen et al. 1992). Selected leks were evenly distributed across both study areas to ensure equal capture effort and to obtain a random sample of the population (Manly et al. 2002). I secured VHF radio transmitters (Model A4060; Advanced Telemetry Systems Incorporated, Isanti, Minnesota, USA) to females with a PVC-covered wire necklace. Transmitters weighed 22 g (~1.4% of mean female sage-grouse body mass); had a battery life expectancy of 789 days; and were equipped with motion-sensors (radio-transmitter pulse rate increased in response to inactivity after 8 hours). Sage-grouse were located using hand-held receivers and 3-element Yagi antennas through the nesting (May–June) period mainly between the hours of 08:00 to 18:00. I located nests of radio-marked birds by circling the signal source until I could visually observe the bird on a nest or isolate the nest to a few shrubs.

After determining a female grouse was nesting, I monitored the nest at a frequency of ≤7 days until the conclusion of the nesting effort from a distance of ≥30 m by triangulating to the exact nest point or nest shrub. I left nests in a meandering or zig-zag pattern to reduce the potential of predators following human scent to the nest. I recorded the location of nests (± 1 m) with a hand-held 12-channel global positioning system (GPS; Garmin Etrex; Garmin International, Olathe, Kansas, USA). The fate of the nest was later determined by the condition of the eggshells and shell membranes (Wallestad and Pyrah 1974). When nest fate could not be determined, I monitored females to assess whether they were brooding because a brooding female indicated a successful nest. If possible, I determined the number of hatched eggs by counting the number of egg shell caps. After the conclusion of nesting, the fate date was estimated as the day midway between consecutive visits unless other diagnostic signs allowed for a better approximation. This approximated date represented each nest's conclusion day in the nest survival analysis. A nest was considered to be successful if it hatched ≥1 egg (Schroeder et

al. 1999); otherwise it was recorded as naturally abandoned, abandoned due to researcher disturbance, nest predation, or unknown fate. If a nest was depredated I noted diagnostic evidence such as nest bowl disturbance, eggshell remains, scat, or tracks at the nest site to determine whether avian or mammalian predation occurred (Thirgood et al. 1998).

STUDY DESIGN

Approach

To provide a framework to evaluate objective 1, I first spatially shifted habitat-specific ARPA nest occurrence and survival models to the SC reference area to explore the accuracy and robustness (i.e., predictive ability in a new area with a distinct sage-grouse population) with out-of-sample data that were not used to train the models (Boyce et al. 2002, Johnson et al. 2006, Aldridge and Boyce 2007) and I measured the realized effects of individual predictor variables forming these models by modeling them against the SC nest occurrence and survival data (Paternoster et al. 1998). Because an animal's selection of resources is dependent on the habitats available to them (Baasch et al. 2010), my validation results provided a measure of habitat likeness between the ARPA and SC. Consequently, if the models performed poorly in SC this suggests that habitat conditions, independent of anthropogenic differences, which drive female sage-grouse nesting selection and survival, are dissimilar between areas.

Research in the ARPA (Chapter 2) demonstrated that the CBNG-related variable, visible wells, was negatively correlated with sage-grouse nest selection, as such this variable was contained in the final nest RSF model (Equation 1). However, no direct correlations between CBNG features and nest survival were detected (Equation 2). Incorporating my reference area and using a control-impact design, I compared sage-grouse nest selection patterns and nest survival demographics between an impacted site (ARPA) to the same parameters in my non-

impacted site (SC; Green 1979, Osenberg and Schmitt 2003). Hence, I explored the question can the reference area function as a control in the place of pre-development data? Specifically, I assessed potential impacts of CBNG development in the ARPA on sage-grouse nest habitat selection patterns and/or nest success by replacing time (i.e., pre-treatment data) with space (i.e., non-impacted reference area (Green 1979). In following with previous research designs (Holloran 2005), I made the assumption that the behavior of birds in a reference area imitated that of sage-grouse in a non-altered setting with expected natural variations in habitat conditions, weather, or other factors.

In SC, I constrained random locations within a 100% minimum convex polygon (MCP; Manly et al. 2002) to allow female sage-grouse habitat use to determine availability (Thomas and Taylor 2006). However, a small portion of my SC sage-grouse sample moved farther than expected from the lek of capture to an area that contained urban dwellings and traditional oil and gas development. This impacted area was in the northeast corner of my MCP near Bairoil, Wyoming. Therefore, to maintain the validity of the reference area as a pseudo-control, I removed any possible effects of energy development on my SC sample from the final MCP by employing a liberal potential influence buffer of 2.5 km, informed by previous research of the effects of distances of energy development on sage-grouse (Braun et al. 2002, Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008). Consequently, this energy influence area and 1 nest location therein were removed from the analysis. Further, a prominent ridgeline forming the Continental Divide separated the energy influence area from my final SC reference area; thus, increasing my confidence that energy development near Bairoil was not influencing nest selection and survival patterns in the SC.

ARPA Nest Occurrence Model

I employed a Type I use versus availability design (Manly et al. 2002) with binary logistic regression (Boyce and McDonald 1999, Thomas and Taylor 2006) to estimate a nest RSF for the ARPA (see Chapter 2). I generated random nest points in GIS at a ratio of 5-times the number of nests (Aldridge and Boyce 2007, Carpenter et al. 2010) and employed Wyoming sagebrush imagery (Homer et al. 2012) to constrain the random locations to sagebrush habitats by excluding areas within the ARPA study area that were inappropriate to be considered as available habitat such as exposed rock, open water, and conifer stands. I used a sequential modeling approach and Akaike's Information Criterion (AIC; Burnham and Anderson 2002) adapted for small sample sizes (AIC_c) to identify the most predictive variables and best-fit models (Hurvich and Tsai 1989). I used Akaike weights (w_i) to identify models within $w_i \leq 10\%$ of my top model to calculate aggregate coefficients, 95% confidence intervals, and odds ratios (i.e., multi-model inference; Burnham and Anderson 2002). The ARPA nest RSF model took the following form:

$$w(x) = \exp\{0.191(\text{Bsage_0.25}) + 0.063(\text{Litter_0.25}) - 21.850(\text{NDVIsd_5.0}) - 0.618(\text{Vwell_1.0})\} \quad (1)$$

Where, the w(x) is the predicted relative probability of a female selecting a 30-m cell in the ARPA landscape to nest. A positive coefficient (+) indicates increased likelihood of selection with an increase in the corresponding variable and the reverse is true for negative (–) coefficients. The GIS-derived spatial variables represented in the ARPA nest RSF included mean big sagebrush cover (%; Homer et al. 2012) at a 0.25-km^2 circular scale (Bsage_0.25); mean litter (%; Homer et al. 2012) at a 0.25-km^2 circular scale (Litter_0.25); standard deviation representing variability of the normalized vegetation index that indicated vegetation greenness at

a 5-km^2 circular scale (NDVIsd_5.0); and a count of visible CBNG wells within a 1-km^2 circular scale (Vwell_1.0).

ARPA Nest Survival Model

While focusing on the ARPA I used the Cox regression model to estimate the effect of landscape variables on time to an event (Cox 1972, Hosmer and Lemeshow 1999). Thus, in this analysis "time" referred to the approximate date of nest initiation and the "event" was the approximate date of nest failure. If a nest hatched successfully then it did not have an "event" (i.e., survived) and was censored. Therefore, the Cox model allowed me to link habitat-specific variables to nest survival or risk on the ARPA landscape (see Chapter 2). I used a derivation of AIC (Burnham and Anderson 2002) adapted for survival modeling (AIC_{SUR}; Liang and Zou 2008) to select the best supported models and most predictive variables. I used Akaike weights (w_i) to identify models within $w_i \leq 10\%$ of my top model to calculate aggregate coefficients, 95% confidence intervals, and risk ratios (multi-model inference; Burnham and Anderson 2002). The final nest survival model was in the form of a risk or hazard function $h(t|x_t)$ as follows:

$$h(t|x_t) = \exp\{-0.099(\text{Shrbhgtsd_1.0}) + 0.247(\text{TWI_0.25}) - 0.295(\text{Wysage_5.0})\} \qquad (2)$$

Positive coefficients indicate increased daily risk of nest failure. The spatial variables in the ARPA nest risk model included standard deviation representing vertical variability in shrub heights (cm; Homer et al. 2012) at a 1.0-km^2 circular scale (Shrbhgtsd_1.0); mean topographic wetness index indicating concave areas accumulating greater surface moisture (Theobald 2007) at a 0.25-km^2 circular scale; and mean Wyoming big sagebrush canopy cover (%; Homer et al. 2012) at a 0.25-km^2 circular scale.

ARPA Predictive Maps

I spatially quantified nesting habitat quality in the ARPA by applying sage-grouse nest occurrence and survival models to the landscape. I mapped these models in a GIS framework, the nest occurrence model was mapped as an RSF and the nest survival model was mapped as a risk function indicating areas of high to low relative probability of selection and relative risk, respectively (see Chapter 2). I distributed the predicted relative occurrence probabilities derived from the nest RSF into quartiles on the basis of 25-percentile breaks in probabilities (Sawyer et al. 2006). For mapping and validation purposes, I classified areas as high occurrence (highest 25% of predicted probabilities for nest occurrence), moderate-high (51 to 75% predicted probabilities for occurrence), moderate-low (26 to 50% predicted probabilities for occurrence), and low (lowest 25% of predicted probabilities for occurrence). The risk function was classified into 2 nest risk bins on the basis of the binary measure of relative risk distribution with the break at the mean value between high and low predicted relative risk values indicating areas predicted as having a high or low relative risk of nest loss.

Comparing Nest Success

I assessed differences in nest survival rates between the ARPA and SC and between years with the Kaplan-Meier (K–M) product-limit estimator (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) and computed the variance for these estimates following Greenwood (1926). I calculated the K–M nest survival estimates to t = 28 days. Further, I tested for statistical differences in the survival function between groups with the log-rank test (Cox and Oakes 1984, Hosmer and Lemeshow 1999).

Predictive Ability of ARPA Nest Models in SC

Nest occurrence model.—The only anthropogenic variable I found predictive of nest selection in the ARPA was visual wells (Equation 1). Because SC was non-impacted and did not contain oil and gas development or associated infrastructure the visual well variable contained within the ARPA full RSF was not applicable in the reference area. Consequently, the visual well variable was left unestimated. Therefore, the ARPA nest RSF applied to the SC was composed only of environmental variables and is describe hereafter as the ARPA nest environmental RSF.

The ARPA nest environmental RSF model performance and fit in SC were evaluated in several ways. First, I used k-fold cross-validation with a Spearman's rank correlation coefficient to evaluate the model's predictive performance against the SC sample (Boyce et al. 2002). A testing ratio of 20% was used with a k-fold partition of 5 bins of area-adjusted RSF scores (Boyce et al. 2002). For each of the 5 data folds (bins) the training data (ARPA) were tested against the SC data (testing data). A good predictive model would have an increasing number of nest locations in concurrence with increasing RSF scores and have a significantly ($\propto = 0.05$) positive Spearman's rank correlation coefficient (Boyce et al 2002). Second, following the methods described above for the ARPA nest RSF maps, the relative probabilities of occurrence derived from the ARPA nest environmental RSF applied to SC were divided into quartile bins with 25 percentile breaks between relative probabilities. The distribution of the SC nests within these bins provided further information on the predictive ability of the ARPA nest model in the SC. Finally, following the same methods used to model the ARPA nest RSF (i.e., binary logistic regression and multi-model inference) I regressed the SC use/available nest data with the ARPA nest environmental RSF model (Equation 1) without the visual wells variable, and for multi-

model inference I regressed all model variable combinations to estimate an SC specific nest RSF. I compared coefficients, such as the magnitude of coefficients and consistent positive or negative effects, for each predictor variable contained within the original ARPA environmental nest RSF to the SC nest RSF, I tested the relevance of each variable in the reference area and examined them for variable-specific differences in female sage-grouse nest habitat selection between the ARPA and SC. I tested for statistically significant ($\propto = 0.05$) differences between coefficients of the two models using a form of the Z-test (Paternoster et al. 1998).

Nest survival model.— If the nest survival model was predictive in the reference area, one would expect that unsuccessful nests would have experienced higher daily risks than successful nests. To validate the ARPA survival model (Equation 2) with the SC nest sample, I tested for a statistical difference in daily risk rates between successful and unsuccessful nests in SC with a one-tailed *t*-test with unequal variance (Aldridge and Boyce 2007). Following the model procedures used for the ARPA nest survival model (see Chapter 2) I used the Cox model to regress the SC nest survival data with the ARPA survival model (Equation 2) and all model variable combinations for multi-model inference to estimate a SC survival model. I compared coefficients for each predictor variable contained within the ARPA nest survival model and the SC nest survival model to examine if variables showed similar effects between areas by assessing the magnitude of coefficients and consistent positive or negative effects. Statistically significant ($\propto = 0.05$) differences between coefficient values between the ARPA and SC nest survival models were assessed using a form of the Z-test (Paternoster et al. 1998). Finally, the daily relative nest risk values for the SC were divided into binary bins with a break at the mean value between high and low daily relative risk. The distribution of successful and unsuccessful

nests within these bins provided further information on the predictive ability of the ARPA survival model in SC.

