Identifying Greater Sage-Grouse source and sink habitats for conservation planning in an energy development landscape

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Abstract. Conserving a declining species that is facing many threats, including overlap of its habitats with energy extraction activities, depends upon identifying and prioritizing the value of the habitats that remain. In addition, habitat quality is often compromised when source habitats are lost or fragmented due to anthropogenic development. Our objective was to build an ecological model to classify and map habitat quality in terms of source or sink dynamics for Greater Sage-Grouse (*Centrocercus urophasianus*) in the Atlantic Rim Project Area (ARPA), a developing coalbed natural gas field in south-central Wyoming, USA. We used occurrence and survival modeling to evaluate relationships between environmental and anthropogenic variables at multiple spatial scales and for all female summer life stages, including nesting, brood-rearing, and non-brooding females. For each life stage, we created resource selection functions (RSFs). We weighted the RSFs and combined them to form a female summer occurrence map. We modeled survival also as a function of spatial variables for nest, brood, and adult female summer survival. Our survival models were mapped as survival probability functions individually and then combined with fixed vital rates in a fitness metric model that, when mapped, predicted habitat productivity (productivity map). Our results demonstrate a suite of environmental and anthropogenic variables at multiple scales that were predictive of occurrence and survival. We created a source–sink map by overlaying our female summer occurrence map and productivity map to predict habitats contributing to population surpluses (source habitats) or deficits (sink habitat) and low-occurrence habitats on the landscape. The source–sink map predicted that of the Sage-Grouse habitat within the ARPA, 30% was primary source, 29% was secondary source, 4% was primary sink, 6% was secondary sink, and 31% was low occurrence. Our results provide evidence that energy development and avoidance of energy infrastructure were probably reducing the amount of source habitat within the ARPA landscape. Our source–sink map provides managers with a means of prioritizing habitats for conservation planning based on source and sink dynamics. The spatial identification of high value (i.e., primary source) as well as suboptimal (i.e., primary sink) habitats allows for informed energy development to minimize effects on local wildlife populations.

Key words: Atlantic Rim Project Area; Centrocercus urophasianus; *energy development; fitness; Greater Sage-Grouse; habitat quality; productivity; resource selection functions; source–sink habitats; south-central Wyoming, USA; survival functions; survival modeling.*

Introduction

The presence of animals in human-altered 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 can be a misleading indicator of population fitness in altered landscapes (Van Horne

1983, Aldridge and Boyce 2007, Chalfoun and Martin 2007). A primary goal of modeling wildlife–habitat relationships should be to understand the suite of habitat features that affect occurrence as well as fitness of a species (Jones 2001, Morrison et al. 2006). Therefore, 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. This information is especially important when managing a species that is imperiled in much of its current range and is expected to face ongoing habitat alteration and loss due to anthropogenic

development and other forms of habitat change, the Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter Sage-Grouse, see Plate 1).

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). 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 (i.e., births exceed deaths; Pulliam and Danielson 1991). 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). Ecological traps can arise when anthropogenic or environmental change act to uncouple the cues that individuals use to assess perceived habitat quality from true quality (Schlaepfer et al. 2002, Aldridge and Boyce 2007). The finite population growth rate or lambda (λ) is a vital metric for judging local population "health" (Pulliam 1988, Nichols and Hines 2002). Although λ fluctuates over the short term, over the long term, 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).

