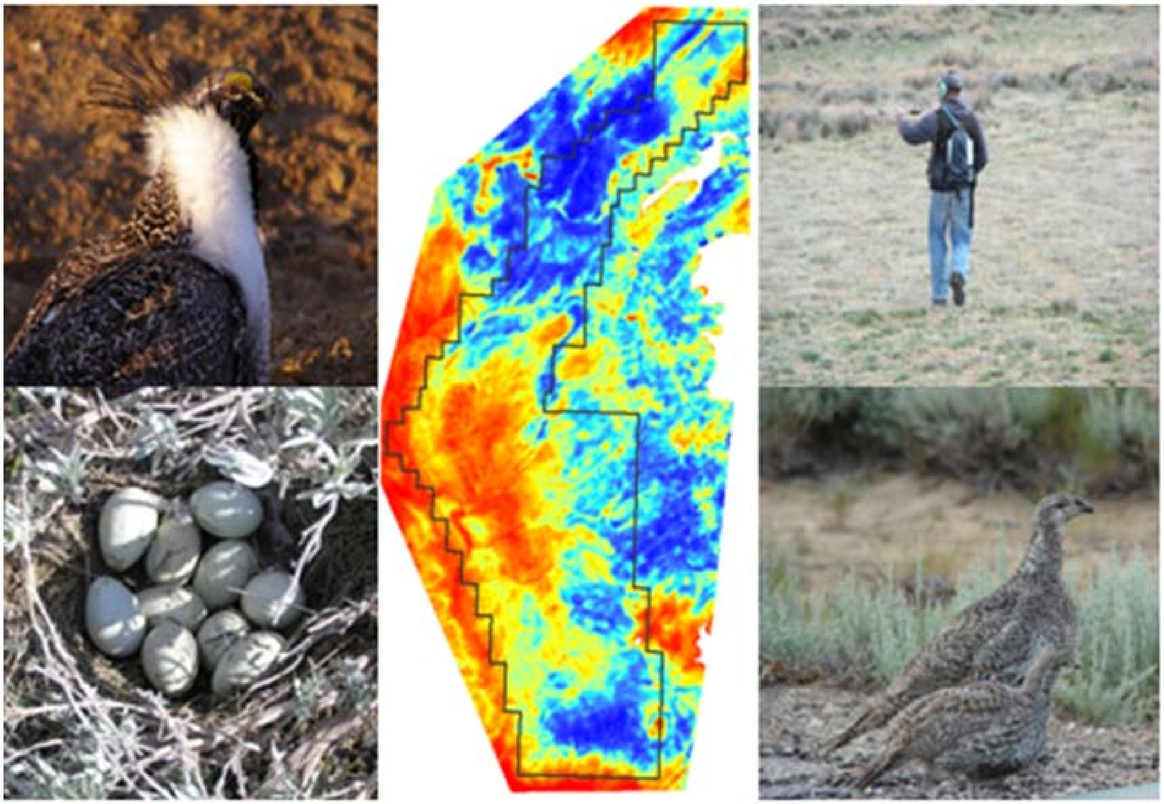
COMPLETION REPORT

Identifying Habitats for Greater Sage-Grouse Population Persistence within the Atlantic Rim, Wyoming



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Christopher P. Kirol and Jeffrey L. Beck, PhD

Department of Ecosystem Science and Management
University of Wyoming
Laramie, Wyoming 82071

EXECUTIVE SUMMARY

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, reducing the overall ability of populations to survive and reproduce within landscapes influenced by energy development. Our 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. To reach our objective we modeled habitat selection, as resource selection functions (RSFs), and habitat-specific survival using data from n = 167 female sage-grouse monitored within the ARPA landscape from May through August 2008 and 2009. By coupling the final habitat selection models and survival models, in a GIS framework, we spatially predicted habitat quality as well as sink and source habitats on the ARPA landscape. Over the reproductive season, we evaluated relationships between environmental (e.g., percent big sagebrush [*Artemisia tridentata*] cover, percent bare ground, and compound topographic 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 our analysis was mainly exploratory we used a sequential modeling approach and Akaike's Information Criterion (AIC) to identify the best-fit models and to make model inferences. We 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, we 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.

Our 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 RSF. 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, our results show that during the summer, non-brooding females did not show selection for the same habitat characteristics as females with broods. For example, unlike late brood-rearing, late non-brooding females were selecting 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 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.

Our survival results illustrated 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 our 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. Daily female survival increased as the distance to anthropogenic edge decreased. That is, female survival was predicted to be higher closer to anthropogenic edge.

Our results suggest 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 probabilities of occurrence. We then combined the RSF's for each life-stage to produce a final occurrence layer that spatially predicted the areas with the highest and lowest 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 into baseline survival probability functions (SPFs). This enabled us to predict survival in GIS on the basis of habitat-specific landscape-scale variables. We combined SPF's with fixed demographic rates into a lambda model that we projected back on the ARPA landscape. Our lambda layer thus predicted habitats that contributed to population surpluses or deficits. Our 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 ($\lambda \geq 1$).

We 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. Our 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. This shift is resulting in selected source becoming non-selected source habitats.

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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). 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 1998). 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.

Our 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 our 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, our 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 to offer a means of prioritizing habitat importance related to sage-grouse population persistence. Because our goal was primarily to predict and map habitat quality, we designed our analysis to identify the best-supported landscape predictor variables, but not to identify all landscape variables that potentially may be correlated to occurrence and/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 our 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 relate these models to survivorship functions, 2) quantify habitat as it relates to λ; thus predicting habitats that contribute to population surpluses or deficits, and 3) 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 between Rawlins and Baggs east of Wyoming Highway 789, 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

We 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). We 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). We 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). We 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 our study. Female sage-grouse were captured and handled according to University of Wyoming Institutional Animal Care and Use Committee approved protocols (03032009).

We located sage-grouse on the ground using hand-held receivers and 3-element Yagi antennas. We 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, we recorded locations for newly discovered nests by projecting the point with the GPS from a distance of ≥20 m. We 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, we mimicked the mooing sounds and loud movements of cattle when approaching a radio-marked bird (Walker 2008). Our field observations suggest that this technique reduced the frequency of bird flushing. After recording a nest location, we retreated in a meandering or zig zagging pattern to prevent predators from following human scent to the nest.

Nest monitoring.—We located radio-marked female sage-grouse at a frequency of ≤7 days throughout the nesting season. We 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. We used triangulation to monitor nests from a distance of ≥50 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, we monitored females to assess whether they were brooding; a brooding female indicated a successful nest. If possible, we determined the number of hatched eggs by counting the number of egg shell caps. We 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 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 we 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.—We 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, we 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). We considered the brood the experimental unit, rather than individual chicks. Therefore, a brood was considered to have survived if we 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, we 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. We 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. Furthermore, 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. We 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.—We monitored female survival by field observation from early May through August 2008 and 2009. We 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. We 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

The predictor variables we considered in our landscape analysis were based on *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 we 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. We performed spatial analyses with ArcGIS 9.3 software (Environmental Systems Research Institute, Redlands, California, USA). We 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); we thus theorized that this was also true for survival. Correspondingly, we 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 the reproductive season. 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 our 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 we examined in occurrence and survival modeling are described in Table 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). We assessed 3 secondary habitat characteristics: percentage bare ground, herbaceous cover, and litter; 3 primary habitat characteristics, percentage sagebrush, big sagebrush, and Wyoming big sagebrush canopy cover; and a shrub height estimate with spatial data developed by the United States Geological Survey (USGS) designed for sage-grouse habitats in Wyoming (Homer et al. 2012). We also 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.

We 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 our study. Furthermore, we 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), we classified conifer stands to create a categorical variable we termed Forest. The variable Forest was verified using NAIP imagery. Utah juniper (*Juniperus osteosperma*) was the dominant conifer in our study area.

We 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). We 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).. We quantified anthropogenic variables at each spatial scale including distances (km) from grouse use and random available locations to anthropogenic edge (Distedge), nearest improved gravel road (Disthaul), nearest unimproved road (dist2-track), nearest fence (Distfence), and nearest energy well (Distwell); total linear distances (km) within each spatial scale for fences (Fence), improved gravel roads

(Haulrd), and unimproved roads (2-track); counts of energy wells (Well) and visual energy wells (Vwell); and the percentage of total surface disturbance (Dstbarea) 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). We evaluated potential influences of energy infrastructure and access roads in a temporal context because energy development was ongoing over the duration of our 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. We 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, we used 2009 NAIP imagery to inspect the analysis area to validate well and road locations. We compiled linear distance variables (Haulrd, 2-track, and Fence) using Geospatial Modeling Environment (GME) tools (Hawthorne 2010).

We 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. We 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.

We 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 our study area.

We quantified the human footprint or percentage surface disturbance, that is, areas of bare ground areas resulting from complete vegetation removal in our study area. To accomplish this, we 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. We 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), we assessed possible relationships between fences and survival or possibly occurrence. Fence data were provided by the BLM-Rawlins Field Office and mostly consisted of grazing allotment boundary and cross fences.

Experimental Design and Statistical Analysis

***Occurrence analysis.*—**We 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:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots\ldots + \beta_p x_p) \quad (1)$$

Where w is the RSF for the predictor variables, x_i, and the β_i,s are coefficient estimates for each predictor variable, and w(x) is the probability proportional to use (Manly et al. 2002).

We incorporated a Type I Design where we 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 occurrence (Manly et al. 2002, Thomas and Taylor 2006). We 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). We 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. We 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, we 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 our logistic regression analyses we down weighted available units to be proportional to used units (Aldridge and Boyce 2007, Carpenter et al. 2010).

We used a 2nd-order Akaike's Information Criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989) for model support inference. In our decision to use AIC_c, we followed the tenet that $n/K < 40$, where n was the sample size, and K was the number of parameters for model selection. In our 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, we 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 we 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, we 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). We used variable screening to remove unsupported predictor variables, thereby reducing the likelihood of overfitting models in our model selection process (Burnham and Anderson 2002, Arnold 2010).