ARPA Nest Selection without CBNG Development

While considering the environmental model validity evidence gained from SC (i.e., selection in a non-impacted setting), I examined what female sage-grouse habitat selection for nesting may have looked like prior to the addition of CBNG development using SC as a spatial control. To accomplish this, I spatially shifted the SC adjusted nest RSF back on the ARPA landscape. I am making the assumption that SC represents female sage-grouse habitat selection for nesting in the absence of CBNG influences. So by applying the SC adjusted RSF (i.e., the ARPA environmental model with adjusted coefficients) back on the ARPA I attempted to explore nesting habitat selection without anthropogenic habitat modification by comparing the relative selection probabilities to the original ARPA RSF (see Chapter 2). I conducted all statistical analyses with Statistical Analysis Software (SAS), version 9.2 (SAS Institute 2009). K-M survival estimates are reported as estimated survival [$\hat{S}$] ± standard error [SE]).

RESULTS

Predictive Ability of ARPA Environmental Nest Occurrence Model in SC

The ARPA nest environmental RSF models performance in SC based on 5-fold validation and Spearman's rank correlation demonstrated a significantly positive relationship ($r_s = 0.87$, $P < 0.01$, $n = 10$) suggesting good predictive ability. Further, 73.0% of the nests in the SC sample were within the nest RSF occurrence areas predicted to be high and moderate-high. This area encompassed 38.4% of the SC landscape while only 9.0% of the nests were within the lowest predicted occurrence areas, which encompassed 36.3% of the landscape (Fig. 3.1). The SC nest distribution of probability bins was similar to those for the ARPA (i.e., training data). In the

ARPA 90.0% of the nests were in the high and moderate-high categories, which included 58.5% of the landscape and only 3.3% of the nests were within the lowest predicted occurrence area encompassing 20.0% of the landscape. The moderate-low quartile in the ARPA contained 18.0% of the nests and encompassed 25.0% of the area, while in SC the moderate-low quartile contained 6.7% of the nests and encompassed 22.0% of the area (Fig. 3.1).

The magnitude and direction of the effects of variable coefficients contained in the ARPA nest environmental RSF were similar when regressed against the SC nest data. The coefficients for Bsage_0.25 and Litter_0.25 increased, whereas the NDVIsd_5.0 coefficient decreased in SC (Table 4.1). However, none of the coefficients were significantly different between the ARPA and SC (Bsage_0.25 [$Z = 0.96$, $P = 0.17$], Litter_0.25 [$Z = 1.21$, $P = 0.11$], and NDVIsd_5.0 [$Z = 0.44$, $P = 0.32$]). Hence, the variable effects predicting female sage-grouse nest selection appear similar between areas.

ARPA Nest Selection without CBNG Development

The ARPA environmental RSF model proved to be highly predictive of nest occurrence in the non-impacted reference area substantiating my assumption of habitat consistency between the areas with the exception of CBNG infrastructure.

Assessing the impacts of CBNG development on nest selection patterns by utilizing SC as a spatial control and by spatially shifting the SC adjusted nest RSF back on the ARPA landscape proved ineffective. This method was not effective because the SC adjusted nest RSF did not demonstrate any predictive ability on the ARPA landscape. When the relative probabilities were distributed into binary bins with a break at the mean probability, this model predicted 78.0% of the ARPA as low relative probability of nest occurrence. The predicted low probability areas included 58.1% of the nest locations. Further, the SC adjusted RSF applied to

the ARPA had an inflated standard deviation, approximately 8 times the mean, preventing me from distributing the probabilities into quartile bins. The poor functionality of the SC adjusted model in the ARPA is likely a consequence of extrapolation out of the range of the SC habitat data used to adjust the RSF. In particular, the environmental variables contained in the adjusted RSF had lower mean values and a more restricted value range than in the ARPA-trained RSF. For example, in the ARPA predictor variable values of Bsage_0.25 averaged 12.1% (range = 0.5–27.8%), Litter_0.25 averaged 21.5% (range = 7.9–33.6%) and NDVIsd_5.0 averaged 0.07 (range = 0.03–0.17) compared to SC variable values of Bsage_0.25 averaged 8.1% (range = 1.4–14.2%), Litter_0.25 averaged 12.5% (range = 4.0–31.3%), and NDVIsd_5.0 averaged 0.04 (range = 0.02–0.14).

Nest Demographics

The average clutch size estimated after hatching for the ARPA was 6.5 (range = 5–9; n = 46) and the average clutch size for the SC was 6.5 (range = 5–8; n = 15). Kaplan–Meier nest survival estimates to 28 days (i.e., nests that successfully hatched) and K–M survival function plots differed between the ARPA and SC, but were similar between 2008 and 2009 in each area (Fig. 3.2). In 2008 and 2009, the ARPA K–M nest survival estimates were 45.2% ± 7.7% (n = 42) and 41.5% ± 7.7% (n = 41), respectively. The K–M nest survival estimates for SC were 61.5% ± 13.5% (n = 13) in 2008 and 66.7% ± 11.1% (n = 18) in 2009. I found no evidence of a statistical difference in survival between years in the ARPA ($\chi^2_1 = 0.09$, $P = 0.76$) or the SC ($\chi^2_1 = 0.03$, $P = 0.88$). I used this evidence to pool the data for each area across years. Nest survival with years combined was greater ($\chi^2_1 = 3.67$, $P = 0.05$) in SC ($\hat{S}$ = 64.5% ± 8.6%) than in (ARPA $\hat{S}$ = 43.4% ± 5.4).

Predictive Ability of ARPA Nest Survival Model in SC

When the ARPA survival model was regressed against the SC nest survival data, some differences emerged in the magnitude of the Cox model coefficients and the direction of effects (Table 3.2). Coefficient change for the predictor variable TWI_0.25 was marginal and not siginficantly different (Z = 0.07, P = 0.47) between models. The direction of the effect was the same for Shrubhgtsd_5.0 in both models, but the effect of coefficient increased in SC, however, the difference was marginally significant (Z = 1.52, P = 0.07). The predictor variable Wysage_5.0 was statistically different (Z = 1.80, P = 0.04) between models. Also, the magnitude of the coefficents for Wysage_5.0 changed dramatically and the direction of the effect switched from being negative in the AR to positive in the SC. However, the 95% confidence intervals for Wysage_5.0 from the SC specific model included zero (Le 1997, Hosmer and Lemeshow 1999), suggesting that nest survival in SC may have no relationship to the subspecies Wyoming big sagebrush canopy cover.

My ARPA survival model accurately identified successful and unsuccessful nests in the SC. Unsuccessful nests increased (t_{14} = 2.28, P = 0.02) in cumulative daily relative risk rates indicating greater exposure to riskier habitats (Fig. 3.3). Mean risk values in the SC for n = 20 successful nests was 0.32 ± 0.30 versus a mean of 0.49 ± 0.06 for n = 10 unsuccessful nests. Further, when the risk values in the SC were divided into binary bins with a break at the mean risk value the higher risk areas contained a greater percentage of unsuccessful nests. In higher risk areas 60.0% of the nests failed compared to only 25.0% in lower risk areas (Fig. 3.3).

DISCUSSION

The integration of a reference area into this research allowed me to test the robustness of my nest models and modeling procedure used in the ARPA against a distinct sage-grouse population.

Because the reference area was available for comparison, I was able to identify discrepancies in nest success between an area being impacted by CBNG development and an adjacent non-impacted area. However, this research elucidated an issue of using a reference area as a spatial control to assess development impacts (control-impact design; Green 1979, and Osenberg and Schmitt 1996) on landscape level selection because of greater variability in habitat conditions in the impacted and non-impacted areas.

Predictive Ability of ARPA Environmental Nest Occurrence Model in SC

The predictive strength of my nest models in an off-site reference area (SC) with independent data increased my confidence in the statistical procedures and model-building process that I used to spatially predict occurrence and survival in the ARPA for nesting (see Chapter 2). My second validation approach allowed me to compare the effects of individual predictor variables that compose the environmental RSF on a non-impacted area. Both methods used to validate the nesting environmental RSF in SC, showed good predictive ability. In fact, the RSF validation results were very similar to those from the RSF model when it was assessed against the training data (ARPA). When the RSF model was regressed with the SC data none of the individual predictor variable coefficients compared between the samples were significantly different suggesting that similar mechanisms were driving nest selection in the ARPA and SC in 2008 and 2009. As with the ARPA environmental RSF model, and findings from other landscape-scale sage-grouse nesting habitat selection studies (Aldridge and Boyce 2007, Doherty et al. 2010), female sage-grouse in SC selected for greater big sagebrush canopy cover. Further, litter proved predictive of nest selection in both areas with the effects of the variable increasing slightly in SC. Research on sage-grouse and other gallinaceous species at the microhabitat scale supports the positive relationship between nest occurrence and increased litter cover (Sveum et al. 1998,

Reese et al. 2005, Kirol et al. 2012). My results suggest that the predictor variables from the ARPA environmental RSF assessed independently demonstrated the same relationship to sage-grouse nest selection in SC as in the ARPA giving further support for these variables as predictors of sage-grouse nest selection.

Predictive Ability of ARPA Nest Survival Model in SC

The ARPA nest survival model proved predictive of nest survival in SC on the basis of two validation techniques. First, successful and unsuccessful nests in SC had statistically different exposure to habitats than the nest survival model predicted as having increased relative daily risk. Inclusively, unsuccessful nests were exposed to habitats predicted by the ARPA model as being riskier in SC. Second, when habitats were distributed into binary bins with a break at the mean daily relative risk value the areas predicted as having higher risk contained a greater percentage of unsuccessful nests when compared to the lower risk habitat bin.

However, individual predictor variables in the ARPA nest survival model regressed against SC nest data demonstrated some effect differences. The variability in shrub heights within a 1.0-km^2 area was not statistically different between areas, but the effect was more pronounced in SC. This predictor variable is of particular interest because, in addition to being predictive of nest survival in both SC and the ARPA, at this same scale it was predictive of survival for every summer life-stage in the ARPA including brood survival and adult female summer survival (see Chapter 2). Consequently, this finding provides strong evidence that large stands that contained greater heterogeneity in vertical cover of sagebrush and other shrub species were less risky habitats for female sage-grouse during the breeding season. The effect of Wyoming big sagebrush canopy cover within 5.0-km^2 area surrounding a nest was statistically different between areas and the direction of the effect changed. Based on the performance of the

ARPA nest survival model in SC, it is likely that sagebrush canopy cover at a landscape scale was important to nest success, but it appears to be independent of a specific sagebrush subspecies; such as, mountain or Wyoming big sagebrush.

ARPA Nest Selection without CBNG Development

Environmental conditions can vary greatly among locations so habitat-specific models are often unreliable for new areas (Morris et al. 2006). Consequently, the reliability of the nesting environmental RSF model and nest survival model in SC provided evidence of the similarities in environmental conditions between the ARPA and SC in the absence of CBNG development. Research conducted by Kirol et al. (2012) on sage-grouse nesting and brood-rearing habitat selection at the microhabitat scale also in the ARPA and SC did not identify significant site differences when the ARPA and SC data were modeled together.

In my previous research, the anthropogenic predictor variable visual well density at a 1.0-km^2 scale was highly predictive (Equation 1). This relationship indicated that female sage-grouse were avoiding visual wells when selecting nest sites (Chapter 2). To more robustly assess potential impacts of anthropogenic development (Green 1979, Osenberg and Schmitt 2003), I incorporated the SC reference area to determine if it could function as a spatial control in the place of pre-development data. When the ARPA environmental nest RSF was adjusted to the SC nest data (representing nest selection in a non-impacted setting) and spatially shifted back to the ARPA landscape inference was limited because of the poor predictive ability of the SC adjusted model in the ARPA. Specifically, even in the non-impacted portions of the ARPA the adjusted RSF predicted nest occurrence no better than a random null model (Boyce et al. 2002). I believe the failure of the SC as a spatial control was a consequence of extrapolation out of the range of the SC habitat data used to adjust the nest RSF. That is, when the nest RSF was adjusted to the

SC data it was adjusted to an area with reduced variability in habitat conditions and specifically the habitat variables contained within the RSF. So when the environmental RSF was extrapolated to the ARPA I was attempting to predict beyond the range of x-values used to adjust the model.

Model shifting to assess impacts of CBNG development also suffered from limited spatial data. The spatial data used in this analysis were from imagery taken between 2006 and 2009 (USDA 2010, Homer et al. 2012) after much of the CBNG infrastructure was in place. Hence, much of the conversion of native vegetation to improved gravel roads, pipeline corridors, compressor stations, and well pads had already occurred. For example, while focusing exclusively on the largest CBNG field in the central portion of the ARPA, I calculated that surface disturbance (see Chapter 2 for methods) exceeded 4.0% of the total area. Thus, predictor variables such as mean big sagebrush at a 0.25-km^2 scale within these modified habitats would likely be lower than the same measure prior to habitat modifications resulting in the ARPA nest environmental RSF predicting lower relative probabilities. Unfortunately, spatial data of the same quality were not available prior to the introduction of CBNG infrastructure on the ARPA landscape.