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, Aldridge et al. 2012, Smith et al. 2014) and fitness (Robinson et al. 1995, Reid et al. 2006, Aldridge and Boyce 2008, Smith et al. 2014). Further, habitat fragmentation may affect productivity through different mechanisms at different spatial scales (Diez and Giladi 2011). Sage-Grouse studies incorporating geographic information systems (GIS) and remote sensing have identified habitat selection at several landscape scales (e.g., Homer et al. 1993, Wisdom et al. 2002, Doherty et al. 2008, Doherty et al. 2010, Aldridge et al. 2012). Habitat quality can also vary at different scales (Diez and Giladi 2011). Accordingly, for landscape-scale species with large ecological neighborhoods, such as Sage-Grouse (Connelly et al. 2011), variables that are biologically relevant to the particular species should be measured at multiple scales (Johnson 1980, Morris 1987, Aldridge et al. 2012). The first researchers to successfully assess and map Sage-Grouse fitness relative to habitat use did so at a single landscape scale, 1 km^2 (Aldridge and Boyce 2007). We built upon their research by exploring relationships between occurrence and survival 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 coal, natural gas, and oil 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). 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 Sage-Grouse populations may result in lower male lek attendance and reduced lek persistence (Walker et al. 2007, Harju et al. 2010, Hess and Beck 2012); lower yearling male recruitment to disturbed leks (Holloran et al. 2010); avoidance of critical seasonal habitats (Lyon and Anderson 2003, Doherty et al. 2008, Smith et al. 2014); lower nest initiation rates (Lyon and Anderson 2003); reduced nest success (Dzialak et al. 2011); 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 Sage-Grouse populations within the sagebrush biome.

Because habitat quality is a function of an occupied habitat's conduciveness to survival and production, our primary research objective was to spatially quantify Sage-Grouse habitat quality on the basis of occurrence and fitness models dictated by landscape predictor variables. This approach offered a means of prioritizing habitat importance related to Sage-Grouse population persistence. Our research focused on the Atlantic Rim Project Area (ARPA), a coalbed natural gas (CBNG) field in the early stages of development in south-central Wyoming, USA. Previous attempts at identifying habitat quality for Sage-Grouse have been based on nesting and brood-rearing life stages (Aldridge and Boyce 2007, Dzialak et al. 2011). By integrating female summer survival and a fitness metric, our goal was to estimate habitat quality more comprehensively and to present this in terms of sink and source habitats. In addition, by definition, source habitats should yield a demographic surplus (Pulliam and Danielson 1991). To reach our objective, we used female-based resource selection functions (RSFs; Manly et al. 2002) and survival probability functions (SPFs; Hosmer and Lemeshow 1999), specific to each female Sage-Grouse life stage during the reproductive period, to generate and map spatially explicit estimates of habitat quality as a
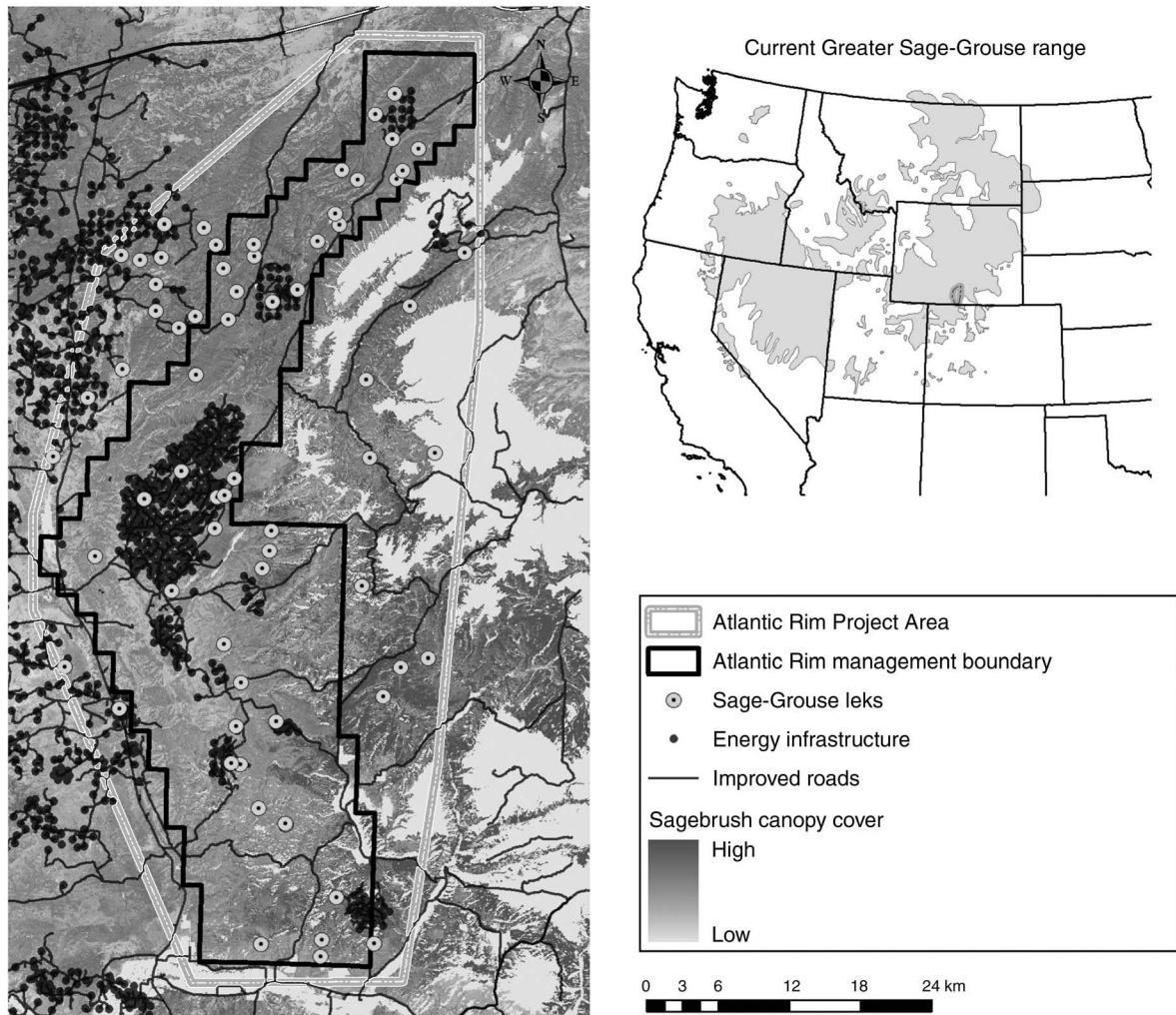
FIG. 1. The Atlantic Rim study area in relation to current range-wide Greater Sage-Grouse (*Centrocercus urophasianus*) distribution and occupied leks (WGFD 2012). The study area is located in south-central Wyoming, USA.