We 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, we 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). We 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 $AICc$ score was retained. On occasion, findings from previous research informed the decision to retain a variable (Aldridge and Boyce 2007, Doherty et al. 2010). We did not permit correlated variables to compete in the same model at any level of model selection.

Survival analysis.—We explored relationships between landscape-scale preditor variables and sage-grouse survival or risk for 3 distict life-stages: nesting, brooding, 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 incoporating 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 our 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 our analysis:

$$h(t|\mathrm{x}_t) = h_0(t)\ \exp(\beta_{i1}\,\mathrm{x}_{i1} + \beta_{i2}\,\mathrm{x}_{i2} + \ldots \beta_{in}\,\mathrm{x}_{in}) \qquad (2)$$

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.

Our 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, we 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 our female and brood Cox models, a “counting-process” method was used that allowed time-dependent variables to be distributed into time intervals (Allison 2010). We 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. 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), we 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 we 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. We 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 also accounts for possible errors associated with determining the exact point of an event. 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. When the fate of an individual or brood was unknown they were right-censored.

We calculated survival estimates for each of these demographics 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 lambda model. Following the fitting of the Cox model and after calculating K-M survival estimates for each demographic, we 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:

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

Where, $S_0(t)$ is the K-M survival estimate at the end of the survival period for that demographic (nest [$t = 28$ days], brood [$t = 40$ days], and female summer [$t = 110$ days]), and $\mathrm{x}'\beta$ is the variable adjusted coefficient from the Cox model. The SPF allowed us to transform daily risk (e.g., daily risk of nest loss) derived from the Cox models, to survival probabilities corresponding to the entire demographic period that we were able to map back on the landscape.

We calculated influence statistics for each variable to determine if any observations were unusually influential in survial models because they had inflated residuals or leverage (Hosmer and Lemeshow 1999, Allison 2010). We did not remove any observations following this diagnostic procedure. We used a derivation of the AIC_c technique adapted for survival modeling ($\mathrm{AIC}_{\mathrm{SUR}}$) to select the best supported models of survival (Liang and Zou 2008). In the same manner as our occurrence modeling effort, we examined 3 spatial scales to determine the scale that best explained survival by testing each variable-scale individually and comparing ($\mathrm{AIC}_{\mathrm{SUR}}$) scores (Arnold 2010, Carpenter et al. 2010, Doherty et al. 2010) for scale-dependent variables. We retained the variable scale with the lowest ($\mathrm{AIC}_{\mathrm{SUR}}$) score. After selection of the appropriate variable scale, we 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, we assessed multicullinearity with a Pearson's correlation matrix and variance inflation factor (VIF) scores combined with tolerance (*t*) values. We omitted variables from correlated groups when (*r*) was ≥ |0.6| or (*t*) was ≤ |0.40| (Allison 2009, SAS Institute 2009). Finally, we checked for stability and consistency of regression coefficient estimates when variables were moderately correlated (|0.3|≤ *r* ≥ |0.6|). When variables were correlated, the variable with the lowest $\mathrm{AIC}_{\mathrm{SUR}}$ score was retained unless findings from previous research informed our decision to retain a certain variable (Aldridge and Boyce 2007). We 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, the variables influence is proportionality over time (Le 1997, Hosmer and Lemeshow 1999). We tested the variables in our top survival models individually for proportionality (Le 1997) and we assessed log (-log(survival) by log(time)) plots to confirm that the proportional hazards assumption was not violated.

Model Development

Our modeling objective was to use our sample of female sage-grouse from the ARPA population to find the best-supported predictor variables. Consequently, we used the variables with the most predictive potential to make population-level inference regarding occurrence and survival; therefore, our final RSFs or SPFs contained only the most predictive variables (Boyce et al. 2002). We evaluated the relative importance of predictor variables for occurrence and survival at 3 spatial scales and within 2 variable subsets. Because our research was mainly exploratory, we 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 we explored all variable combinations (Burnham and Anderson 2002). At this stage, we 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, we 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 we 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 we assessed variable importance by summing Akaike model weights across models that included the variable of interest (Arnold 2010). We 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 ($\geq$ 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), we allowed models to compete across subsets to see if additional information produced a more parsimonious model (Arnold 2010). We 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, we 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) we used multi-model inference to calculate final parameter coefficients, 95% confidence intervals, odds ratios, and risk ratios within confidence sets. We determined confidence sets for those models where Akaike weights were within 10% of the top model (Burnham and Anderson 2002). We explored quadratic transformations because the quadratic form of a variable can often identify non-linear relationships that would otherwise go undetected. We followed the convention that the linear term was always included in the model with the quadratic. At the final level of model selection we further filtered variables with poor support for a true statistical difference between groups that had parameter estimates with 95% CIs that considerably overlapped (Hosmer and Lemeshow 1999; 2000). Yet, in a few instances we 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).

Our 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, we 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

We assessed goodness-of-fit for our final occurrence and survival models using the likelihood ratio χ^2 test statistic (Hosmer and Lemeshow 1999, 2000). We did not have independent data to test the predictive accuracy of our final models. As such, for our occurrence models, we performed a 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, we 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, we 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 our 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). We conducted all statistical analyses with Statistical Analysis Software (SAS), version 9.2 (SAS Institute 2009). We report all K-M survival estimates as estimate ± standard error [SE]).

Mapping Ecological Models on the ARPA Landscape

We mapped our 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 the final female summer occurrence map the GIS layers specific to nesting, early brooding, early non-brooding, late brooding, and late non-brooding RSFs were combined as a means to classify habitat importance on the basis of female occurrence during different life-stages throughout the summer. For each RSF we distributed our predicted occurrence probabilities into quartiles on the basis of percentile breaks in predicted probabilities (Sawyer et al. 2006). We 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 merged into a single layer; thus, every cell contained a summer occurrence probability score. 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 has an occurrence probability based on the combined values derived from each of the different life-stage layers.

Holloran and Anderson (2004) provided a model that combines sage-grouse demographics into an estimate of lambda for grouse inhabiting 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 our research objective to identify habitats contributing to sage-grouse population persistence in the ARPA, we incorporated this model to predict habitat quality on the landscape in terms of population growth. Thus we integrated our SPFs specific to nests, broods, and adult female summer as well as our K-M female winter survival estimates and nest initiation rates into the lambda model that took the following form:

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

Where, *Nest Initiation* was a fixed value from the mean of our initiation rates from 2008 and 2009. *Nest Survival* was a shifting value, based on the final predictor variables, from our nest SPF; *Brood survival* was a shifting value from our 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 shifting value from our female summer SPF; and ♀*Adult Female Winter Survival* was a fixed value from our K-M female winter survival estimate. For the demographic rates that did not come directly from our research (♀*Chick* and *Chick Winter Survival*), we were conservative in our estimation of lambda 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 our K-M female winter survival estimate and nest initiation rate in addition to demographic rates from the sage-grouse literature into the lambda model (Equation 4). The lambda model was then mapped onto the ARPA landscape to predict lambda as a function of variability in habitat quality. The map is adjusted per each 30-m cell as a result of changing lambda model values that are driven by habitat-specific changes in the SPFs for nest, brood and female summer.

The combination of our female summer occurrence map and lambda map formed our 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 lambda map. We classified areas as high quality (highest 25% of predicted probabilities for summer occurrence and lambda**)**, moderate-high quality (51 to 75% predicted probabilities for summer occurrence and lambda), moderate-low quality (26 to 50% predicted probabilities for summer occurrence and lambda), and low quality (lowest 25% of predicted probabilities for summer occurrence and lambda). Second, predicted sink and source habitats were mapped on the ARPA landscape by grouping occurrence and survival into quartiles based on the lambda 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). These source-sink habitat categories include selected source, non-selected source, selected sink, and non-selected sink habitats.

RESULTS

In spring 2007 and 2008 we captured 90 radio-marked female sage-grouse. In 2009, we captured 71 female sage-grouse and included those birds with 6 birds from 2007 and 2008 that still had functioning collars for a total of 77 birds. During 2008 and 2009 we 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, 282 m radius), big sagebrush canopy cover (Bsage) and litter (Litter) were strongly correlated with nest occurrence (Table 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 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 (Figure 1). The likelihood ratio χ^2test statistic suggested that the nest RSF model had good fit ($\chi^2_4 = 33.80$, $P < 0.001$). 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, we 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 8). The variability in percent herbaceous cover within a 1-km^2 area (564 m radius) was negatively correlated with selection during the early brood-rearing period, suggesting selection for habitats with more homogenous herbaceous cover. Within 564 m 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 1).

The anthropogenic model combined with the environmental model substantially increased model support (w_i = 0.99; Table 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 564 m 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 1260 m 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 (Figure 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 282 m (Litter_0.25), less variability in NDVI values (NDVIsd_1.0) and lower terrain roughness values (VRM_1.0) within 564 m (Table 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 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. We rescaled and mapped the final early non-brooding RSF model including the above mentioned environmental and anthropogenic variables to the ARPA landscape (Figure 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 and 3. Within 282 m 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, we 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, we found that habitat selection by late brood-rearing females and late non-brooding females also diverged (Table 8). Because of the predicted differences in occurrence based on our modeling, we 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 1260 m. 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 we believe the increase was sufficient to justify including these anthropogenic variables in the final RSF model (Table 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 (Figure 4).

Multiscale environmental predictor variables were supported in our 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 282 m (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 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 (Figure 5). Differences in spatial selection patterns are evident when comparing the mapped late non-brooding RSF with the late brooding RSF (see Figures 4 and 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 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 (Figure 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 1260 m 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 282-m 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 examined in our nest survival modeling proved predictive. Specifically, no 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. We 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 (Figure 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 11). The accumulative environmental variables relating to daily brood survival included the percent herbaceous cover (Herb) and Shrbhgtsd. Herbaceous cover within a 564 m 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 (Figure 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 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 (Figure 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 on average using habitats with 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%. We 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 (Figure 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 564 m 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 (Figure 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% increase 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 $7.05 \times 10^{-4} \pm 6.0 \times 10^{-5}$ 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 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 (Figure 10).