Nest Success Differences

Research has suggested that lower nest success in sage-grouse is likely a significant factor in population declines (Bergerud 1988, Crawford et al. 2004, Baxter et al. 2008). Reported nest success rates from radio-marked greater sage-grouse studies over the species' range vary from 12% to 71% with an average nest success rate of 46% (Connelly et al. 2011). In both years of my study nest success rates in the ARPA were lower than the range-wide average. Furthermore, the nest success rate in SC was 21.5% higher compared to the rate in the ARPA over both years.

Because of the divergence in nest success between areas, I examined if the environmental variables forming the nest survival model (Equation 2) explained the differences in nest success rates between the ARPA and SC. More specifically, I assessed if the ARPA nests in general were exposed to riskier habitats as predicted by the ARPA nest survival model. However, I found the inverse to be true in that the model predicted that mean daily risk rate for the ARPA nest sample was 0.13 and the mean risk rate for the SC nest sample was 0.38. Thus, the habitat-specific nest survival model accurately identified habitats with lower or higher nest survival in both areas, but did not explain the difference in survival between the areas.

Prairie grouse nests are very susceptible to predation; thus, nest loss in sage-grouse and other prairie grouse is most often a consequence of predation (Schroeder and Baydack 2001, Hagen 2011). Research has shown that habitat fragmentation and the introduction of anthropogenic features can augment existing predator populations or provide resources for new predators (Knight and Kawashima 1993, Boarman 2003). Greater predator abundance and the introduction of new nest predators (e.g., corvids) can adversely affect nest success of ground-nesting birds such as sage-grouse (Evans 2004, Manzer and Hannon 2005, Coates and Delehanty 2010, Hagen 2011). Range-wide nest success rates reported for radio-marked sage-grouse in human altered habitats averaged 37.0% compared to 51.0% in unaltered habitats (Connelly et al. 2012). Thus, the different nest success rates between the areas may be explained by an increase in sage-grouse nest predators as a result of CBNG development in the ARPA. But this difference could also be explained by natural variation in predator communities and/or abundance between the areas. The possible mechanisms behind the different nest success rates between my impacted study area and reference area warrant further research.

In conclusion, model validation using the SC reference area suggested good predictive ability of my ARPA nest environmental RSF and survival models and similar habitat effects on selection and survival in an area not used to train the models. The nest survival model did not explain the significantly higher nest success rate in the SC compared to the ARPA; thus, the difference may or may not be due to human activity related to CBNG development. When following a control-impact design in conjunction with spatial modeling the variability in habitat conditions and specifically the habitat variables in the final spatial models in the non-impacted spatial control must include the same amount of habitat variability as those in the impacted area. Otherwise, as experienced in this analysis, one is attempting to apply a model to predict beyond the range of the data used to train the model that may cause the model predictive ability and accuracy to suffer because relationships between variables may not hold or continue to be accurate when the model is extrapolated beyond this range. In this research spatial inference (Green 1979) provided additional information on impacts of anthropogenic development, but inference is limited without pre-development data.

MANAGEMENT IMPLICATIONS

When model predictions inform management decisions or future research it is critical that the models predict selection accurately (Boyce et al. 2002). My primary objective was to use the SC reference area as a validation of my ARPA nest models as well as my model-building approach; consequently, my results provide information to further inform sage-grouse nesting habitat management. My results provide support for the importance of intact sagebrush stands with adequate canopy cover and litter at large scales for sage-grouse nesting. Furthermore, habitats with homogeneous vertical shrub cover at large scales seem to be less conducive to nest success. I am unaware of any others who have specifically accessed variability in shrub heights and nest

survival at the landscape-scale; but, Aldridge and Boyce (2007) found that nest survival improved in habitats containing a heterogeneous mix of silver sagebrush (*A. cana*) cover.

My research findings support the importance of non-impacted reference areas to provide a comparison to assess possible implications of anthropogenic habitat alteration to sage-grouse populations as well as identifying specific mechanisms that warrant future research. For example, the mechanisms driving lower nest success in the ARPA compared to the non-impacted reference area are likely be a result of differences in nest predator abundance and composition between the areas and CBNG development may explain these differences. My research suggests that to make accurate inference on impacts of development by utilizing a reference area as a spatial control not only is it necessary that the reference area include similar habitat as the impacted area, but also contain a similar range of habitat conditions.

Reference areas can provide a baseline to assess variability in sage-grouse demographic rates (e.g., nest success) to impacted areas with similar habitat conditions. These comparative landscapes are useful to provide managers with information to assess if demographic changes are a consequence of ongoing disturbance or attributed to natural fluctuations such as annual weather variability. Finally, a goal of restoration ecology is to move an altered system back to an ecological state that is within acceptable limits identified by comparisons to less disturbed systems (Palmer et al. 2006). Therefore, when reclamation of CBNG infrastructure disturbance occurs in the ARPA a reference area such as SC can act as a “testing ground” of ecosystem function in a non-impacted state with sage-grouse serving as a bio-indicator of restoration success (Palmer et al. 2006). The strongest inferences are made when data are collected before and after disturbances occur in impacted study sites as well as comparative data collected at non-disturbed reference sites (i.e., BACI designs; Green 1979). However, the possibility to conduct

wildlife-disturbance studies under these conditions in energy development settings has unfortunately been rare, but would yield greater insights for restoration efforts.

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Table 3.1. A comparison of model coefficients derived from a nest resource selection function model applied to independent nest samples from the Atlantic Rim Study area and Stewart Creek reference area in south-central Wyoming, USA, 2008 and 2009.

	Atlantic Rim project area		Stewart Creek reference area		
Predictor variable	Coefficient	SE	Coefficient	SE	*P*-value
Bsage_0.25	0.19	0.06	0.34	0.15	0.169
Litter_0.25	0.06	0.04	0.16	0.07	0.113
NDVIsd_5.0	−21.85	6.42	−14.01	16.81	0.330

[a]Predictor variables quantified in a geographic information system: Bsage_0.25 = mean big sagebrush cover (%) at a 0.25-km^2 circular spatial scale; Litter_0.25 = mean vegetation litter (%) at a 0.25-km^2 circular spatial scale; and NDVIsd_5.0 = standard deviation representing variability of the normalized vegetation index that indicates vegetation greenness at a 5.0-km^2 circular spatial scale.

Table 3.2. A comparison of model coefficients derived from a nest survival model applied to independent nest samples from the Atlantic Rim Study area and Stewart Creek reference area in south-central Wyoming, USA, 2008 and 2009.

	Atlantic Rim project area		Stewart Creek reference area		
Predictor variable[a]	Coefficient	SE	Coefficient	SE	*P*-value
Shrbhgtsd_1.0	–0.10	0.07	–0.32	0.12	0.065
TWI_0.25	0.25	0.16	0.29	0.56	0.474
Wysage_5.0[b]	–0.29	0.14	0.23	0.26	0.036

[a]Predictor variables quantified in a geographic information system: Shrbhgtsd_1.0 = standard deviation of shrub heights (cm) representing vertical variability at a 1.0-km^2 circular spatial scale; TWI_0.25 = mean topographic wetness index indicating areas with greater surface moisture at a 0.25-km^2 circular spatial scale; and Wysage_5.0 = mean Wyoming big sagebrush cover (%) at a 0.25-km^2 circular spatial scale.

[b]Statistical difference between predictor variable coefficients at the $\propto = 0.05$ level–indicating a different effect of the predictor variable on nest survival between the ARPA and SC.

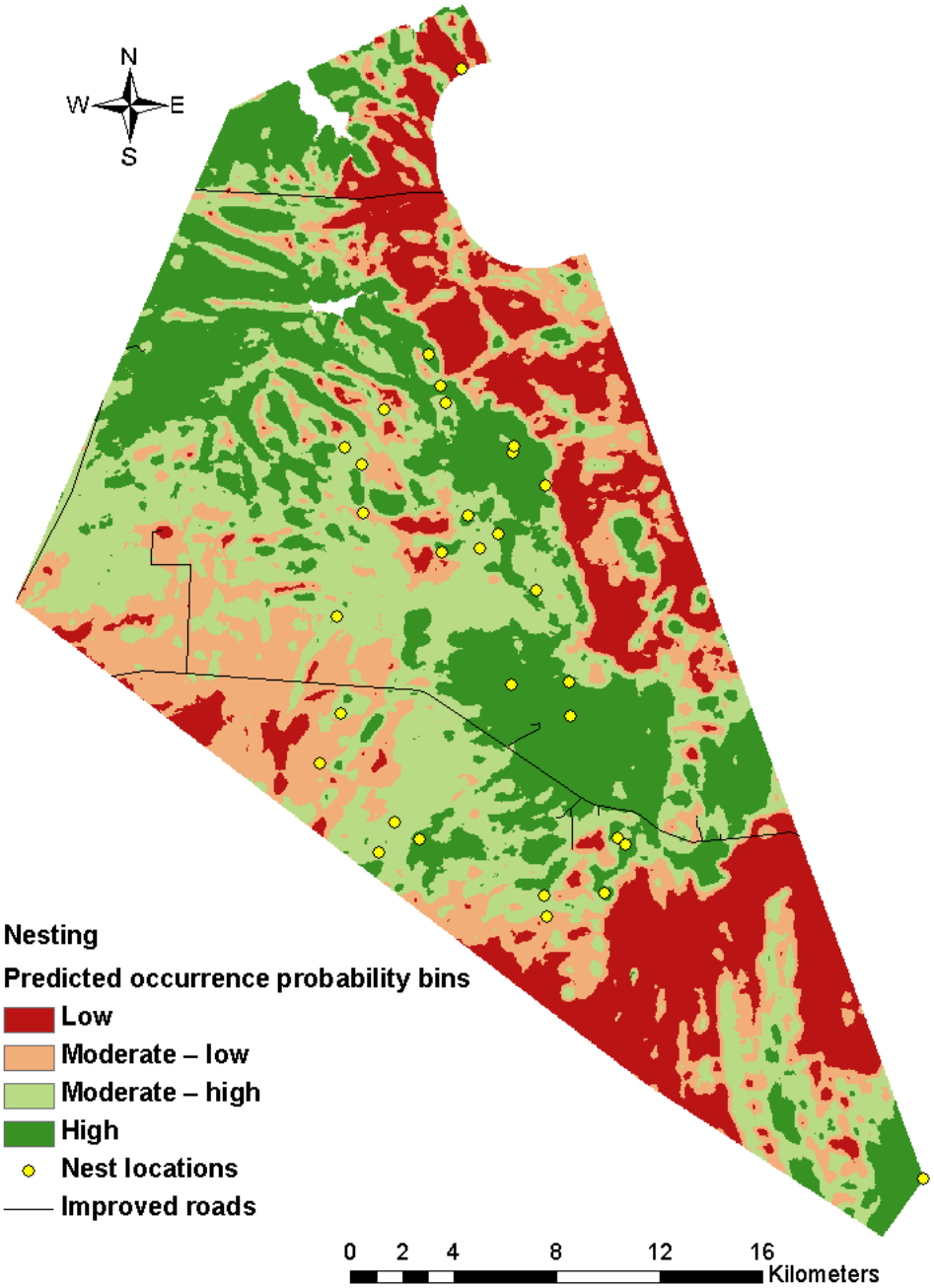

Figure 3.1. Atlantic Rim study area environmental nesting resource selection function predicting the relative probability of nesting sage-grouse occurrence mapped on the Stewart Creek reference area, south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of nest occurrence distributed into 25-percentile quartile bins.