means of informing future development at a landscape scale.

METHODS

Study area

The 1093-km^2 ARPA lies in south-central Wyoming, USA, immediately west of the Sierra Madre mountain range. It includes 64.3% (701.9 km^2) federal, 5.2% (57.0 km^2) state, and 30.5% (334.1 km^2) private lands. The ARPA is within the semidesert grass–shrub zone in the Cool Central Desertic Basin and Plateaus major land resource area (NRCS 2006). The semidesert grass–shrub zone is characterized by a vast sagebrush steppe with a low average annual precipitation of 24 cm (NRCS 2006). Average daily temperatures in the ARPA range between a low of −16°C and a high of 0.5°C in midwinter and between 13°C and 24°C in midsummer (BLM 2006, Kirol et al. 2012). The ARPA is character- ized by drainage basins and rolling hills bisected by deep

drainages with prominent knolls, and escarpments. Elevations within the study area range from 1982 to 2529 m. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) communities at lower elevations and mountain big sagebrush (*A. t. vaseyanas*) communities at higher elevations dominate the majority of the ARPA (BLM 2006). See Kirol et al. (2012) for a description of common herbaceous species forming the big sagebrush communities in the ARPA. The ARPA has supported a substantial Sage-Grouse population, with one of the highest lek densities in Wyoming (Fig. 1). Male Sage- Grouse counted on individual leks ranged from 1 to 112 males in 2008 (WGFD 2012).

The BLM Record of Decision (ROD) for the Atlantic Rim Natural Gas Field completed in 2007 described the development of 2000 natural gas wells, including the drilling of 1800 CBNG wells and 200 deep natural gas wells at a down-spacing of 32.4 ha per well (BLM 2007). Development and drilling began in 2007 and there were

~600 natural gas wells at the conclusion of our field research in August 2009. Other land uses in the ARPA included livestock grazing.