We rescaled the combined female summer occurrence layer to spatially display probabilities of female summer occurrence (Figure 6). The lambda map is displayed as a continuum from the highest predicted lambda value (λ = 1.22) to the lowest (λ = 0.34; Figure 12). Of the sage-grouse habitat within the ARPA, 87% was predicted to have a λ value $\geq$1. The habitat quality map derived from female summer occurrence and lambda represents a continuous prediction of habitat quality and suggests that about 50% of the available habitat is moderate to high quality (Figure 13). The spatial quantification of source and sink habitats on the ARPA landscape (Figure 14) indicated that of the sage-grouse habitat within the ARPA, the source-sink map predicted 40% as selected source, 42% as non-selected source, 14% as selected sink, and 4% as non-selected sink (Figure 14).

DISCUSSION

Our analysis provides critical information for persistence of greater sage-grouse within the ARPA in south-central, Wyoming. In our analyses we 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 our GIS variables. We 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. We used our 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 influencing habitat selection through all summer life-stages of female sage-grouse. Anthropogenic variables do not seem to be broadly driving reduced 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. Our findings do indicate that total surface disturbance ≥4% results in reduced brood survival. However, our 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 our 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, we 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). Our 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 our 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 our 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, we found that sage-grouse fitness parameters were scale-dependent. For example, our 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 our 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, litter was also positively related to nest habitat selection. To our knowledge no other landscape-scale sage-grouse research has identified this relationship. Although, 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, our results show that during summer females without broods were not selecting the same habitats as females with broods (Figures 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.

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 564 m 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 (Figure 4).

Our 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. 1999, Connelly et al. 2011) we found that sage-grouse nest success had a positive relationship to sagebrush canopy cover. Specifically, we found that as Wyoming big sagebrush canopy cover within a 1260 m radius (5-km^2) increased so did the probability of nest survival. Sagebrush communities in our 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), we 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 our 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. We are 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 our brood survival and adult female survival models, but the mechanisms were quite different. We found that brood survival began to decrease when a threshold of about 4% surface disturbance within a 564-m radius of brood-rearing habitat was reached and brood-rearing habitat becomes considerably riskier at approximately 6% surface disturbance (Figure 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 (Figures 8 and 9). Aldridge and Brigham (2007) found that daily chick survival (56-days) decreased with greater well densities also within a 564 m radius. In Wyoming, Holloran et al. (2010) found that yearling females and males that were brooded within natural gas development buffers (>3 km) had 30.6% and 45.3%, respectively, lower annual survival than those that were not brooded within natural gas development buffers. 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, we found that adult female survival decreased with a greater distance from anthropogenic edge. That is, our results indicate that female survival was higher in many of the same habitats where CBNG development was occurring (Figure 10). Thus accumulative exposure to CBNG modified habitats throughout the summer may not have been detrimental to adult female survival. We 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 we found predictive of female summer adult survival. We found that the level of terrain roughness at our largest landscape scale (VRM_5.0) was negatively related to adult female summer survival. Thus, habitats with greater amounts of topographic relief at our largest landscape scale were riskier habitats to female sage-grouse during summer. In the ARPA this would include several prominent drainage basins and ridgelines. 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 we found no evidence of reduced adult female summer survival at the level of CBNG development that occurred during our study.

The lambda 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, lambda 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 lambda 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. Our lambda 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 lambda model and corresponding map suggest that CBNG development was not increasing the amount of habitat with lambda <1 unless surface disturbance exceeded approximately 4% at which the lower predicted brood survival caused lambda to fall below 1. Furthermore, our 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 recognizing potential fitness consequences and avoiding these areas.

It is important to note that the predicted lambda values and corresponding maps we provide have limitations. One limitation is that mechanisms we did not measure directly such as sage-grouse immigration or emigration, predator intensity, and climatic differences are not considered in the lambda model. A second limitation is that the model may over predict lambda 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, we believe we 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 lambda model. Because our habitat quality map is independent of the lambda threshold of 1 (e.g., lambda 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 (Table 12).

Our 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 well density. In fact, our models predict that almost half of the source habitat is falling into the non-selected source category. Therefore, a large percentage of source habitats are contributing little to recruitment because of being largely unoccupied.

Our 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. Our results suggest that occurrence and fitness are influenced by environmental and anthropogenic habitats at multiple spatial scales. Our source-sink map suggests that the ARPA currently has abundant source habitat. Yet, our 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.

Our research shows 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. Our 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 (Figures 13 and 14).

Anthropogenic development in high occurrence brood-rearing habitats (Figures 2 and 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. We 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 we provide.

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Table 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

Table 1. Continued

	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

Table 1. Continued

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. 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 3. Model category combinations (environmental and anthropogenic) considered in our 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 our sequential modeling approach. Refer to Table 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 4. Model category combinations (environmental and anthropogenic) considered in our 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 our sequential modeling approach. Refer to Table 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 5. Model category combinations (environmental and anthropogenic) considered in our 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 our sequential modeling approach. Refer to Table 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 6. Model category combinations (environmental and anthropogenic) considered in our 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 our sequential modeling approach. Refer to Table 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 7. Model category combinations (environmental and anthropogenic) considered in our 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 our sequential modeling approach. Refer to Table 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 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	1.121
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^{2}[b]	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]

Table 8. Continued

VRM	1.0	–571.902	–836.810	–306.994	<0.001	0.423[e]
Anthropogenic model						
Two-trackdist^2[b] (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^2[b]	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 282	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 1260	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 9. Model category combinations (environmental and anthropogenic) considered in our 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 our sequential modeling approach. Refer to Table 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 10. Model category combinations (environmental and anthropogenic) considered in our 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 our sequential modeling approach. Refer to Table 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 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	0.085
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	2.05

[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.

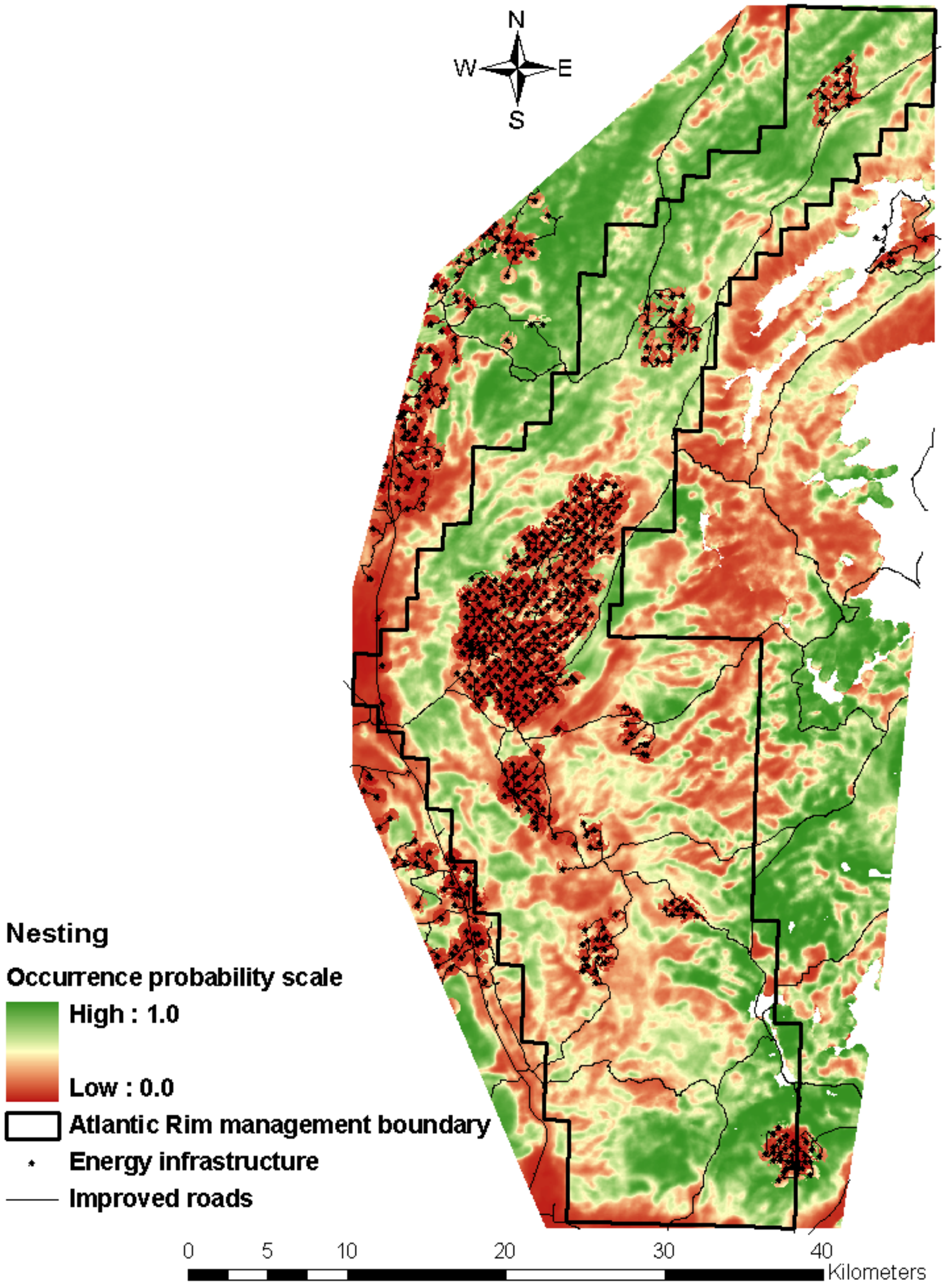

Figure 1. Predicted probability of nesting sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