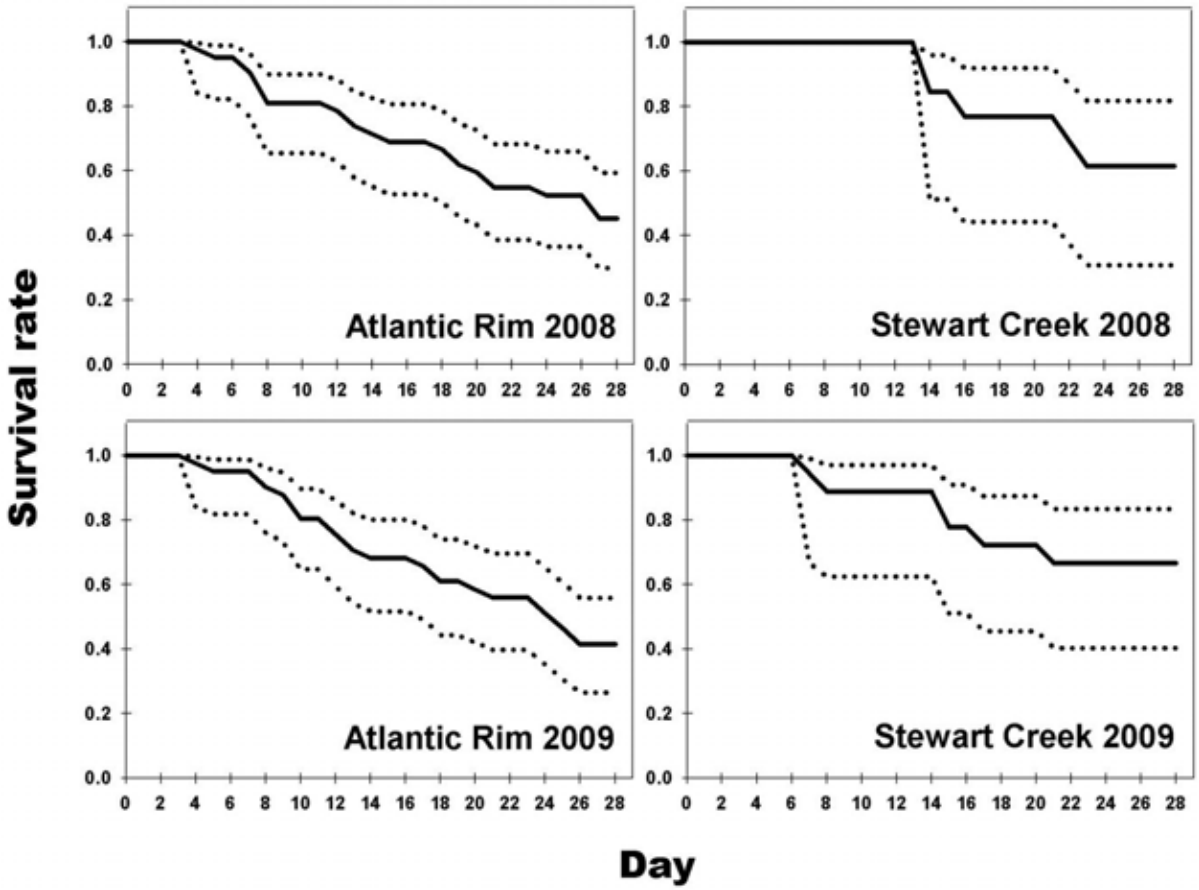

Figure 3.2. Kaplan-Meier survival curves with 95% confidence limits (dotted lines) for sage-grouse nest survival to hatch to ~28 days in the Atlantic Rim study area and Stewart Creek reference area in south-central, Wyoming, USA, 2008 and 2009.

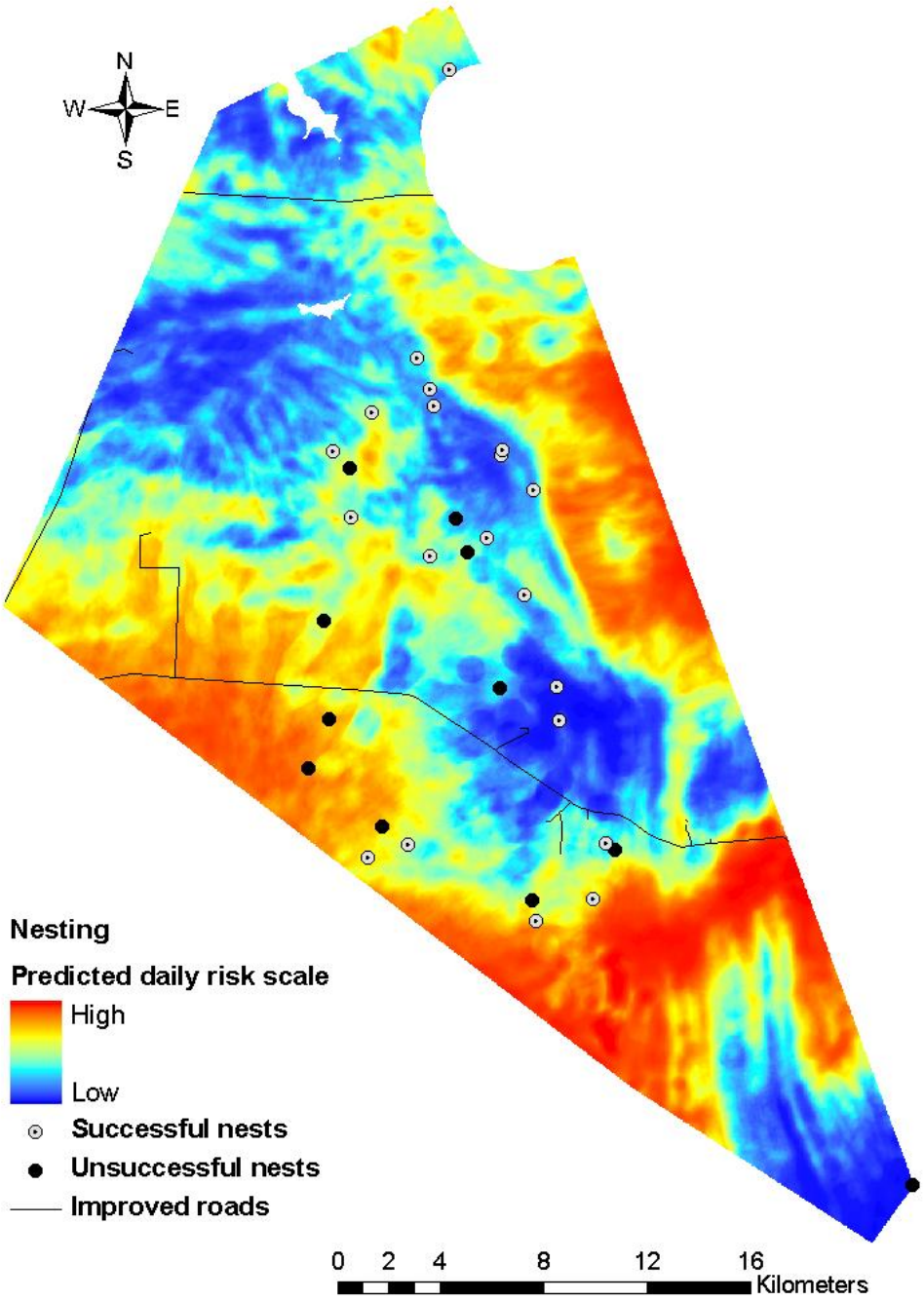

Figure 3.3. Atlantic Rim study area nest survival model predicting the relative daily risk of sage-grouse nest failure mapped on the Stewart Creek reference area, south-central, Wyoming, USA, 2008 and 2009. The map displays a continuum of nest risk from highest to lowest.

CHAPTER 4

MICROHABITAT SELECTION FOR NESTING AND BROOD-REARING BY THE GREATER SAGE-GROUSE IN XERIC BIG SAGEBRUSH

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Abstract. Understanding reproductive habitat selection is critical to conserving and restoring Greater Sage-Grouse (*Centrocercus urophasianus*) habitats, particularly in xeric landscapes (≤25 cm annual precipitation). We monitored radio-marked female sage-grouse in south-central Wyoming, USA in 2008 and 2009 to assess microhabitat use during nesting, early (5–14 days posthatch), and late (21–30 days posthatch) brood-rearing. For each model we grouped variables into 3 hypothesis sets on the basis of the weight of support from previous research (*a priori* information). We used binary logistic regression to compare grouse-use to randomly available locations and used an information-theoretic approach to identify the best supported models. Nest microhabitat selection was positively correlated with mountain big sagebrush (*Artemisia tridentata vaseyana*) compared to Wyoming big sagebrush (*A. t. wyomingensis*) and negatively correlated with cheatgrass. Nesting hens also selected microhabitats with greater litter cover. Early and late brood-rearing microhabitat contained greater perennial grass and sagebrush cover than random locations. Microhabitat variables most supported in the literature, such as forb cover and perennial grass cover, only accounted for 8%

and 16% of the pure variation in our early and late brood-rearing models, respectively. Our findings suggest sage-grouse inhabiting xeric sagebrush habitats rely on sagebrush cover and grass structure for nesting as well as brood-rearing and that these structural characteristics may be more important than forb availability at the microhabitat scale. Therefore, habitat treatment practices designed to increase forb production by markedly reducing sagebrush cover, as a means to increase sage-grouse productivity, in xeric sagebrush habitats may not be justified.

Key Words: Centrocercus urophasianus*, brood-rearing, grass cover, biological soil crust, microhabitat selection, nest occurrence, Wyoming*

INTRODUCTION

Over the past 60 years, researchers have documented range-wide declines in greater sage-grouse (*Centrocercus urophasianus*) populations (Patterson 1952, Connelly and Braun 1997, Braun 1998, Connelly et al. 2004) leading to concerns over long-term sage-grouse population viability. Sage-grouse depend on sagebrush for food and shelter throughout the entire year (Patterson 1952, Bent 1963, Braun et al. 1977, Swenson 1987, Connelly et al. 2011). Extensive loss and fragmentation of big sagebrush (*Artemisia tridentata*)-steppe habitat have reduced the current distribution of sage-grouse to about one-half of their original range (Schroeder et al. 2004). Knowing what vegetation and structural characteristics at the microhabitat scale are important to sage-grouse (i.e., nesting, early, and late brood-rearing) is critical to habitat maintenance and restoration efforts on the remaining lands supporting populations of sage-grouse.

Research has expanded our ecological understanding of sage-grouse nesting habitat selection at the microhabitat scale (e.g., Dunn and Braun 1986, Sveum et al. 1998b, Connelly et al. 2000, Aldridge and Brigham 2002, Holloran et al. 2005, Kaczor 2008, Doherty et al. 2010). The importance of specific habitat features for nesting has been extensively documented

including adequate sagebrush cover (or shrub cover) and sagebrush height (Wallestad and Pyrah 1974, Fischer 1994, Sveum et al. 1998b, Connelly et al. 2000, Braun et al. 2005, Holloran et al. 2005, Hagen et al. 2007, Kaczor 2008), as well as an herbaceous understory (Lyon 2000, Holloran et al. 2005, Hagen et al. 2007).

Microhabitat characteristics at nesting and early brood-rearing habitats often are very similar because brooding females spend their first 2–3 weeks after hatch in the vicinity of their nest (Berry and Eng 1985, Holloran and Anderson 2005). Sage-grouse chicks use foods with high protein content (i.e., insects and actively growing forbs) almost exclusively for the first two weeks posthatch (Johnson and Boyce 1990); as a result, the hen likely selects early brood-rearing habitats based on the abundance of insects and protein-rich forbs (Barnett and Crawford 1994, Holloran and Anderson 2004). Generally, early brood-rearing habitats are characterized by a well-developed sagebrush overstory and a healthy herbaceous understory (Connelly et al. 2000). Sage-grouse chicks consume fewer insects as the summer progresses, and forbs form a larger portion of their diets (Klebenow and Gray 1968, Peterson 1970). Research has suggested that late brood-rearing habitat is generally associated with more mesic sites that provide greater quantities of forbs and insects for both hens and chicks (Schroeder et al. 1999, Connelly et al. 2000). Because of the demonstrated importance of forbs to brooding hens and chicks, conservation efforts commonly focus on habitat treatments involving the removal of sagebrush to increase forb production (Wrobleski and Kauffman 2003, Pyke 2011).

Habitat selection analyses are commonly used to identify resources that are used disproportionately to their availability (Millspaugh and Marzluff 2001), predicated on the idea that animals are making choices (i.e., habitat selection; Garshelis 2000). Thus, it reasons that these choices are influenced by habitat conditions at specific locations within a species range.

Our understanding of sage-grouse nesting and brood-rearing habitat selection comes primarily from studies conducted in more mesic sagebrush habitats (e.g., Drutt 1992, Holloran 1999, Lyon 2000, Aldridge and Brigham 2002, Hausleitner 2003, Slater 2003, Aldridge 2005, Doherty et al. 2010) than those found in our study areas, where precipitation averaged 23.0 cm annually (based on ≥21 years of data compiled from 4 surrounding meteorological stations; Western Regional Climate Center 2010).

Our primary objective was to explore microhabitat selection, considering both physiognomic and floristic characteristics, during the nesting, early brood-rearing, and late brood-rearing periods in south-central Wyoming (USA). We hypothesized that the microhabitat variables that were most predictive of selection in our drier study areas may diverge from findings in more mesic areas. We were able to gain insight into this question using a sequential modeling approach (Arnold 2010) by forming model categories, termed hypothesis sets, for each life stage based on *a priori* information to select the best supported models. On the basis of the weight of evidence in published literature on habitat selection during the reproductive period and sage-grouse biology we grouped microhabitat variables into 3 hypothesis sets.