Radio-marking and monitoring

To obtain a random sample of the population (Manly et al. 2002), we captured female Sage-Grouse from 14 leks situated throughout the ARPA in 2008 and 2009, using established spot-lighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992). We attached VHF radio transmitters (Model A4060; Advanced Telemetry Systems, 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 d; and were equipped with motion sensors (i.e., radio transmitter pulse rate increased in response to inactivity after 8 h) to aid in detecting mortalities. 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 (Eng 1955, Dalke et al. 1963). Female Sage-Grouse were captured and handled according to University of Wyoming Institutional Animal Care and Use Committee approved protocols (03032009) and Wyoming Game and Fish Department Chapter 33 permits 572 and 699.

We located Sage-Grouse on the ground using hand-held receivers and three-element Yagi antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA). We used ground telemetry to monitor radio-marked females through nesting (May–June) and early and late brood-rearing periods (June–August). Sage-Grouse locations were recorded in Universal Transverse Mercator (UTM) coordinates using a handheld 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 Sage-Grouse 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. After recording a nest location, we retreated in a meandering or "zigzagging" pattern to prevent predators from following human scent to the nest.

Nest monitoring.—We monitored Sage-Grouse nests at a frequency of 6.21 ± 0.16 days (mean ± SE) throughout the nesting season. After a nest was recorded, we monitored the nest from long range (>50 m) until the conclusion of the nesting effort. The fate of the nest (successful or unsuccessful) was determined by the condition of the eggshells (eggshell cap) and shell membranes (Wallestad and Pyrah 1974) directly following a female leaving the nesting area. When the hatched nest was undisturbed by scavengers, we counted eggshell caps (initial pipping of the egg generally results in an eggshell cap) to ascertain the number of eggs that hatched. When nest fate could not be determined

conclusively by diagnostic evidence, we found the female within ≤2 days after we determined she was off the nest to ascertain if she was brooding chicks. Nests of females not brooding chicks during this visit were assumed to have failed. A nest was considered successful if one egg hatched and the hatch date was estimated as the day midway between consecutive visits, unless other diagnostic signs allowed for a better approximation. Nest fates were recorded as successful, naturally abandoned, abandoned due to researcher disturbance, eaten by a predator, or unknown.

Brood monitoring.—We monitored females that successfully hatched chicks at a frequency of 5.99 ± 0.17 days (mean ± SE) to assess brood-rearing habitat use and brood fate through August 2008 and 2009. At each visit, we determined 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 to be the experimental unit, rather than individual chicks. Therefore, a brood was considered to have survived if we observed ≥1 chick at approximately 36 days post-hatch. Thirty-six day post-hatch was used as a cutoff for 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 (Hannon and Martin 2006, Gregg et al. 2007, Walker 2008). We estimated dates of brood loss at the midpoint between the last date observed with a brood and the first date without. Females thought to be no longer with broods were checked twice after the initial determination to confirm brood loss. We conducted back-to-back nighttime spotlight counts (Walker 2008) at approximately days 35 and 36 post-hatch to establish final brood fate. Dahlgren et al. (2010) estimated 100% chick count accuracy using nighttime spotlight counts. We considered the duration of the early brood-rearing period to be from hatch to 14 days; the late brood-rearing period was >14 days post-hatch to ~36 days. (Thompson et al. 2006, Connelly et al. 2011).

Female monitoring.—We monitored female survival by field observations and aerial telemetry flights from early May through August 2008 and 2009. Aerial telemetry flights were conducted approximately monthly throughout the summer. In addition to nesting and brooding females, we monitored non-brooding females at a frequency of 10.01 ± 0.21 days (mean ± SE) post-nest or brood loss, or after it was determined that they did not initiate a nest. While monitoring, we consistently scanned for mortality signals; if detected, we would track that female as soon as possible. We did not include females in the survival analysis for a period of two 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 late August. During each year, time was started at $t = 0$ upon the first monitoring

of each female Sage-Grouse. Monitoring began for the entire female sample in early May each year immediately after an aerial telemetry flight. If the female did not survive, dates of mortality were estimated at the midpoint 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 the first documentation of the mortality signal or diagnostic signs (e.g., fresh or decomposed body).