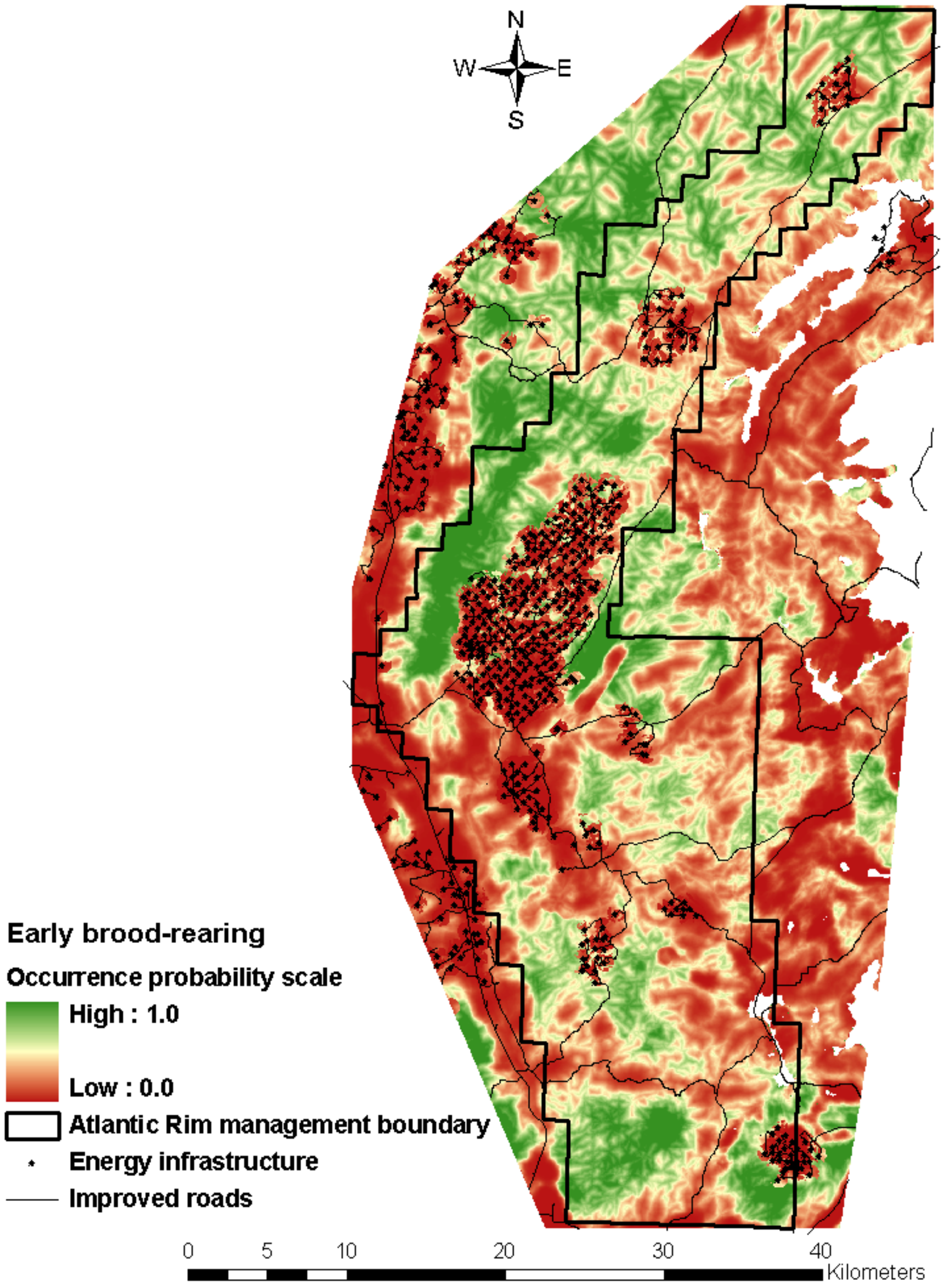

Figure 2. Predicted probability of early brood-rearing sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

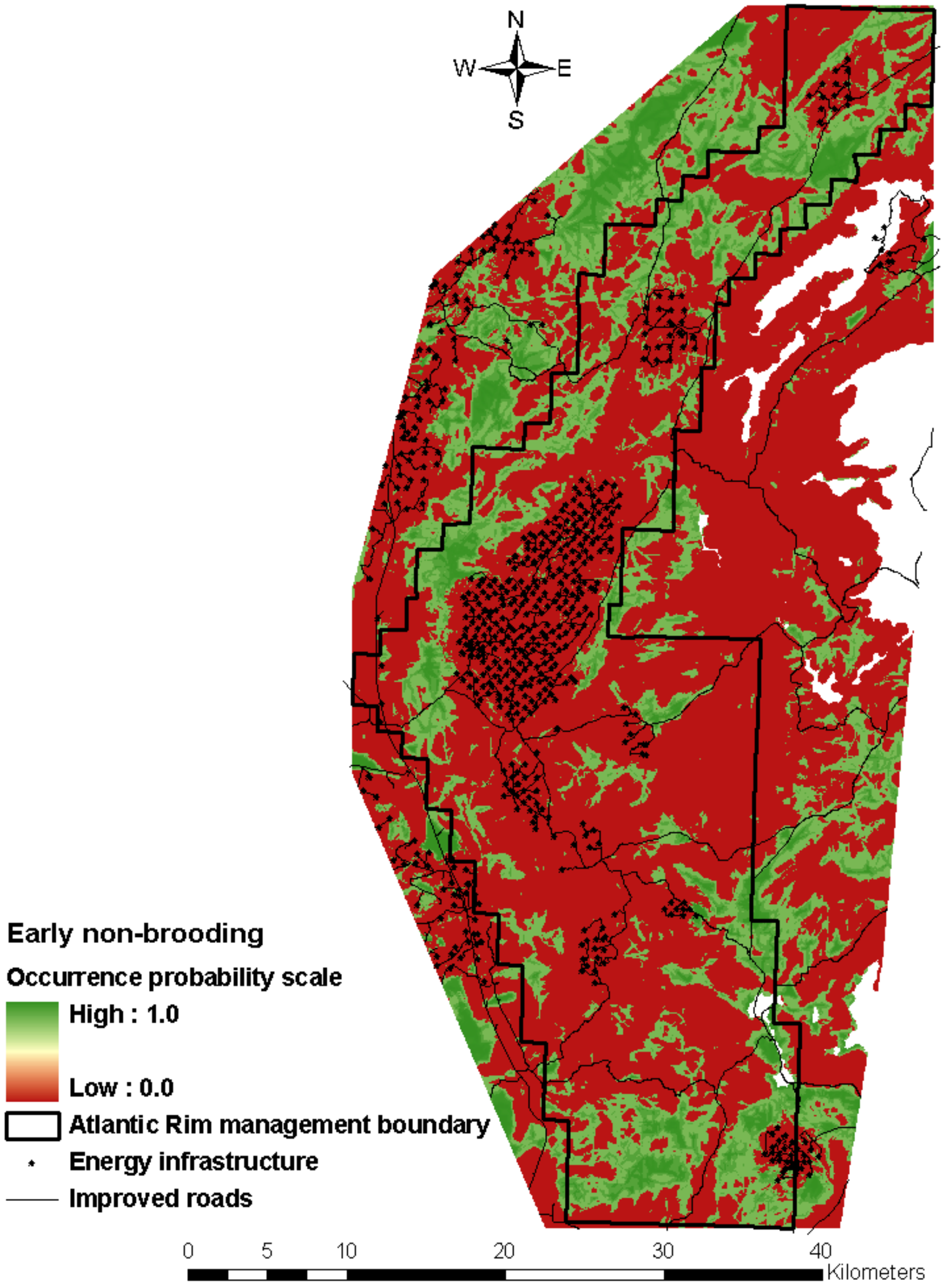

Figure 3. Predicted probability of early non-brooding sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