METHODS

STUDY AREA

The Atlantic Rim (AR) and Stewart Creek (SC) study areas were located in south-central Wyoming (USA) within a semi-desert grass-shrub zone characterized by expansive sagebrush-steppe with low average annual precipitation (Natural Resources Conservation Service 2006). Combined, the study areas encompassed approximately 1,913 km² (AR = 1,093 km² and SC = 820 km²) with elevation ranging from 1,981 m to 2,529 m. The majority of land in both areas is federally owned and administered by the BLM. Cattle and domestic sheep grazing is a major

land use in both the AR and SC. The AR is also being developed for coalbed natural gas reserves. Both study areas were dominated by Wyoming big sagebrush (*A. t. wyomingensis*) at lower elevations and mountain big sagebrush (*A. t. vaseyana*) along higher elevation foothills (BLM 2006b). Common forbs composing the understory included arrowleaf balsamroot (*Balsamorhiza sagittata*), desert parsley (*Cymopterus* spp.), Phlox (*Phlox* spp.), sego lily (*Calochortus nuttallianum*), sulfur buckwheat (*Eriogonum umbellatum*), and wild onion (*Allium* spp.). Common grasses included, bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*; BLM 2006a).

RADIO-MARKING AND MONITORING SAGE-GROUSE

We captured female sage-grouse from mid-March through late April 2008 and 2009 on or near 14 leks in the AR and 5 leks in the SC using established spot-lighting and hoop-netting protocols (Giesen et al. 1982, Wakkinen et al. 1992). Selected leks were evenly distributed across both study areas to ensure equal capture effort and to obtain a random sample of the population (Manly et al. 2002). We secured VHF radio transmitters (Model A4060; Advanced Telemetry Systems Incorporated, Isanti, Minnesota, USA) to females with a PVC-covered wire necklace. Transmitters weighed 22 g (~1.4% of mean female sage-grouse body mass); had a battery life expectancy of 789 days; and were equipped with motion-sensors (radio-transmitter pulse rate increased in response to inactivity after 8 hours).

Sage-grouse were located using hand-held receivers and 3-element Yagi antennas on a weekly basis through the nesting (May–June), and early and late brood-rearing (late June–August) periods mainly between the hours of 08:00 to 18:00. We located nests and brood locations of radio-marked birds by circling the signal source until the surveyor could visually

observe the bird on a nest or with her brood or isolate the nest or brood to a few shrubs. After determining a female grouse was nesting, we monitored the nest on a bi-weekly basis until the conclusion of the nesting effort. We left nests in a meandering or zig-zag pattern to reduce the potential of predators following human scent to the nest. To further minimize human-induced nest predation or nest abandonment, we monitored incubating females from a distance of ≥30 m by triangulating to the exact nest point or nest shrub. At each brood visit, we attempted to determine if the female was still with chicks by visually locating the chicks with binoculars or by observing the brooding female's behavior (e.g., distraction displays, feigning injury, clucking, and hesitation to flush). We recorded the location of nests and broods (± 1 m) with a hand-held 12-channel global positioning system (GPS; Garmin Etrex; Garmin International, Olathe, Kansas, USA).

We established random sampling locations by using a Geographic Information System (GIS) to generate a 1-km^2 grid overlaying the AR and SC study areas. The intersection points were numbered then randomized to represent sampling locations (random locations) and employed the Northwest GAP landcover data (2008) to constrain the random locations to sagebrush habitats while excluding areas within this habitat that were inappropriate to be considered as available habitat such as exposed rock, open water, and conifer stands.

MICROHABITAT MEASUREMENTS

We used established protocols to measure microhabitat vegetative characteristics surrounding nests, brood-rearing locations, and random locations (Connelly et al. 2003). We measured microhabitat characteristics along 2 perpendicular 10-m surveyor tapes centered on nests and random locations (Gregg et al. 1994) and 2 perpendicular 20-m surveyor tapes centered on brood-rearing and random locations to sample characteristics within 5 m and 10 m from each

nest and brood location, respectively (K. P. Reese, University of Idaho, Moscow, Idaho, USA, personal communication, 2008). We recorded general habitat characteristics at nests including vegetation association following hatch in late May and June and concluded our measurements at nest and random locations in June and early July, while microhabitat characteristics were recorded at early and late brood-rearing locations and random locations between July and August. We conducted measurements of microhabitat characteristics at grouse use locations concurrent with measurements at random locations. We considered the duration of the early brood period from hatch to 14 days (Connelly et al. 1988, Thompson et al. 2006) and subsequently recorded habitat characteristics for early brood-rearing at 1 location occupied by each brood during this period and late brood-rearing habitat characteristics at 1 location occupied by each brood between approximately 20 and 30 days posthatch (Connelly et al. 1988, Connelly et al. 2011).

The location of a simulated nest site (random) was determined by selecting the closest shrub taller than or equal to 30 cm, the average nest shrub height in Wyoming (Patterson 1952, Holloran et al. 2005). This same convention was not followed to establish random brood-rearing locations, because hens with chicks select a variety of vegetation structure including shrubs, grasses, and forbs. We measured a suite of physiognomic and plant taxa (Rotenberry 1985) microhabitat variables at nests, early brood-rearing, late brood-rearing, and random locations consisting of overstory, understory, and ground cover (Table A1).

We used the line intercept technique (Canfield 1941) to quantify shrub canopy cover by species at each location (Wambolt et al. 2006). We measured height (cm) of each sagebrush or other shrub (tallest leader, excluding inflorescences) encountered along the line intercept and averaged these per location. The average sagebrush height included all sagebrush species,

mainly mountain and Wyoming big sagebrush, but on occasion basin big sagebrush (*A. t. tridentata*), and silver sagebrush (*A. cana*). We quantified shrub density as the number of shrubs rooted in a 1-m wide belt transect along each line transect. To accurately differentiate between Wyoming and mountain big sagebrush, we took a representative sample at each location and identified them to subspecies with a UV-light fluorescence test (Rosentreter 2005). We estimated visual obstruction with a modified Robel pole (3-cm diameter × 1-m; Robel et al. 1970, Griffith and Youtie 1988) placed in the center of each location (nest bowl or center of brood-rearing or random locations) and recorded measurements from each cardinal direction. We ocularly estimated canopy or ground cover of invasive annual grasses, perennial grasses, residual perennial grasses, forb cover, food forb cover, gravel and rock, bare soil, biological soil crust, and litter within 6 cover classes in 20 × 50 cm (0.1-m^2) quadrats (Daubenmire 1959) placed along each surveyors' tape (nest: transect intersection, 2 m, 4 m, 6 m, and 8 m; brood: transect intersection, 4 m, 6 m, 8 m, 10 m, 12 m, and 14 m) and radiating from the transect intersection. This yielded 9 quadrats per location for each nest or random nest and 13 for each brood or random brood location. Designated cover classes included: 1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%. Forbs that are known to be eaten by sage-grouse (Patterson 1952, Peterson 1970, Wallestad and Eng 1975, Barnett and Crawford 1994) were grouped as food forbs (Table A2) and others as non-food forbs. We measured residual and perennial grass heights (cm) as the tallest naturally growing portion of the plant excluding flowering stalks (droop height) within 1-m from each Daubenmire quadrat to yield 9 or 13 height measurements for each microhabitat location.

EXPERIMENTAL DESIGN AND DATA ANALYSIS

We employed a use versus availability design to evaluate fourth-order habitat selection, or selection of items from a habitat patch (e.g., a nest site; Johnson 1980, Manly et al. 2002). Used locations were pooled across individual grouse to represent a population level response (i.e., Type I Design of Thomas and Taylor 2006; Manly et al. 2002). Random locations were also pooled and constrained within the boundaries of each study area (Manly et al. 2002).

We conducted statistical analyses with Statistical Analysis Software (SAS), version 9.2 (SAS Institute 2009). We evaluated microhabitat selection with binary logistic regression modeling. For each reproductive period (nesting, early, and late brood-rearing), we determined the probability of use where used (e.g., early brood-rearing locations) and available locations (e.g., random locations) were the dependent variables (Johnson et al. 2006). Random locations, representing available habitat, were not assigned as unused resources because the absence of a nest or brooding female cannot be determined without error (i.e., we are not certain that the random sample locations were not universally unused). Random locations that had evidence of nesting or brood-rearing use were not included in the sample so contamination was likely negligible (Johnson et al. 2006).

Prior to modeling, we computed a Pearson's correlation matrix to test for multicollinearity among the variables (linear dependencies among the explanatory variables) and omitted one of each correlated variables when correlation coefficients (r) were $\geq | 0.6 |$. Using a correlation matrix alone is often not sufficient because, when combined, multiple variables may be highly interdependent, but may not be detected by the matrix procedure (Allison 2009). Consequently, we further examined multicollinearity by estimating the global model (e.g., containing all variables) in PROC REG and specified the collinearity tolerance option. Low

tolerance, approximately (t) ≤ 0.40, suggests multicollinearity (Allison 2009, SAS Institute 2009), which we used as a basis to omit correlated variables. When omitting correlated variables we relied on variable importance established in the literature and those we believed were most biologically relevant to sage-grouse. Finally, we checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($|0.3| \leq r \geq |0.6|$). Undetected correlations between variables can cause instability in the signs of coefficients and also result in inflated standard errors (Doherty 2008). We did not permit variables to compete in the same model at any level of model selection when variable interactions in the same model caused the signs of coefficients to switch. Of the correlated variables causing instability in the model, the variable(s) that had the most impact on model fit were kept in the analysis. Re-nests were not considered in our nest analyses to avoid pseudoreplication.

To control for spatial and temporal variability, we included site-year combinations in each candidate model as fixed effects (dummy variables; Manly et al. 2002). Thus, because we standardized site and year in each model, differences between models were due to the explanatory power of the microhabitat variables (Holloran et al. 2005, Ludwig et al. 2010). To make results more interpretable, we did not report site and year responses. However, we reported statistically significant ($P \leq 0.05$) site or year effects.

We used 2nd-order Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) to rank candidate models by degrees of support. AIC_c penalizes for the number of model parameters, providing an unbiased estimate of the support of a particular candidate model. The candidate model with the lowest AIC_c value has the most support from the data but models within 2 ΔAIC_c points are competitive with that model (Burnham and Anderson 2002:70, 131). Consequently, we considered models within 2 ΔAIC_c

points of the top model to be plausible models. We computed cumulative Akaike weights (w_i) for all candidate models to provide weights of evidence in support of each model being the most parsimonious, compared to the other models being considered (Burnham and Anderson 2002:451, Rushton et al. 2004). Furthermore, we quantified the relative importance (RI) for each microhabitat variable by summing the Akaike weights for each variable across all of the models they appeared in (Burnham and Anderson 2002). Parameters having 95% confidence intervals with odds ratios that included 1 were considered uninformative predictors (Hosmer and Lemeshow 1989:100).

We used the area under the receiver operator curve (ROC) to measure the predictive accuracy of the models. ROC is derived from plotting the true positives against the false positive fractions for a range of thresholds in a prediction probability (e.g., how good our best model was at discriminating between nests and random locations; Rushton et al. 2004).

Our objective was to find the most parsimonious model and the most informative microhabitat variables for each reproductive period. Consequently, we used a sequential modeling procedure (Arnold 2010) consisting of two steps. First, we formed three model categories grouped into hypothesis sets for nesting, early, and late brood-rearing (Table 4.1). The three hypothesis sets for each life stage were organized as follows: Hypothesis set 1 was restricted to variables described in the literature as the most supported variables for sage-grouse microhabitat selection, and primarily based on a meta-analysis conducted by Hagen et al. (2007); Hypothesis set 2 was based on variables described in the literature as having moderate support; and Hypothesis set 3 contained variables that have not been verified in sage-grouse research, but we believe may be biologically relevant on the basis of sage-grouse biology. To arrive at a best-fit model, we tested multiple variable combinations (Burnham and Anderson 2002:101-102,125)

within each hypothesis set. The best model or models in each hypothesis set were then compared to the null model. If the best model was not at least 2 AIC_c points lower than the null model, it was not brought forward to the next level (Burnham and Anderson 2002:70,131, Doherty et al. 2010). This design allowed us to evaluate model fit in simpler models (≤ 4 microhabitat variables) and, in turn, avoid issues with over parameterized models (Burnham and Anderson 2002:32,131). Second, after finding the best model(s) in each hypothesis set (e.g., Nest I, Nest II, and Nest III), we allowed models to compete across sets to see if additional information produced a more parsimonious model (i.e., reduced the AIC_c value by at least 2 points; Burnham and Anderson 2002, Doherty 2008). For example, did the top model(s) from Nest I have the most support individually or did a combination of top models from Nest I + Nest II produce a model with greater support? When a single top model was not apparent based on the weight of evidence (w_i), we performed a model averaging procedure to calculate mean coefficients and associated standard errors and confidence intervals for each variable in the confidence set (Akaike weights that were within 10% of the top model [Burnham and Anderson 2002]). We reported means and standard errors of variables found to have predictive power in our modeling effort. We presented results of all models that were within 2 AIC_c points of the top model in each of the final model sets.