Spatial predictor variables

We developed anthropogenic and environmental predictor variables for our analysis on the basis of a priori information from previous Sage-Grouse research (Homer et al. 1993, Lyon and Anderson 2003, Aldridge and Boyce 2007, Walker et al. 2007, Doherty et al. 2008, Carpenter et al. 2010, Doherty et al. 2010, Holloran et al. 2010, Connelly et al. 2011) as well as hypothesized predictors of ecological relationships. We processed spatial data with ArcGIS 9.3.1 (Environmental Systems Research Institute (ESRI), Redlands, California, USA), and Geospatial Modeling Environment (Beyer 2010). We calculated summary statistics for most of the continuous predictor variables for each scale using neighborhood statistics (hereafter referred to as a moving window) in GIS.

Based on the biology of Sage-Grouse (Holloran and Anderson 2005, Aldridge and Boyce 2007, Doherty et al. 2010), we evaluated explanatory variables at three 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). The radius for the largest landscape scale, 1.260 km, 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 seasons. 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 nesting and brood-rearing selection and survival at this scale in southern Alberta, Canada. The biological relevance of our patch scale, 0.25 km^2 or 0.282 km radii, was 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. Moreover, a scale of radius 0.35 km proved predictive of nest-site selection in the Powder River Basin, Wyoming (Doherty et al. 2010). When appropriate, we explored quadratic transformations because the quadratic form of a variable can often identify nonlinear relationships that would otherwise go undetected (Doherty et al. 2010, Aldridge et al. 2012). We followed the convention that the linear term was always included in the model with the quadratic. Table 1 provides a description of the suite of environmental and anthropogenic spatial predictor variables that we examined in occurrence and survival modeling.

Environmental predictor variables.—Using remotely sensed continuous-cover maps (30-m resolution) developed by Homer et al. (2012) for sagebrush habitats in Wyoming, we assessed eight habitat characteristics: percent cover of bare ground, herbaceous cover, and litter; shrub height; and percent canopy cover of sagebrush, big sagebrush, Wyoming big sagebrush, and total shrub cover. These variables were summarized as means within the different spatial scales examined. Litter was defined as an estimate of detached plant and animal organic matter as well as dead standing woody vegetation (Homer et al. 2012). We calculated the standard deviation (SD) of herbaceous, sagebrush, big sagebrush, and Wyoming big sagebrush cover and shrub height measures as a proxy for the amount of habitat diversity or heterogeneity (Kastdalen et al. 2003, Carpenter et al. 2010) at each scale examined.

We generated a normalized difference vegetation index (NDVI) from the August 2009 National Agriculture Imagery Program (NAIP) 1-m resolution color aerial imagery (USDA 2009; see Enwright et al. 2011) and rescaled this to 30-m resolution. NDVI is a measure of surface greenness, generally correlating well with live green vegetation and aboveground biomass. We derived a categorical (0 or 1) mesic habitat variable from NDVI by reclassifying into mesic or non-mesic, based on ground-truthing and visual verification with NAIP imagery. Mesic habitats represented riparian areas along stream channels, ponds, and wet meadows containing abundant herbaceous cover. Using NW ReGap data (Lennartz 2007), we classified conifer stands to create a categorical variable that we termed Forest. The variable Forest was also visually 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 digital elevation model, 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). VRM uses the variation in slope and aspect to create a single measure of terrain ruggedness (Sappington et al. 2007).