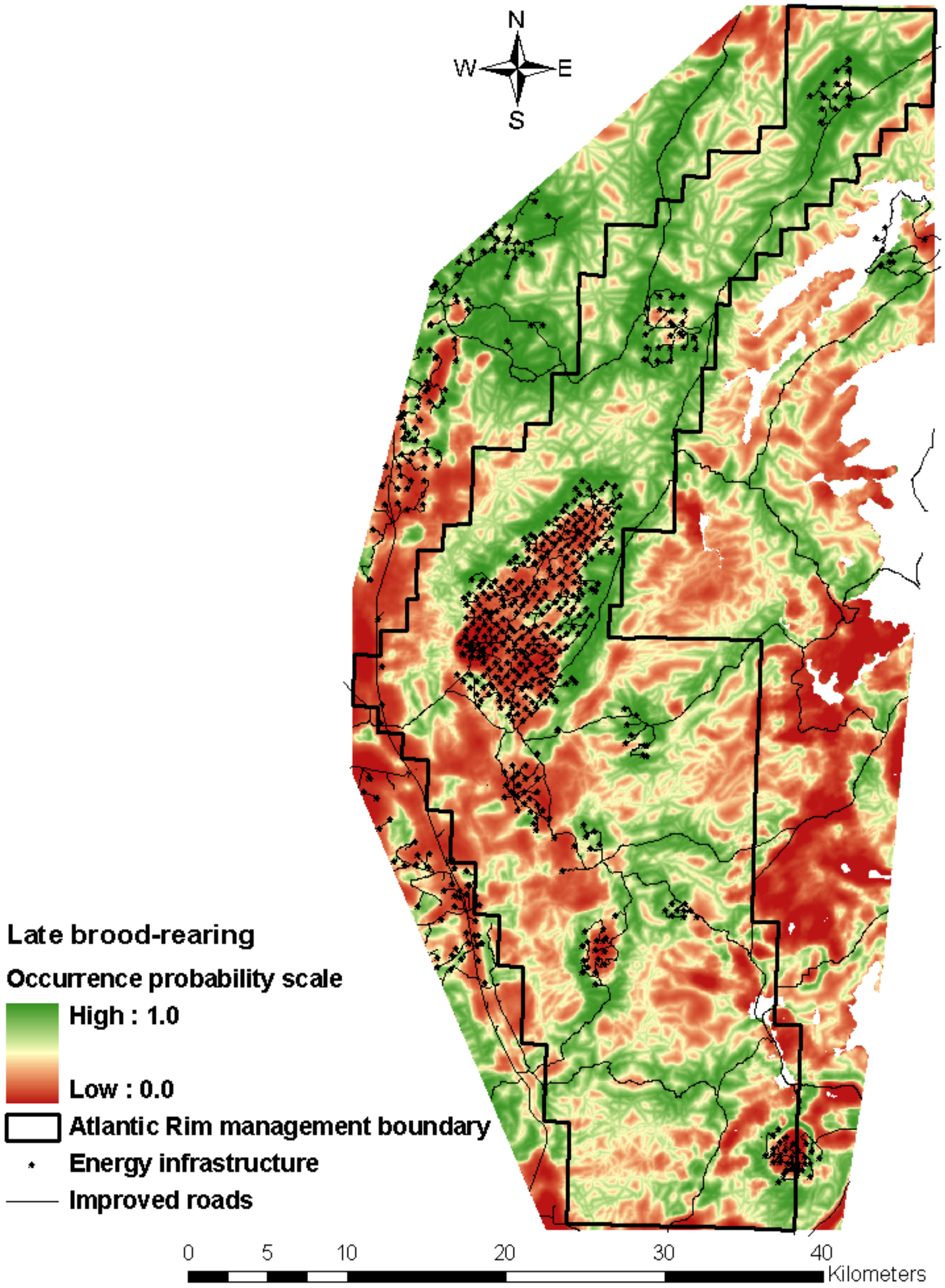

Figure 4. Predicted probability of late brood-rearing sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

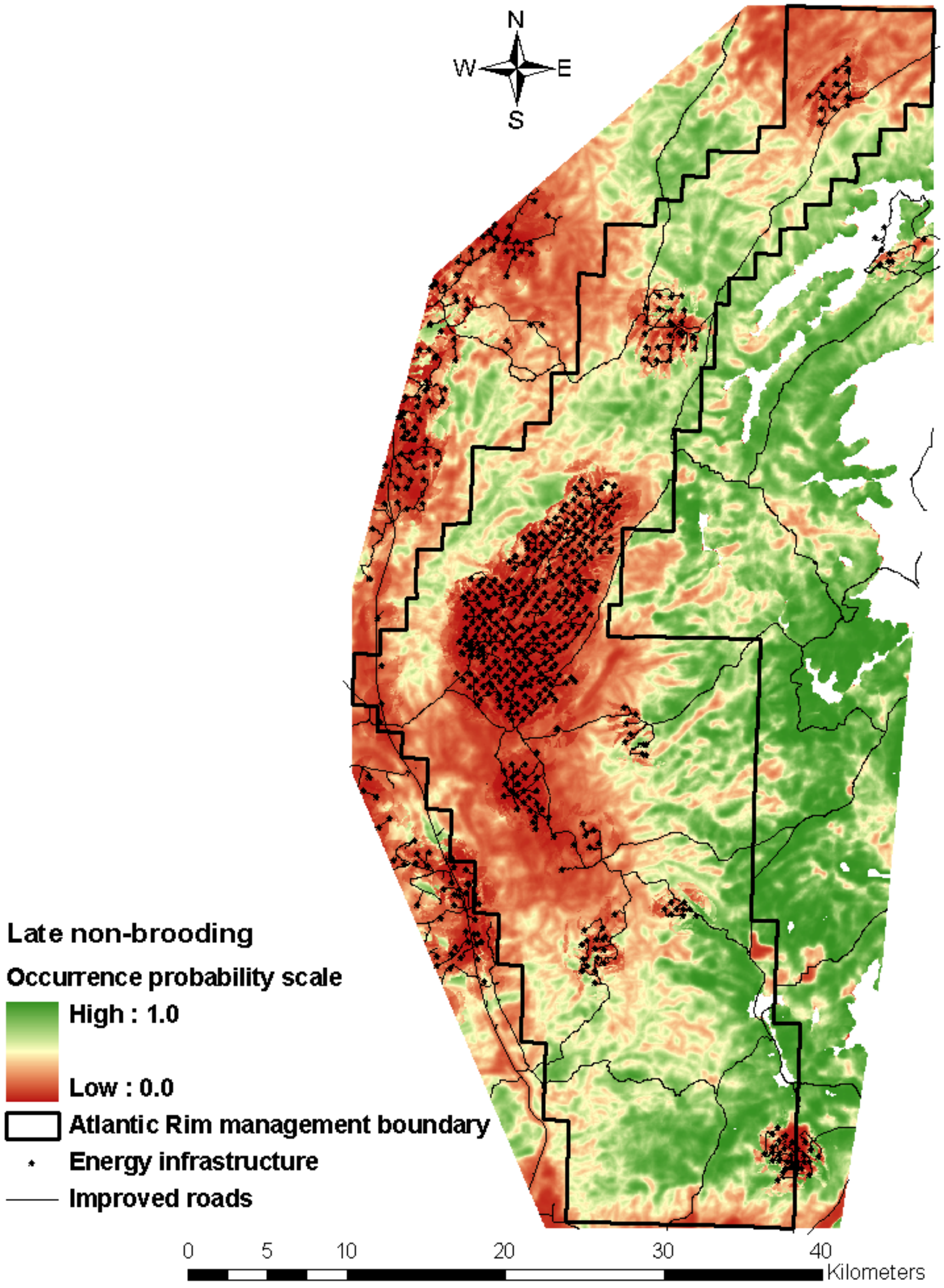

Figure 5. Predicted probability of late non-brooding sage-grouse occurrence in south-central, Wyoming, USA, 2008 and 2009. The map displays a rescaled (0 to 1) resource selection function with 1 (green) being the highest and 0 (red) being the lowest probability.

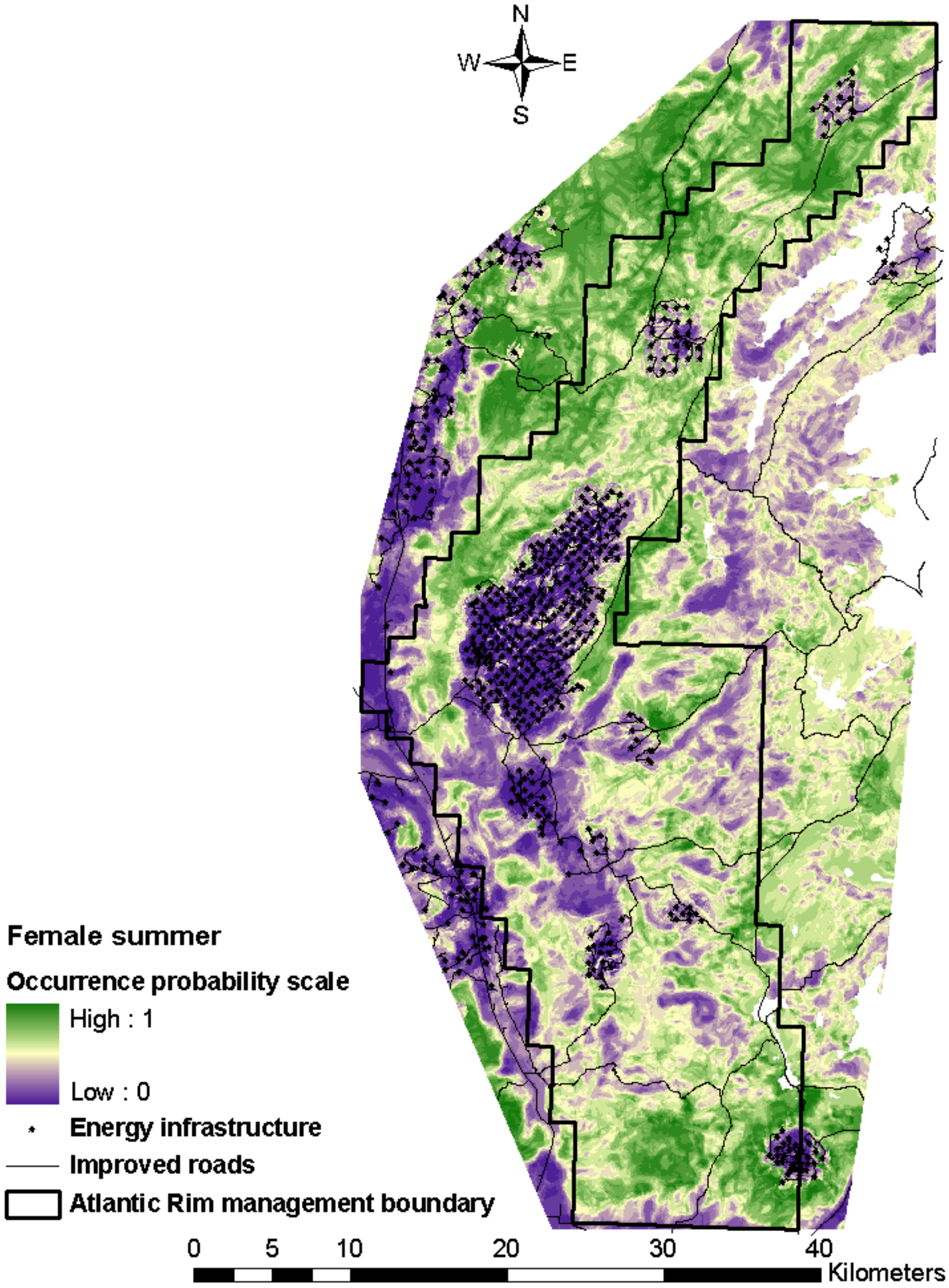

Figure 6. Predicted probability of female sage-grouse occurrence throughout the summer in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of selection by females with 1 (blue) being the highest and 0 (orange) being the lowest probability.