Hagen et al.'s (2007) meta-analysis suggested that overstory cover variables had the greatest support from previous nest microhabitat studies across the distribution of sage-grouse. Therefore, our Nest I hypothesis set included total sagebrush cover (SAGECVR), shrub density (SHRUBDEN), and visual obstruction (VOBST). Hypothesis set 2, for each reproductive period, were based on explanatory variables that published research has identified as being predictive of sage-grouse microhabitat selection (Heath et al. 1998, Sveum et al. 1998b, Holloran

1999, Lyon 2000, Aldridge and Brigham 2002, Aldridge 2005, Holloran et al. 2005, Herman-Brunson 2007, Kaczor 2008, Doherty et al. 2010), but are not ubiquitous in the literature or were not as conclusive (i.e., a lower overall effect size) in the Hagen et al. (2007) meta-analysis. Consequently, Nest II included total forb cover (FORBS), grass cover (GRSCVR = live perennial and residual perennial grass cover), and litter (LITTER). For each reproductive period, our final hypothesis set was less dependent on *a priori* information and more exploratory than Hypothesis sets 1 and 2. That is, these are variables we theorized may be related to sage-grouse microhabitat selection, but are not omnipresent in sage-grouse selection literature. Thus, Nest III included presence or absence of Wyoming big sagebrush (ARTRW), presence or absence of cheatgrass (CHEAT), biological soil crust (BIOCRUST; proxy for ecological condition) and gravel and rock (GANDR).

Hagen et al.'s (2007) designation of early brood-rearing and late brood-rearing periods differed from ours so we focused on the pooled brood-rearing analysis presented by Hagen et al. (2007) that did not differentiate between the early and late brood-rearing periods. Following others (Berry and Eng 1985, Connelly et al. 1988, Holloran and Anderson 2005, Thompson et al. 2006) we defined early brood-rearing as the period between hatch to 2 weeks and late brood-rearing >2 weeks posthatch. Across early and late brood-rearing, Hagen et al. (2007) demonstrated that broods selected habitats with greater herbaceous cover (forbs and grass). Thus, Early-brood I and Late-brood I (Hypothesis sets 1) contained the variables perennial grass cover (PERGRS), and FORBS. Early-brood II and Late-brood II (Hypothesis sets 2), contained the variables food forbs (FOODF), SAGECVR, SHRUBDEN, sagebrush height (SAGEHGHT), and grass height (GRSHGHT). Early-brood III (Hypothesis set 3) included ARTRW, CHEAT,

BIOCRUST, LITTER, and VOBST. Whereas ARTRW, CHEAT, BIOCRUST, and GANDR were considered in our Late-brood III hypothesis set.

When our final model was a combination of >1 of the subset models (e.g., top model[s] from individual hypothesis sets) we used variance decomposition to assess the relative influence of each of the subset models in our top model (Lawler and Edwards 2006, Doherty et al. 2010). Variance decomposition is a statistical approach that uses the maximum likelihood function to partition out the total variation into the pure variation explained by the component parts (Wittaker 1984, Lawler and Edwards 2006). For example, if our best model was a combination of subset models Nest I + Nest II + Nest III, variance decomposition enabled us to quantify the variation associated with each subset model into pure components (Lawler and Edwards 2006, Doherty et al. 2010).

RESULTS

During 2008 and 2009, we sampled microhabitat conditions at 115 nest locations, 114 random nest locations, 52 early brood-rearing locations, 52 random early brood-rearing locations, 52 late brood-rearing locations, and 55 random late brood-rearing locations. Of the total, 84 nests (2008, n = 41; 2009, n = 43) and 80 random nest locations (2008, n = 42; 2009, n = 38) were sampled in the AR and 31 nests (2008, n = 14; 2009, n = 17) and 34 random nest locations (2008, n = 18; 2009, n = 16) were sampled in the SC. Thirty-one early brood-rearing locations (2008, n = 18; 2009, n = 13) and 33 random early brood-rearing locations (2008, n = 18; 2009, n = 15) were sampled in the AR and 21 early brood-rearing locations (2008, n = 9; 2009, n = 12) and 19 random early brood-rearing locations (2008, n = 8; 2009, n = 11) were sampled in the SC. Thirty-one late brood-rearing locations (2008, n = 18; 2009, n = 13) and 34 random late brood-rearing locations (2008, n = 22; 2009, n = 12) were sampled in the AR and 21 late brood-rearing

(2008, n = 9; 2009, n = 12) and 20 random late brood-rearing locations (2008, n = 7; 2009, n = 13) were sampled in the SC. Ninety-five percent of all sage-grouse nests were located under big sagebrush (big sagebrush spp. = 17%, mountain big sagebrush = 45%, and Wyoming big sagebrush = 33%).

NEST HABITAT SELECTION

Continuous variables that were predictive in our final nest model included gravel and rock, litter, sagebrush canopy cover, total grass canopy cover, and visual obstruction (Table A3). Categorical variables that were predictive in our final nest model included presence of cheatgrass and presence of Wyoming big sagebrush. The nest selection model with the most support in the final level of model selection was a combination of models from all hypothesis sets (Nest I, Nest II, and Nest III). Variance decomposition suggested that Nest I contained 27% of the pure variation, Nest II contained 15% of the pure variation, and 26% of the pure variation was contained by Nest III whereas 32% of the variation was shared. The top model had moderate support (w_i = 0.44) and was 2.2 times more likely to be the best approximating model when compared to the second model in the set (Table 4.2). Because the top model lacked overwhelming support, we conducted model averaging for all of the models within the confidence set. Four of the variables contained in the confidence set of models (BIOCRUST, FORBS, and SHRUBDEN) were considered ineffective predictors because the CI of the odds ratios included 1 (Table 4.4). Statistically supported variables included ARTRW, CHEAT, GANDR, GRSCVR, LITTER, SAGECVR, and VOBST with relative importance weights from 0.6 to 1.0. Nest selection was positively related to greater grass cover, litter, sagebrush cover, and visual obstruction. For every 10% increase in sagebrush cover, the likelihood of sage-grouse nesting increased by approximately 10% (Figure 4.1). Nest selection was negatively related to

the presence of cheatgrass and Wyoming big sagebrush when compared to available habitat (Table 4.4). Cheatgrass occurred at 6% of the nest locations and 19% of the random nest locations. Wyoming big sagebrush occurred at 46% of our random locations, but only at 35% of our nest locations. Conversely, mountain big sagebrush occurred at 32% of our random nests and 50% of our nest locations.

EARLY BROOD-REARING HABITAT SELECTION

All of the predictive variables in our final early brood-rearing model were continuous and included perennial grass canopy cover, perennial grass height, and sagebrush canopy cover (Table A3). No variables grouped in Early-brood III were predictive. Consequently, the final level of early brood-rearing model selection contained a combination of the top models from Early-brood I and Early-brood II. Early-brood I contained 8% and Early-brood II 37% of the pure variation. The top model had good support (w_i = 0.61) and was 2.4-times more likely than the second model to best explain early brood-rearing habitat selection (Table 4.3). Variables composing the top model included SAGECVR, PERGRS, and GRSHGHT, which had RI values of 1.0, 1.0, and 0.9, respectively. Brood hens selected early brood-rearing habitats with greater sagebrush canopy and perennial grass cover and shorter grass heights when compared to available habitat (Table 4.4). A 10% increase in sagebrush cover increased the odds of early brood-rearing use by approximately 20% (Figure 4.1). Although the means for both food forb cover and total forb cover were slightly higher at grouse-use versus random locations (6.7 ± 1.3% vs. 5.9 ± 0.7% and 7.5 ± 0.9% vs. 7.1 ± 0.7, respectively), they were not supported in our models.

LATE BROOD-REARING HABITAT SELECTION

Continuous variables that were predictive in our final late brood-rearing model included biological soil crust, gravel and rock, perennial grass height, perennial grass canopy cover, sagebrush canopy cover, sagebrush height, and shrub density (Table A3). There were no categorical variables that were predictive in our final late brood-rearing model. The combination of models from each hypothesis set (Late-brood I, II, and III) best explained late brood-rearing habitat selection. However, 8 models in the final model set were competitive ($AIC_c \leq 2$) with the top model. The top model had poor support ($w_i = 0.16$) when compared to the other models in the set (Table 4.3). Four variables, GRSHGHT, PERGRS, SAGECVR, and SAGEHGHT, were in all models in the confidence set and had relative importance values of approximately 1.00. Other variables in the confidence set with some support included BIOCRUST (RI = 0.79), GANDR (RI = 0.79), and SRUBDEN (RI = 0.31). The CI for the odds ratios around several of these variables, including ARTRW, FOODF, LITTER, overlapped 1 indicating that they were not supported as predictive variables (Table 4.4). In the top model, Late-brood I explained approximately 16%, Late-brood II 58%, and Late-brood III explained 14% of the pure variation. Sagebrush cover, sagebrush height, and perennial grass cover were positively associated with late brood-rearing sites. Conversely, late brood-rearing grouse selected against taller grass, greater shrub density, and greater biological soil crust. The probability of use of late brood-rearing habitat increased by 3% for every 1% increase in perennial grass cover and by 1.5% for every 1% increase in sagebrush cover. Food forbs were present in the final confidence set, but had little predictive power because the CI for odds ratio included 1. Similar to early brood-rearing, food forb cover and total forb cover had little to no support in our late brood-rearing

models yet the mean values for grouse-use compared to random locations were slightly higher (9.5 ± 1.1% vs. 8.5 ± 1.1% and 11.0 ± 1.1% vs. 10.8 ± 1.0%, respectively).

DISCUSSION

Our study design enabled us to assess the importance of several microhabitat variables in the context of *a priori* information derived from sage-grouse selection research while exploring additional microhabitat variables we theorized may be biologically relevant. By grouping variables into hypothesis sets for each reproductive stage we were able to compare selection in our study areas to predictive microhabitat variables with varying degrees of support from previous sage-grouse research. Variance decomposition enabled us to quantify how much information was explained by each hypothesis set and compare this to existing sage-grouse selection research (e.g., Hagen et al. 2007).

In our study we demonstrated that sage-grouse in south-central, Wyoming showed strong selection for physiognomic characteristics including sagebrush cover and visual obstruction (both represented in hypothesis set Nest I) for nesting. Similarly, we found that during early and late brood-rearing, female grouse also preferred areas with greater sagebrush cover (represented in Early-brood II and Late-brood II) than randomly available. Late brood-rearing hens used areas with taller sagebrush plants (represented in Late-brood II) than randomly available. During early and late brood-rearing, females disproportionately used habitats with greater perennial grass cover compared to random locations (represented in Early-brood I and Late-brood I). Likewise, nest selection was positively associated with greater total grass cover (represented in Nest II). We did not identify a correlation between greater forb cover or food forb cover (represented in Early-brood I, Late-brood I, Early-brood II, and Late-brood II, respectively) and microhabitat selection during the early and late brood rearing periods.

Less studied microhabitat variables proved predictive of nest and late brood-rearing site selection in our models. Nest selection was positively correlated with greater litter and negatively correlated with cheatgrass (represented in Nest II and Nest III, respectively) and late brood-rearing hens selected microhabitats with less biological soil crust (represented in Late-brood III). Floristically, we found Mountain big sagebrush was preferred over Wyoming big sagebrush for nesting (represented in Nest III).

We predicted that the greatest amount of the pure variation in our data would be explained by Hypothesis set 1, that considered variables with the most support in the literature (Hagen et al. 2007) in each life stage that we modeled (i.e., Nest I, Early-brood I, and Late-brood I). However, using variance decomposition, we found that this was true only for nest selection modeling where a slight margin of the pure variation was explained by Nest I (27%) compared to Nest III (26%). Early-brood II and Late-brood II explained the majority of the pure variation in our final brood-rearing models (37% and 58%, respectively).

The importance of sagebrush and other obstructing cover to nesting sage-grouse (Wallestad and Pyrah 1974, Connelly et al. 1991, Fischer 1994, Heath et al. 1998, Sveum et al. 1998b, Popham and Gutie´rrez 2003, Holloran et al. 2005, Herman-Brunson 2007, Hagen et al. 2007, Kaczor 2008, Doherty et al. 2010) and to other prairie grouse such as Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus columbianus*; Giesen and Connelly 1993), and Lesser Prairie-chicken (*Tympanuchus pallidicinctus*; Hagen et al. 2004) has been well documented. Sage-grouse selection for greater grass cover during nesting has also been reported in many studies (Heath et al. 1998, Holloran et al. 2005, Sveum et al. 1998b, Lyon 2000, Hagen et al. 2007). The total combination of these cover attributes likely provides olfactory, visual, and physical barriers to predators (Bowman and Harris 1980, Crabtree et al. 1989, Delong et al.

1995) and thermal protection (Forrester et al. 1998, Heath et al. 1998, Schroeder et al. 1999, Reese et al. 2005).