Anthropogenic predictor variables.—We quantified anthropogenic variables independent of scale including distances (km) to anthropogenic edge (Distedge; mainly infrastructure sites and roads), nearest improved gravel road (Disthaul), nearest unimproved road (Two-trackdist), nearest fence (Distfence; BLM-Rawlins Field Office data consisting of grazing allotment boundary and cross fences), and nearest energy well (Distwell). At each spatial scale, we quantified total linear distances (km) of fences (Fence), improved gravel roads (Haulrd), and unimproved roads (Two-track), as well as counts of energy wells

TABLE 1. Spatial predictor variables used for Sage-Grouse nest, brood, female occurrence, and survival modeling in south-central Wyoming, USA.

Model category, predictor variable	Scale (km^2)	Description
Environmental		
Baresoil	0.25, 1.0, 5.0	mean bare ground % cover (Homer et al. 2012); MW
Bsage†	0.25, 1.0, 5.0	mean big sagebrush (*Artemisia tridentata*) % cover (Homer et al. 2012); MW
Bsage$_{SD}$	0.25, 1.0, 5.0	SD big sagebrush (*Artemisia tridentata*) % cover (Homer et al. 2012); MW
Forestdist†		distance (km) to nearest conifer stand from NW ReGap (Lennartz 2007), verified using NAIP imagery (2009)
Herb†	0.25, 1.0, 5.0	mean herbaceous % cover (Homer et al. 2012); MW
Herb$_{SD}$	0.25, 1.0, 5.0	SD herbaceous cover (%; Homer et al. 2012); MW
Litter	0.25, 1.0, 5.0	mean % litter (Homer et al. 2012); MW
Mesic	0.25, 1.0, 5.0	percentage of area that is mesic habitat derived from converting NAIP imagery (2009) to NDVI and ground-truthed to determine value break (categorical [0,1])
Mesicdist†		distance (km) to nearest mesic area derived from converting NAIP imagery (2009) to NDVI ground-truthed to determine cell value break (categorical [0,1])
NDVI	0.25, 1.0, 5.0	mean NDVI values derived from NAIP imagery; MW
NDVI$_{SD}$	0.25, 1.0, 5.0	SD NDVI values; MW
Sage†	0.25, 1.0, 5.0	mean sagebrush (all *Artemisia* spp.) % cover (Homer et al. 2012); MW
Sage$_{SD}$	0.25, 1.0, 5.0	SD sagebrush (all *Artemisia* spp.) % cover (Homer et al. 2012); MW
Shrbhgt	0.25, 1.0, 5.0	mean shrub height, cm (Homer et al. 2012); MW
Shrbhgt$_{SD}$	0.25, 1.0, 5.0	SD shrub height, cm (Homer et al. 2012); MW
Slope	0.25, 1.0, 5.0	mean slope (%); MW
TWI	0.25, 1.0, 5.0	mean topographic wetness index, TWI (high values = increased soil moisture; Theobald 2007); MW
VRM†,‡	0.25, 1.0, 5.0	mean topographic roughness (vector roughness measure, VRM; Sappington et al. 2007); MW
Wysage†	0.25, 1.0, 5.0	mean Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) % cover (Homer et al. 2012); MW
Wysage$_{SD}$	0.25, 1.0, 5.0	SD Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) % cover (Homer et al. 2012); MW
Anthropogenic		
Dstbarea†	0.25, 1.0, 5.0	surface disturbance 30-m cell count (bare ground resulting from vegetation removal): combination of energy infrastructure (energy well sites§, improved gravel roads¶, compressor sites¶, and human dwellings digitized or confirmed using NAIP imagery
Edgedist		distance (km) to nearest anthropogenic edge: combination of energy infrastructure (energy well sites§, improved gravel roads¶, compressor sites¶, and human dwellings digitized or confirmed using NAIP imagery
Fence	0.25, 1.0, 5.0	total linear distance (km) of fence (mainly grazing allotment fences) within analysis region
Fencedist†		distance (km) to nearest fence (mainly barbwire grazing allotment fences)
Haulrd	0.25, 1.0, 5.0	total linear distance (km) of haul road¶ (improved gravel road) within analysis region, verified using NAIP imagery
Hauldist†		distance (km) to nearest haul road¶ (improved gravel road), verified using NAIP imagery
Two-track	0.25, 1.0, 5.0	total linear distance (km) of unimproved road (two-track road) within analysis region
Two-trackdist†		distance (km) to nearest unimproved road (two-track)
Vwell	0.25, 1.0, 5.0	count of visible energy wells§ within analysis region, verified using NAIP imagery
Well	0.25, 1.0, 5.0	count of energy wells§, within analysis region, verified using NAIP imagery
Welldist†		distance (km) to nearest energy well site§, verified using NAIP imagery