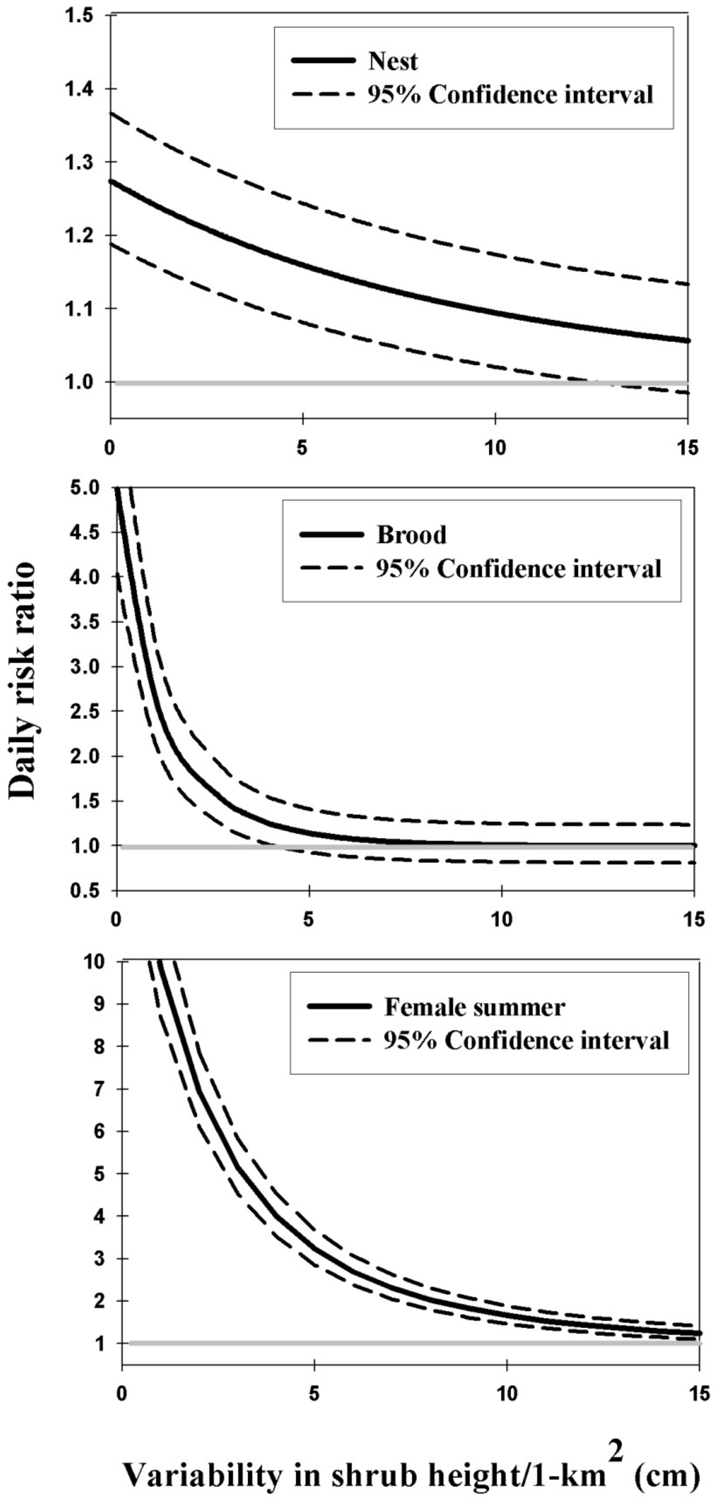

Figure 7. Shrub height variability and daily survival risk for nest, brood, and adult female summer daily survival at the 1-km^2 scale, south-central, Wyoming, USA, 2008 and 2009.

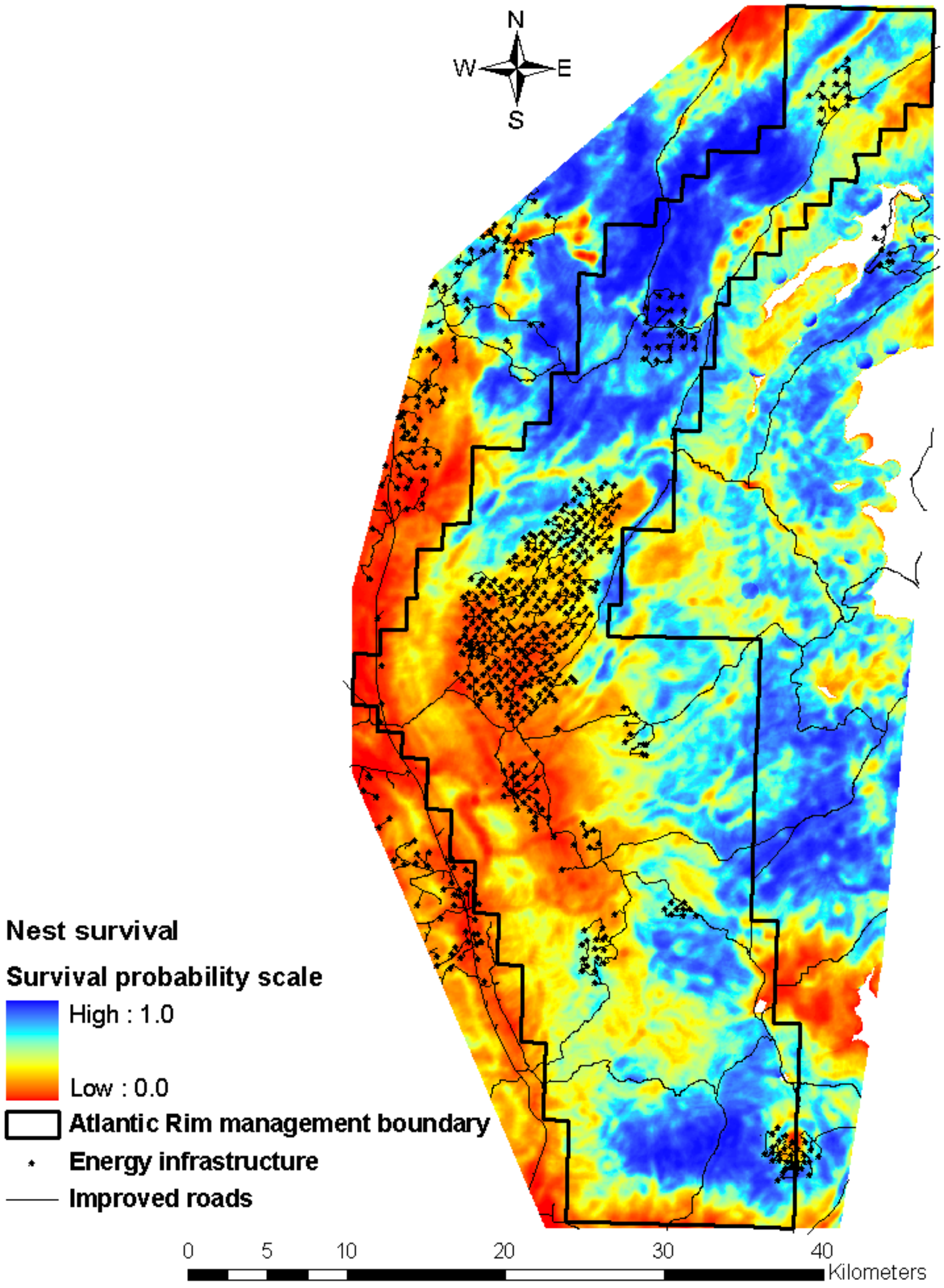

Figure 8. Predicted probability of sage-grouse nest survival to 28 days. Mapped as a survival probability function in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of 40-day brood survival with 1 (blue) being the highest and 0 (red) being the lowest probability.

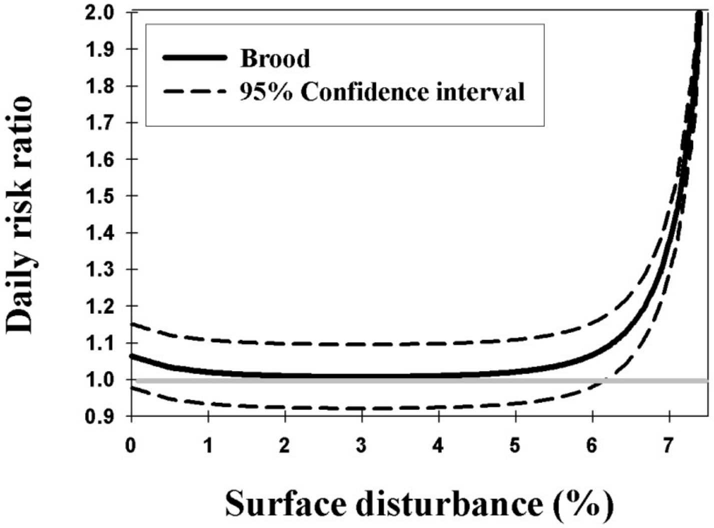

Figure 9. Risk of daily brood loss over successive brood locations as a function of the percent of surface disturbance area at the 1-km^2 scale, south-central, Wyoming, USA, 2008 and 2009.