Similar to Sveum et al. (1998b), we found a positive relationship between sage-grouse nest selection and litter. Research on other gallinaceous species such as Mountain Quail (*Oreortyx pictus*) also suggests an association between nest site selection and litter (Reese et al. 2005). This relationship may be a conferred adaptive advantage related to hen concealment from predators during incubation. Hens have a cryptic grayish-brown plumage (Patterson 1952, Schroeder et al. 1999) likely enabling them to conform more easily to nesting areas with a high percent of litter cover that is similar in color and patterning. Further support for this suggestion comes from Kaczor (2008) who found that successful sage-grouse nests in South Dakota had a higher percentage of litter cover than unsuccessful nests.

Sagebrush communities in our study areas were dominated by nearly equal distributions of Wyoming and mountain big sagebrush (BLM 2006a, Rodemaker and Driese 2006). Yet, our results indicated that sage-grouse preferred nesting in mountain over Wyoming big sagebrush. When compared to Wyoming big sagebrush, mountain big sagebrush often occurs at higher elevations in areas with lower mean temperatures, greater precipitation, increased vegetation production potential, and a more developed herbaceous understory (Goodrich 2005, Davies and Bates 2010). In addition, food forbs in close proximity to cover may be more available in mountain big sagebrush than Wyoming big sagebrush (Goodrich 2005, Rosentreter 2005, Davies and Bates 2010). Therefore, we suspect this response is a direct result of the dry conditions in our study areas as nesting sage-grouse may be seeking out cooler and wetter microhabitats.

Cheatgrass was not widespread in either the AR or SC but when it was found it was often associated with human infrastructure. Thus female sage-grouse may avoid nesting in areas

dominated by cheatgrass because cheatgrass is more prevalent in areas with anthropogenic disturbance (Pyke 2011). A likely explanation for this is that disturbance may be a mediating variable for cheatgrass, which is acting as a proxy for nest selection. In other words, sage-grouse may not have directly selected against cheatgrass, but may have avoided locations in our study areas with roads and infrastructure (Naugle et al. 2011) where cheatgrass was more common (Bergquist et al. 2007). The ecological mechanisms behind this finding warrant further research.

In agreement with some studies we found that female sage-grouse selected early brood-rearing microhabitats with greater sagebrush (Patterson 1952, Dunn and Braun 1986, Aldridge and Brigham 2002, Thompson et al. 2006) and perennial grass (Thompson et al. 2006, Hagen et al. 2007, Kaczor 2008) canopy cover. Yet, our research showed that early and late brood-rearing hens did not select areas with the tallest grass when compared to random locations, which may suggest a threshold where vertical cover is avoided. Aldridge and Boyce (2008) found that increased grass height was negatively related to chick survival. Moreover, Gregg and Crawford (2009) found that sage-grouse chick survival increased as the cover of short grasses (<18 cm) increased, but found no relationship between tall grass (>18 cm) cover and chick survival. Thus, brooding females may recognize the fitness consequences of using taller grass. As with early brood-rearing habitats, we found cover characteristics were important to late brood-rearing hens. In comparison, others have identified the importance of grass cover (Hagen et al. 2007, Hermun-Brunson 2007), sagebrush cover (Dunn and Braun 1986, Hermun-Brunson 2007, Aldridge and Brigham 2002), and visual obstruction (Kaczor 2008) for sage-grouse brood-rearing habitat encompassing both early and late brood-rearing. Similarly, Hagen et al. (2005) found strong selection by brooding female Lesser Prairie-chickens for habitats with greater visual obstruction

and Lehman et al. (2010) found that brooding Merriam's Turkey (*Meleargris gallopavo merriami*) females preferred areas with high visual obstruction.

Contrary to our findings, several researchers have reported that brood-rearing female sage-grouse often select microhabitats with greater forb abundance (Sveum et al. 1998a, Holloran 1999, Connelly et al. 2000, Hausleitner 2003, Hagen et al. 2007) and less sagebrush cover than random locations (Hagen et al. 2007). A likely explanation for the patterns of brood-rearing selection in our study areas is reflected in the different and sometimes contradictory findings from other studies. For example, most of the brood-rearing studies noted previously and considered by Hagen et al. (2007) were not located in xeric (≥25 cm of annual precipitation [Clifton 1981, Fischer et al. 1996]) sagebrush habitats (e.g., Drutt 1992, Hermun-Brunson 2007, Holloran 1999, Lyon 2000, Aldridge and Brigham 2002, Hausleitner 2003, Slater 2003, Aldridge 2005). Galliform chicks are born with poorly developed thermoregulatory systems and have been shown to be vulnerable to heat stress (Forrester et al. 1998, Flanders-Wanner et al. 2004). We theorize that because the habitat available to sage-grouse in our study areas is more-xeric, cover characteristics likely providing microclimates conducive to hen and brood thermoregulation may be driving microhabitat selection. Further support for this theory comes from another sage-grouse study in a xeric sagebrush habitat in south-central Wyoming that also did not find a correlation between forb cover and early or late brood-rearing microhabitat selection (Heath et al. 1998). Bell et al. (2010) showed the importance of shrub communities in providing thermal refugia for Lesser Prairie-chicken broods and Patten et al. (2005) found that Lesser Prairie-chickens avoided microclimates that were hotter, drier, and more exposed to wind and survival increased in sheltered microhabitats with lower temperatured and higher relative humidity.

Predation is a major factor contributing to reduced chick survival rates in sage-grouse (Aldridge 2005, Gregg and Crawford 2009, Hagen et al. 2011) and other Galliformes (Larson et al. 2001). Thus, it reasons that refugia from avian and mammalian predators likely also contributes to selection for greater screening cover, regardless of the vegetation type, during the early and late brood-rearing periods.

Our results stress that the factors most important to sage-grouse nesting, early brood-rearing, and late brood-rearing microhabitats in xeric habitat in south-central Wyoming are related more to cover than food. Additional microhabitat characteristics we identified as being predictive of nesting, early and late brood-rearing use, such as sagebrush type, litter, biological soil crust, and the absence of cheatgrass warrant future research. Our results concur with Hagen (2011) that the prevailing theme of sage-grouse seasonal habitat selection is a balance between concealment (e.g., predator avoidance) and meeting biological demands (e.g., food and thermal regulation).

On the basis of our findings managers should consider efforts to conserve sagebrush and increase perennial grass and residual grass cover. Furthermore, management targeting sage-grouse nesting and brood-rearing habitat in xeric sagebrush habitats should avoid practices that increase forb abundance at the expense of cover (e.g., sagebrush removal).

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TABLE 4.1. Measured variables grouped into three hypothesis sets considered in the sequential model selection analysis evaluating nesting, early brood-rearing, and late brood-rearing habitat selection in south-central Wyoming, USA, 2008 and 2009.

Candidate sets / variable names	Description
Nest I[a]	
SAGECVR	Sagebrush canopy cover (%)
SHRUBDEN	Shrub density (plants/m^2)
VOBST	Visual obstruction (horizontal cover; dm)
Nest II[b]	
FORBS	Total forb cover (%)
GRSCVR	Perennial and residual grass cover (%)
LITTER	Litter ground cover (%)
Nest III[c]	
ARTRW	Wyoming big sagebrush or other sagebrush type
BIOCRUST	Biological soil crust (%)
CHEAT	Presence or absence of cheatgrass
GANDR	Gravel and rock cover (%)

Candidate sets / variable names	Description
Early-brood I[a]	
FORBS	Total forb cover (%)
PERGRS	Perennial grass cover (%)
Early-brood II[b]	
FOODF	Food forb cover (%)
SAGECVR	Sagebrush canopy cover (%)
SAGEHGHT	Average sagebrush height within location (cm)
SHRUBDEN	Shrub density (plants/m^2)
GRSHGHT	Averaged maximum perennial grass droop height (cm)
Early-brood III[c]	
ARTRW	Wyoming big sagebrush or other sagebrush type
BIOCRUST	Biological soil crust (%)
CHEAT	Presence or absence of cheatgrass
LITTER	Litter (%)
VOBST	Visual obstruction (horizontal cover; dm)
Late-brood I[a]	
FORBS	Total forb cover (%)
PERGRS	Perennial grass cover (%)
Late-brood II[b]	
FOODF	Food forb cover (%)

Candidate sets / variable names	Description
GRSHGHT	Averaged maximum perennial grass droop height (cm)
SAGECVR	Sagebrush canopy cover (%)
SAGEHGHT	Average sagebrush height within location (cm)
SHRUBDEN	Shrub density (plants/m^2)
Late-brood III[c]	
ARTRW	Wyoming big sagebrush or other
BIOCRUST	Biological soil crust (%)
CHEAT	Presence or absence of cheatgrass
GANDR	Gravel and rock cover (%)
LITTER	Litter (%)

[a]Nest I, Early-brood I, Late-brood I hypothesis sets 1 contains the microhabitat variables that have been shown to be important in a suite of published sage-grouse habitat selection studies.

[b]Nest II, Early-brood II, Late-brood II hypothesis sets 2 contains microhabitat variables that have been examined in published sage-grouse habitat selection studies but their importance is not well established.

[c]Nest III, Early-brood III, Late-brood III hypothesis sets 3 contains microhabitat variables that we theorize may be biologically relevant to sage-grouse habitat selection but are not prevalent in published sage-grouse habitat selection studies.

TABLE 4.2. Top and competing ($\Delta AIC_c \leq 2.0$) models best explaining sage-grouse nest microhabitat selection in south-central Wyoming, USA, 2008 and 2009. Nest I, II, and III represent the hypothesis sets used in sequential modeling.

Model Nest[a]	K[b]	ΔAIC_c[c]	w_i	ROC[d]
[SAGECVR, SHRUBDEN, VOBST]$^{\text{Nest I}}$ + [GRSCVR, LITTER]$^{\text{Nest II}}$ + [ARTRW, CHEAT, GANDR]$^{\text{Nest III}}$	11	0.00	0.44	0.84
[SAGECVR, SHRUBDEN, VOBST]$^{\text{Nest I}}$ + [LITTER]$^{\text{Nest II}}$ + [ARTRW, CHEAT, GANDR]$^{\text{Nest III}}$	10	1.53	0.20	0.84
[SAGECVR, SHRUBDEN, VOBST]$^{\text{Nest I}}$ + [GRSCVR, LITTER]$^{\text{Nest II}}$ + [ARTRW, BIOCRUST, CHEAT, GANDR]$^{\text{Nest III}}$	12	1.69	0.19	0.85
Null	1	77.20	0.00	

[a]Conducted model averaging.

[b]Number of parameters (K) with site and year included in all models.

[c]Lowest AIC_c = 244.84 for nest.

[d]Receiver operating curve (ROC) statistic indicating the true positive rate.

TABLE 4.3. Top and competing ($\Delta AIC_c \leq 2.0$) models best explaining sage-grouse early and late brood-rearing microhabitat selection in south-central Wyoming, USA, 2008 and 2009. Early-brood I, II, and III and Late-brood I, II, and III represent the hypothesis sets used in sequential modeling.

Model	K[b]	ΔAIC_c[c]	w_i	ROC[d]
Early brood-rearing				
[PERGRS]$^{\text{Early-brood I}}$ + [GRSHGHT, SAGEVCR]$^{\text{Early-brood II}}$	6	0.00	0.61	0.81
[PERGRS]$^{\text{Early-brood I}}$ + [FOODF, GRSHGHT, SAGECVR]$^{\text{Early-brood II}}$	7	1.66	0.27	0.82
Null	1	15.35	0.00	
Late brood-rearing[a]				
[PERGRS]$^{\text{Late-brood I}}$ + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT]$^{\text{Late-brood II}}$ + [BIOCRUST, GANDR]$^{\text{Late-brood III}}$	10	0.00	0.16	0.89
[PERGRS]$^{\text{Late-brood I}}$ + [GRSHGHT, SAGECVR, SAGEHGHT, SHRUBDEN]$^{\text{Late-brood II}}$ + [BIOCRUST, GANDR]$^{\text{Late-brood III}}$	10	0.67	0.11	0.89
[PERGRS]$^{\text{Late-brood I}}$ + [GRSHGHT, SAGECVR, SAGEHGHT]$^{\text{Late-brood II}}$ + [BIOCRUST, GANDR]$^{\text{Late-brood III}}$	9	0.78	0.11	0.88

Model Early brood-rearing	K[b]	ΔAIC_c[c]	w_i	ROC[d]
[PERGRS]$^{\text{Late-brood I}}$ + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT]$^{\text{Late-brood II}}$	8	1.15	0.09	0.87
[PERGRS]$^{\text{Late-brood I}}$ + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT]$^{\text{Late-brood II}}$ + [ARTRW, BIOCRUST, GANDR]$^{\text{Late-brood III}}$	11	1.67	0.07	0.89
[PERGRS]$^{\text{Late-brood I}}$ + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT]$^{\text{Late-brood II}}$ + [BIOCRUST, GANDR, LITTER]$^{\text{Late-brood III}}$	11	1.71	0.07	0.89
[PERGRS]$^{\text{Late-brood I}}$ + [GRSHGHT, SAGECVR, SAGEHGHT]$^{\text{Late-brood II}}$	7	1.93	0.06	0.86
[PERGRS]$^{\text{Late-brood I}}$ + [GRSHGHT, SAGECVR, SAGEHGHT, SHRUBDEN]$^{\text{Late-brood II}}$	8	1.95	0.06	0.87
Null	1	36.14	0.00	

[a]Conducted model averaging.