Notes: Data are 30-m resolution and spatial scales are circular unless indicated otherwise. MW indicates calculation using a moving window; NAIP is the USDA National Agriculture Imagery Program (USDA 2009); NDVI is the normalized differential vegetation index.

† Quadratic transformations assessed.

‡ Square analysis regions.

§ Time-stamped on the basis of spud dates monthly 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.

¶ When constructed in concurrence with energy well sites, feature time-stamped monthly 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.

(Well), visual energy wells (Vwell), and the percentage of total surface disturbance (Dstbarea^2) within each scale. We obtained energy well data, including type, location, status, production, and spud date (date when the drill bit from a rig penetrates the surface), from the Wyoming Oil and Gas Conservation Commission database (WOGCC 2010). We used 2009 NAIP imagery to validate well and road locations. Variables associated with energy development, including Dist-edge, Disthaul, Distwell, Dstbarea^2, 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 based all spatial analyses on monthly increments. The spatial analysis for each month only included infrastructure and associated well sites spudded prior to that month.

Research has found that visible wells can be negatively associated with chick survival (Aldridge and Boyce 2007). We determined wells visible from any given location (Vwells) by using the ArcView Spatial Analyst 9.3 Viewshed tool (ESRI, Redlands, California, USA). We used 3 m as the standard well height for this analysis because this is a conservative height for the standard structure at most CBNG wells in the ARPA. We calculated viewsheds from ground height. We summed the number of visible wells for each spatial scale.

We separated roads into haul roads (i.e., improved gravel roads generally used for accessing energy infrastructure) and unimproved roads (i.e., high-clearance four-wheel drive or two-track). We quantified percentage of surface disturbed by anthropogenic activity, areas with complete vegetation removal resulting in bare ground, for each spatial scale. To accomplish this, we created a disturbance layer that consisted of all energy infrastructure, including well pads, compressor sites, transfer stations, and haul roads, and non-energy-related human structures. We digitized energy infrastructure and dwellings using 2009 NAIP imagery and buffered haul roads at 10 m, which represented the average road width in the study area.

Experimental design and occurrence analysis

We employed a use vs. availability design (Manly et al. 2002) with binary logistic regression (Boyce and McDonald 1999) to estimate each resource selection function (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 form

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

where $w(x)$ was the RSF (relative probability of selection; Lele et al. 2013) for each cell in the landscape for the environmental and anthropogenic predictor variables, x_1 through x_k. The β_ks are coefficient estimates for each predictor variable. Herein we refer to what is the relative probability of selection (see Lele et al. 2013) as the relative probability of occurrence or occurrence.

We incorporated a Type I habitat selection design in which we pooled used locations across individual Sage-Grouse and evaluated habitat availability for all Sage-Grouse with pooled random locations to represent a population-level response to habitat variables (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 at the scale of the use data (Thomas and Taylor 2006). We explored five 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-brood-ing. 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 the same or different habitats during the same temporal period. We employed Wyoming sagebrush products (Homer et al. 2012) to constrain the random locations to sagebrush habitats (i.e., sagebrush habitats) and excluded habitats such as exposed rock, open water, and conifer stands. We generated random points at a ratio of five times the number of used points (Aldridge and Boyce 2007, Carpenter et al. 2010). To account for possible overrepresentation 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 (Hirzel et al. 2006, Aldridge and Boyce 2007, Carpenter et al. 2010). This resulted in a used to available ratio of 1:1.