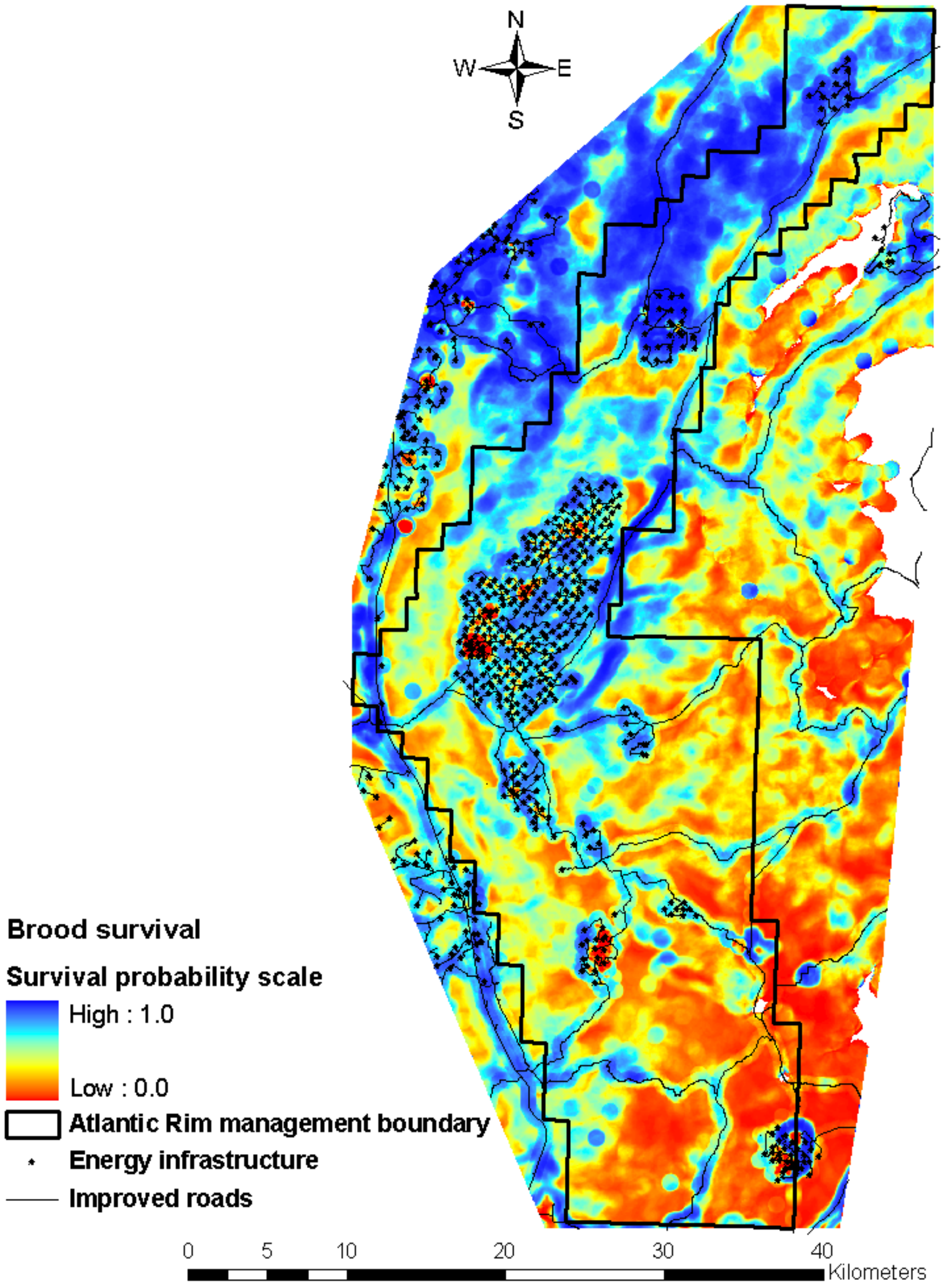

Figure 10. Predicted probability of sage-grouse brood survival to 40 days. Mapped as a survival probability function in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of 40-day brood survival with 1 (blue) being the highest and 0 (red) being the lowest probability.

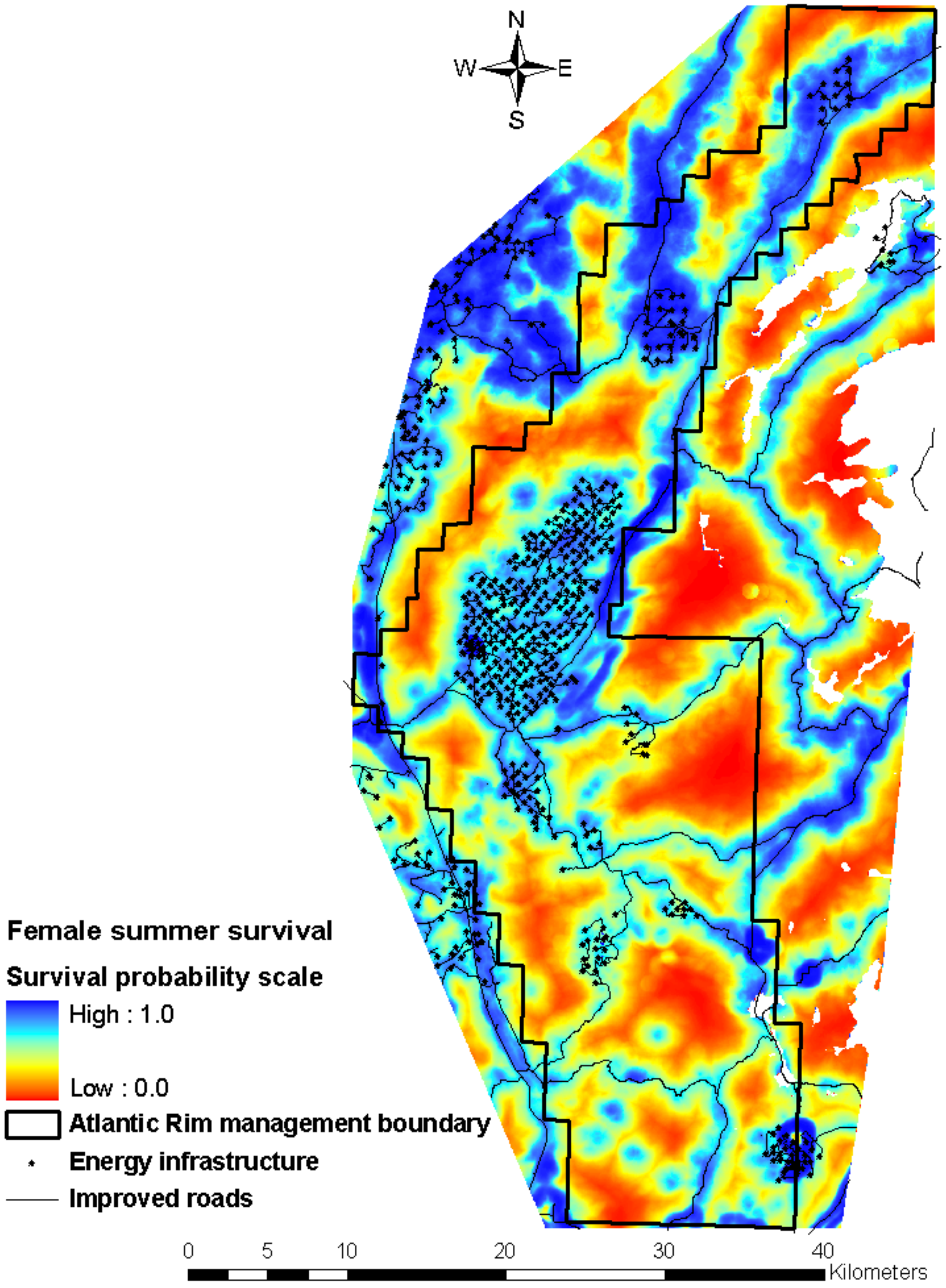

Figure 11. Predicted probability of sage-grouse summer female survival to 110 days. Mapped as a survival probability function in south-central, Wyoming, USA, 2008 and 2009. The map displays the relative probability of 110-day brood survival with 1 (blue) being the highest and 0 (red) being the lowest probability.