[b]Number of parameters (K) with site and year included in all models.

[c]Lowest AIC_c = 128.05 for early brood-rearing, 110.78 for late brood-rearing.

[d]Receiver operating curve (ROC) statistic indicating the true positive rate.

TABLE 4.4. Parameter estimates, variable importance values, and odds ratios for microhabitat variables that were included in top model(s) depicting nesting, early brood-rearing, and late brood-rearing microhabitat selection in south-central Wyoming, USA.

Parameter	Estimate	95% CI		*P*-value[c]	RI[d]	Odds ratio	95% CI	
		Lower	Upper				Lower	Upper
Nest selection[a]								
Intercept	–3.252	–4.080	–2.423	<0.001				
ARTRW	–0.737	–1.065	–0.409	0.04	1.0	0.478	0.344	0.664
BIOCRUST[b]	0.061	–0.023	0.146	0.45	0.3	1.063	0.977	1.157
CHEAT	–2.286	–2.882	–1.690	<0.001	1.0	0.102	0.056	0.185
FOODF[b]	0.001	–0.020	0.023	0.48	0.9	1.001	0.980	1.023
GANDR	–0.053	–0.080	–0.027	0.05	1.0	0.948	0.923	0.974
GRSCVR	0.028	0.014	0.041	0.05	0.6	1.028	1.014	1.042
LITTER	0.038	0.026	0.049	<0.001	1.0	1.038	1.027	1.050
SAGECVR	0.057	0.042	0.073	<0.001	1.0	1.058	1.043	1.075
SHRUBDEN[b]	0.066	–0.050	0.182	0.61	1.0	1.068	0.951	1.200
VOBST	0.143	0.005	0.282	0.32	1.0	1.154	1.005	1.325
Early brood-rearing[a]								
Intercept	–0.834	0.605	–2.272	0.73				
GRSHGHT	–0.098	–0.181	–0.015	0.02	0.9	0.907	0.834	0.986
PERGRS	0.108	0.177	0.039	0.002	1.0	1.114	1.039	1.193
SAGECVR	0.052	0.084	0.020	0.002	1.0	1.053	1.020	1.088

Parameter	Estimate	95% CI		*P*-value[c]	RI[d]	Odds ratio	95% CI	
		Lower	Upper				Lower	Upper
Late brood-rearing[a]								
Intercept	–1.011	–1.965	–0.060	0.64				
ARTRW[b]	–0.549	–1.195	0.097	0.19	0.2	0.578	0.303	1.102
BIOCRUST	–0.652	–0.680	–0.624	0.07	0.8	0.521	0.507	0.536
FOODF[b]	0.009	–0.025	0.043	0.06	0.4	1.009	0.975	1.044
GANDR	–0.039	–0.076	–0.003	0.23	0.8	0.961	0.927	0.997
GRSHGHT	–0.010	–0.149	–0.050	0.05	1.0	0.905	0.861	0.951
LITTER[b]	–0.029	–0.064	0.006	0.65	0.2	0.971	0.938	1.006
PERGRS	0.107	0.067	0.147	0.009	1.0	1.113	1.069	1.158
SAGECVR	0.055	0.036	0.075	0.002	1.0	1.057	1.036	1.078
SAGEHGHT	0.052	0.029	0.075	0.03	1.0	1.053	1.029	1.078
SHRUBDEN	–0.538	–0.886	–0.189	0.10	0.3	0.584	0.412	0.828

[a]Contains model-averaged parameters estimates.

[b]Parameters having no predictive power as the 95% confidence intervals of the odds ratios include 1.

[c]*P*-value from combined model containing all variables in top model(s).

[d]Relative importance (RI) was calculated by adding Akaike weights for all models in the candidate set that variable was present in; the closer the value is to 1 the more important the variable was in the set.

FIGURE LEGENDS

FIGURE 4.1. Probability of sage-grouse use of microhabitat for nesting, early brood-rearing, and late brood-rearing as a function of sagebrush canopy cover with 95% confidence intervals around predictions, south-central, Wyoming, USA, 2008 and 2009. Probability graphs derived from single-variable models. Sagebrush canopy cover was truncated based on its median values in our data or its upper limits reported in the Hagen et al. (2007) meta-analysis.

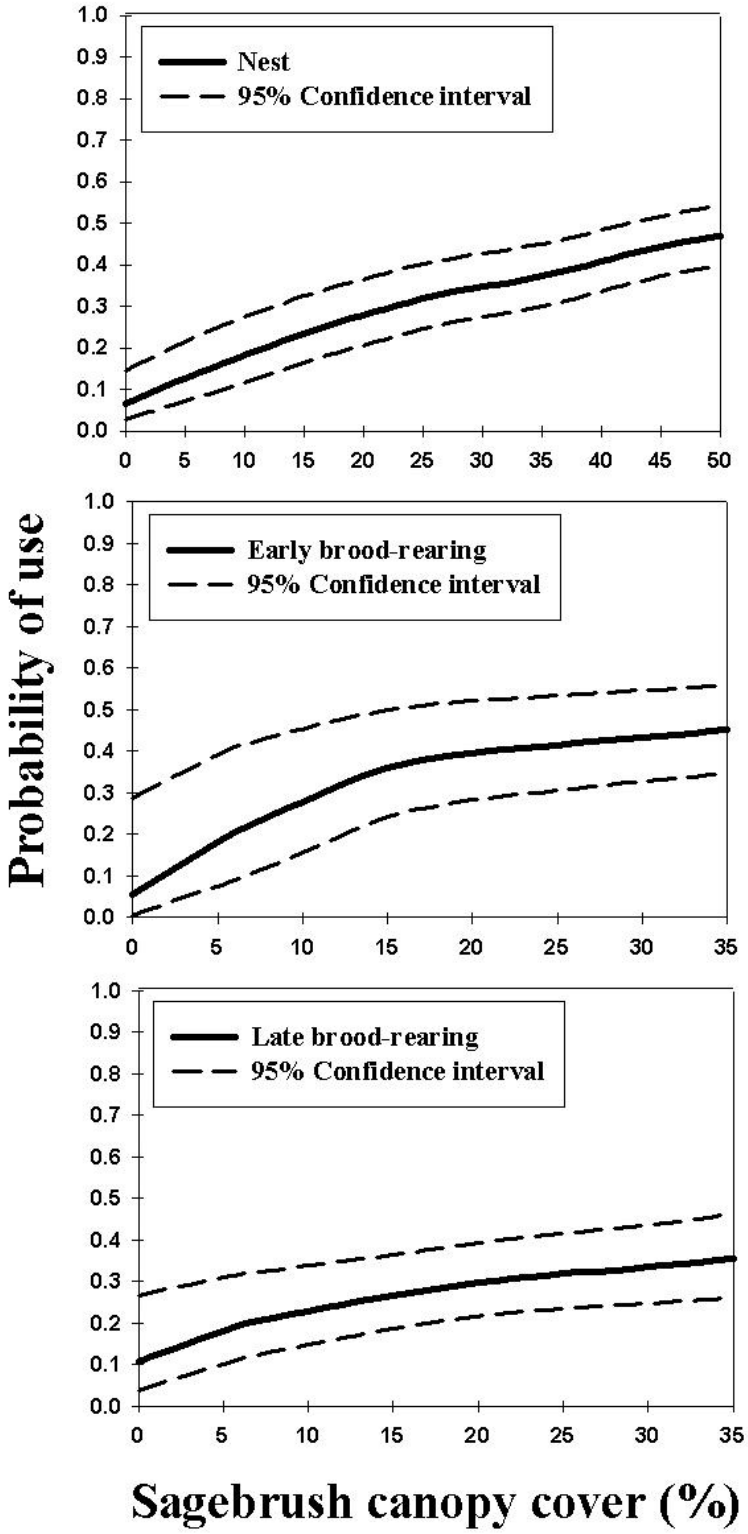
Nest
95% Confidence interval
Early brood-rearing
95% Confidence interval
Late brood-rearing
95% Confidence interval
Probability of use
Sagebrush canopy cover (%)

FIGURE 4.1.

APPENDIX

TABLE A1. Microhabitat vegetation characteristics measured at nest, early brood-rearing, late brood-rearing locations and random locations, south-central, Wyoming, USA, 2008 and 2009.

	Physiognomic	Plant taxa
Overstory characteristics	Mean shrub height	Sagebrush subspecies
	Shrub density	
	Sagebrush density	
	Total shrub canopy cover	
	Total sagebrush canopy cover	
	Visual obstruction	
Understory characteristics	Food forbs	
	Non-food forbs	
	Perennial grass canopy cover	Cheatgrass (*Bromus tectorum*)
	Perennial grass height	
	Residual grass canopy cover	
	Residual grass height	
	Total grass canopy cover	
	Total forb canopy cover	
Ground cover	Bare soil	
	Biological soil crust	
	Cactus canopy cover	
	Gravel and rock	
	Litter	

TABLE A2. Forbs known to be present and likely consumed by Greater Sage-Grouse in south-central Wyoming, USA.

Common name	Scientific name	Status
Agoseris	*Agoseris* spp.	Native
Alfalfa	*Medicago sativa*	Introduced
Aster	*Symphyotrichum* spp.	Native
Balsamroot	*Balsamorhiza* spp.	Native
Bluebells	*Mertensia* spp.	Native
Broomrape	*Orobanche* spp.	Native
Buckwheat	*Eriogonum* spp.	Native
Clover	*Trifolium* spp.	Native/introduced
Common pepperweed	*Lepidium densiflorum*	Native
Common dandelion	*Taraxacum officinale*	Native/introduced
Curlycup gumweed	*Grindelia squarrosa*	Native
Deathcamas	*Zigadenus* spp.	Native
Desert Parsley/Biscuitroot	*Lomatium* spp.	Native/introduced
Flax	*Linum* spp.	Native/introduced
Fleabane	*Erigeron* spp.	Native
Globemallow	*Sphaeralcea* spp.	Native
Goatsbeard	*Tragopogon* spp.	Introduced
Hawksbeard	*Crepis* spp.	Native/introduced
Indian paintbrush	*Castilleja* spp.	Native

Common name	Scientific name	Status
Lupine	*Lupinus* spp.	Native
Milkvetch	*Astragalus* spp.	Native
Monkey Flower	*Mimulus* spp.	Native
Northern sweetvetch	*Hedysarum boreale*	Native
Penstemon	*Penstemon* spp.	Native
Phlox	*Phlox* spp.	Native
Prickly lettuce	*Lactuca serriola*	Introduced
Prairie clover	*Dalea* spp.	Native
Microseris	*Microseris* spp.	Native
Pussytoes	*Antennaria* spp.	Native
Sego lily	*Calochortus nuttallii*	Native
Shootingstar	*Dodecatheon* spp.	Native
Slender phlox	*Microsteris gracilis*	Native
Small burnet	*Sanguisorba minor*	Introduced
Vetch	*Vicia* spp.	Native/introduced
Wild onion	*Allium* spp.	Native
Yarrow	*Achillea millefolium*	Native
Yellow sweetclover	*Melilotus officinalis*	Introduced

TABLE A3. Means (± SE) for all variables determined to have support in the final AIC_c models to assess sage-grouse microhabitat selection during nesting, early brood-rearing, and late brood-rearing, south-central, Wyoming, USA, 2008 and 2009.

	Grouse locations	Random locations
Variable category/name[a]	Mean ± SE	Mean ± SE
Nest		
Cover (%)		
Gravel and rock	2.8 ± 0.6	7.5 ± 1.0
Litter	45.1 ± 1.7	31.6 ± 1.7
Sagebrush	39.0 ± 1.4	25.2 ± 1.0
Total grass	17.5 ± 1.0	16.6 ± 1.2
Visual obstruction (dm)		
Robel pole	3.8 ± 0.2	2.8 ± 0.1
Early brood-rearing		
Cover (%)		
Perennial grass	14.7 ± 1.5	9.6 ± 0.8
Sagebrush	35.3 ± 3.0	22.5 ± 2.2
Height (cm)		
Perennial grass	17.7 ± 0.8	18.5 ± 1.1
Late brood-rearing		
Cover types (%)		
Gravel and rock	4.4 ± 1.0	10.0 ± 1.8

Variable category/name[a]	Grouse locations Mean ± SE	Random locations Mean ± SE
Sagebrush	37.7 ± 2.8	21.5 ± 1.7
Perennial grass	17.4 ± 1.8	12.3 ± 1.6
Biological soil crust	0.3 ± 0.1	1.1 ± 0.2
Density (plants/m^2)		
Shrub	2.3 ± 0.14	2.5 ± 0.3
Height (cm)		
Perennial grass	20.2 ± 0.9	21.8 ± 2.5
Sagebrush	40.8 ± 2.6	25.9 ± 2.3

[a]Microhabitat variables that were supported in our final models.