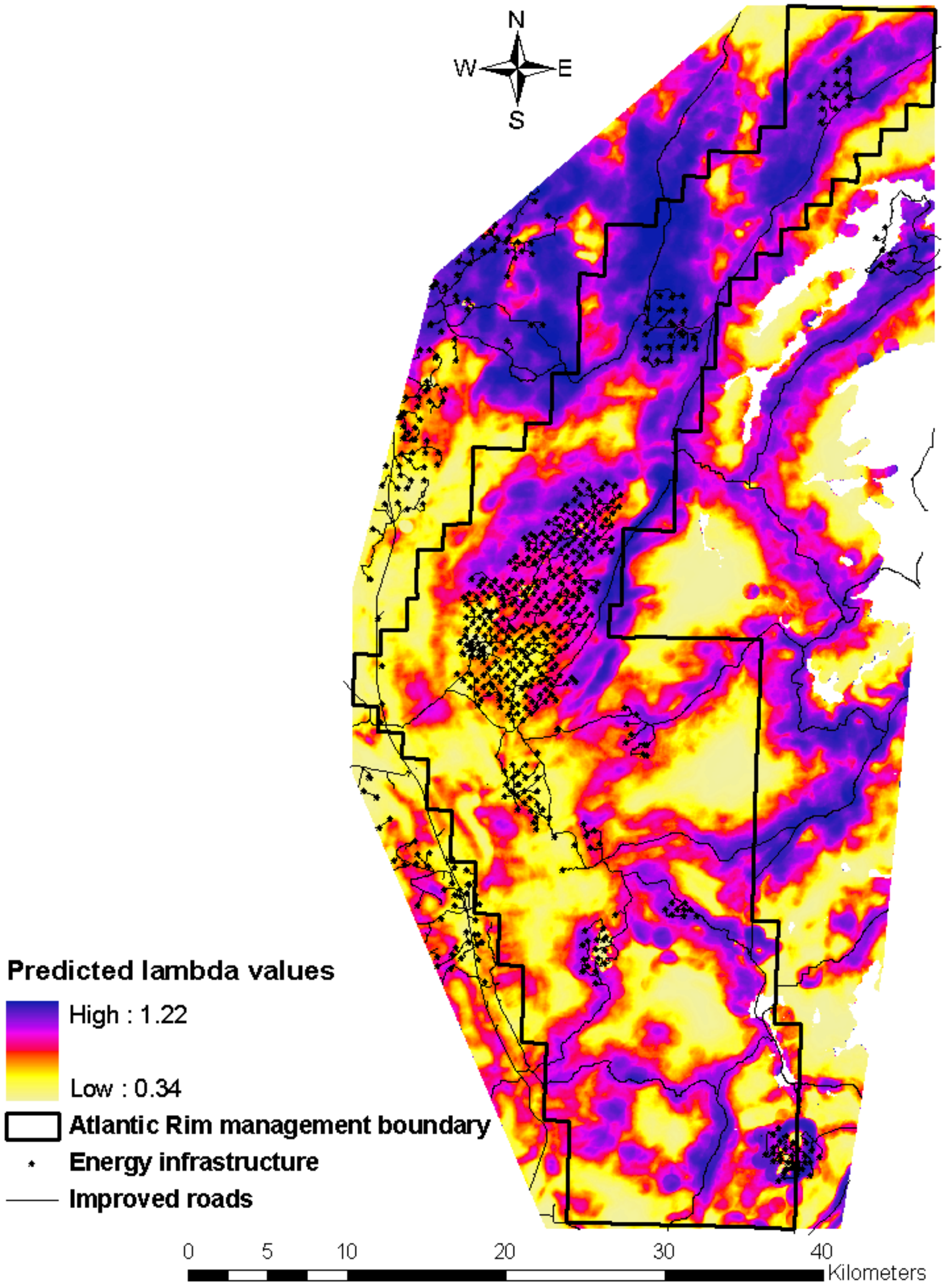

Figure 12. Predicted sage-grouse population growth rate (lambda) based on variable adjusted survival probability functions specific to nest, brood, and summer female (brooding or non-brooding) survival in south-central, Wyoming, USA, 2008 and 2009, as well as fixed demographic rates. The map displays a continuum from the highest predicted lambda value (dark blue) to the lowest (light yellow).

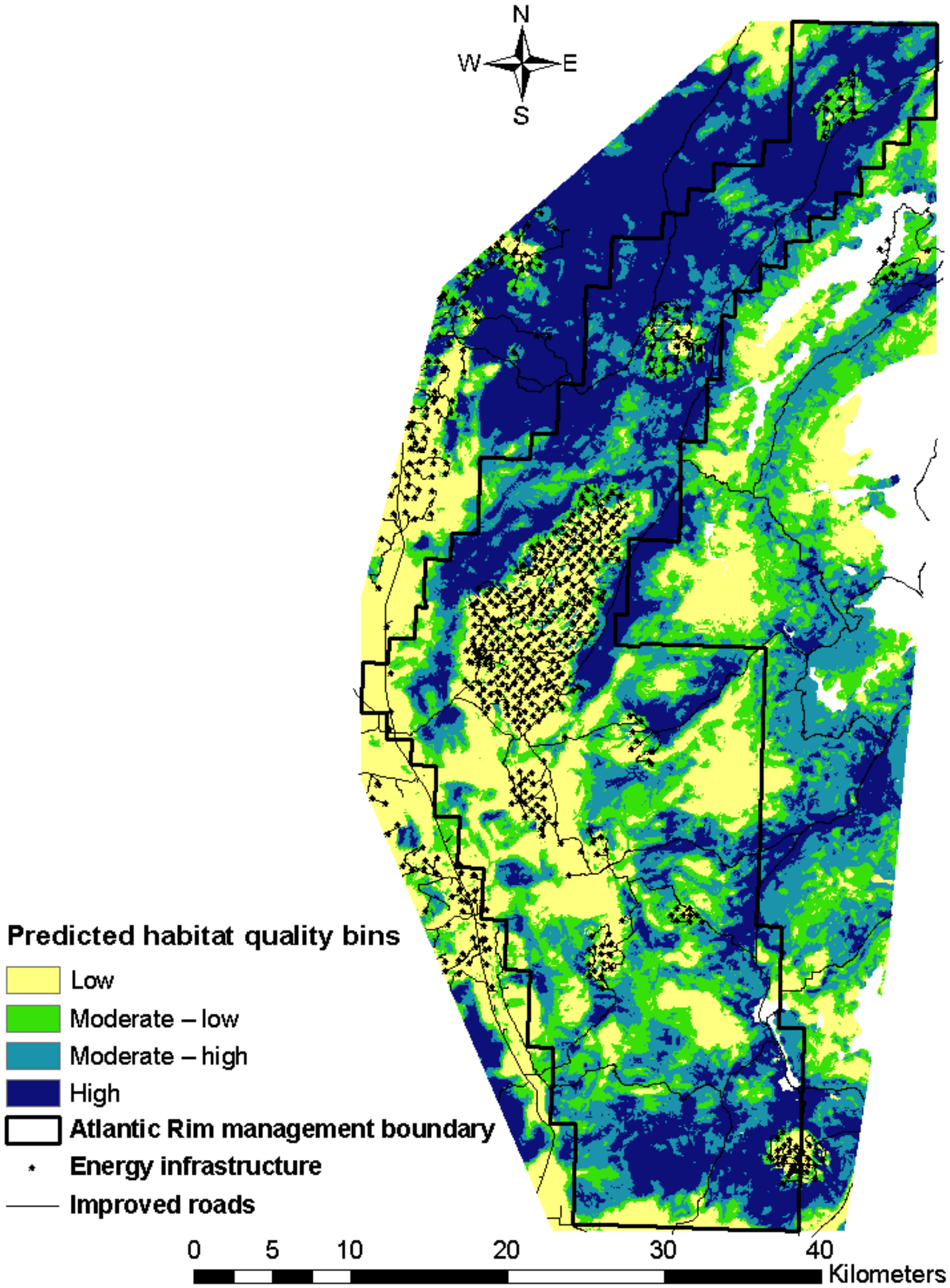

Figure 13. Predicted habitat quality (female summer occurrence + lambda prediction) for sage-grouse during the reproductive season in south-central, Wyoming, USA, 2008 and 2009. The map displays habitat quality bins derived from the distribution of female summer occurrence and lambda predictions divided into quartiles containing 25 percentile values.

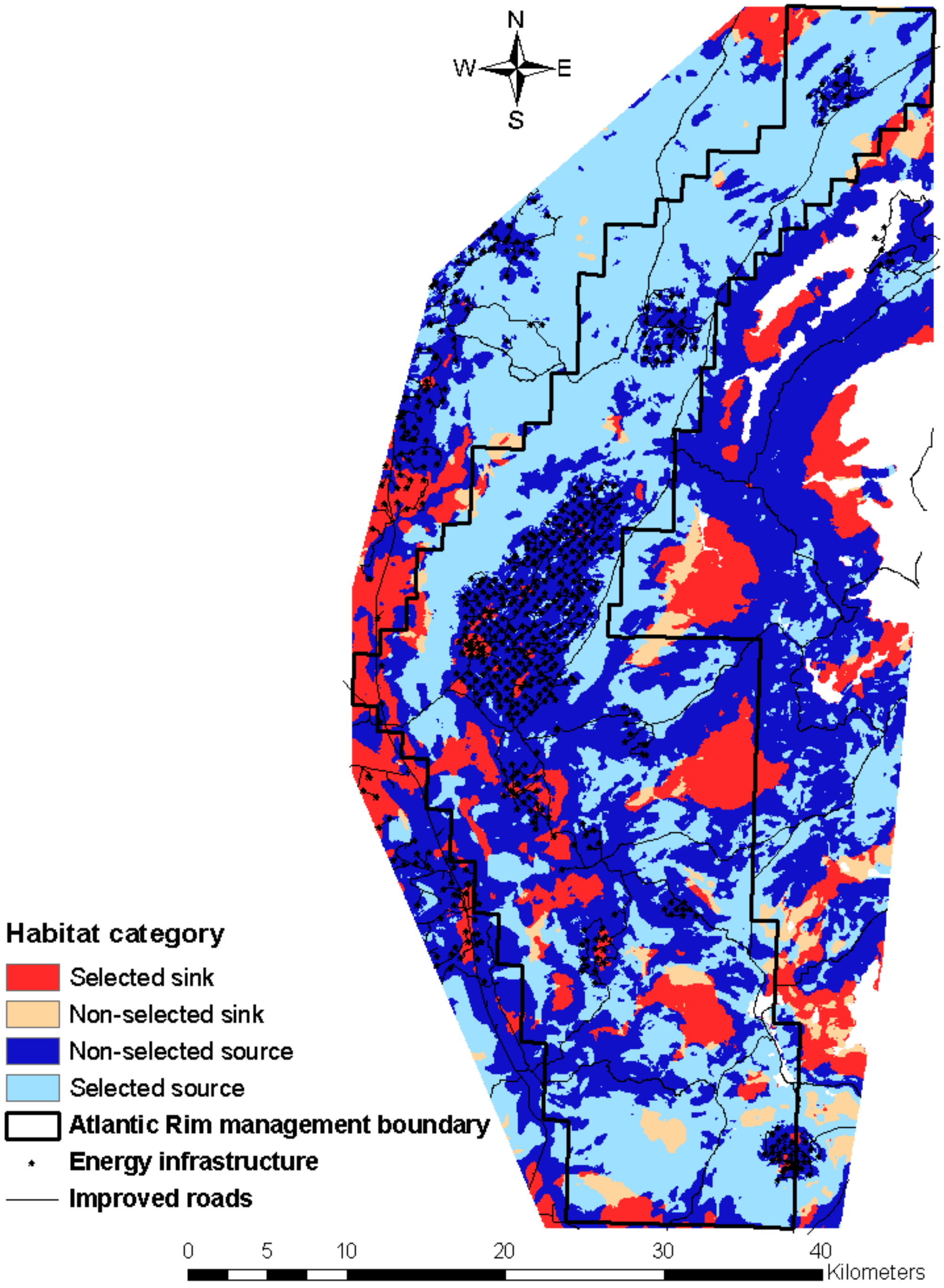

Figure 14. Predicted sink and source habitats for sage-grouse in south-central, Wyoming, USA, 2008 and 2009. The habitat categories are based on the lambda threshold of 1 and a binary measure of occurrence probability with the break at the mean value between high and low probability. The quantification of source-sink categories is described in Table 2.