We used a second-order Akaike's information criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989) to assess model support. We modeled all variables univariately and, for scale-dependent variables, we determined the scale that was most correlated with occurrence by comparing AIC_c scores across variable scales (Arnold 2010, Carpenter et al. 2010, Doherty et al. 2010). We retained the scale with the lowest AIC_c score, which corresponded to the greatest predictive potential (Burnham and Anderson 2002). Further, we screened unsupported predictor variables that had an 85% confidence interval (CI) around parameter estimates that included 0, thereby reducing the likelihood of over-fitting models in our model selection process (Hosmer and Lemeshow 2000, 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 ≥ 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). We checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($0.3 \leq r \leq 0.6$). Generally, if variables were correlated, the variable with the lowest AIC_c score was retained. On occasion, findings from previous research informed the decision to retain a variable (Aldridge and Boyce 2007, Doherty et al. 2010). We did not permit correlated variables to compete in the same model at any level of model selection.

Experimental design and survival analysis

We explored relationships between landscape-scale predictor variables and Sage-Grouse survival or risk for three distinct life stages: nest, brood, and adult (including yearling) female summer survival. In general, survival analyses are used for investigating time-to-event data. Cox's (1972) proportional hazards regression

model (hereafter Cox model) is a robust survival model that provides a method of estimating the effect of variables on time to an event such as death. For example, in this analysis "time" refers to the approximate date of nest initiation and the "event" is the approximate date of nest failure. If the nest hatched successfully, then it did not have an "event" and was censored. The Cox model allows for incorporating time-dependent variables or variables that change with time and space, and right- and left-censored survival data (Hosmer and Lemeshow 1999). Right- and left-censoring allows for incorporating individuals into the model that may not be observed for an entire period or those whose event is unknown. We used the Cox model to fit our nest survival, brood survival, and adult female survival data to 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 a unit change in a variable on the risk of death (Winterstein et al. 2001). The Cox model took the following form in our analysis:

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

where β_is are the regression coefficients for the x_i variables, and $h_0(t)$ is the baseline hazard at time t. The baseline hazard is unspecified but the effects of the variables are still estimated. Environmental and anthropogenic predictor variable effects were interpreted as hazard ratios ($\exp[\beta_i]$).

Our survival analysis periods (t) for nests, broods, and summer females were $t = 28$ days, $t = 36$ days, and $t = 110$ days, respectively. Thus, female summer survival overlapped the nest and brood survival periods. Left-censoring of females was minimal because we began monitoring the female sample at the same time (early May) each year. For the brood and female survival analyses, some right-censoring did occur for individuals or broods of unknown status (i.e., disappeared during summer monitoring). For the nest survival analysis, we assessed fixed variables in the Cox model 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 vital rate, which we termed average cumulative 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 that this is an important step because it is more appropriate to assess risk based on varying exposure to habitat features over time (cumulative exposure), rather than based solely on the last location were an individual was found dead or a female was no longer with brood. For example, individual chicks may be preyed on as they move through the landscape, and not necessarily all at the same time. Therefore, this approach accounted for possible errors associated with determining the exact point of an event, but also incorporated the point of the event in the analysis.

We calculated survival estimates for each vital rate with the Kaplan-Meier (K-M) product-limit estimator (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989). Following the fitting of the Cox model and after calculating K-M survival estimates for each vital rate, we estimated the baseline survivorship function of the proportional hazards model (Hosmer and Lemeshow 1999). The survival probability function (SPF) took the form

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

where $S_0(t)$ was the K-M survival estimate at the end of the survival period for that vital rate (nest, $t = 28$ days; brood, $t = 36$ days; female summer, $t = 110$ days), and $x'\beta$ was the variable-adjusted coefficient from the Cox model. The SPF allowed us to transform daily risk (e.g., daily risk of nest loss in terms of a hazard ratio) derived from the Cox models to survival probabilities corresponding to the entire demographic period and then map these back on the ARPA landscape.

The Cox model assumes that hazards remain constant over time; thus, a variable's influence is proportional over time (Le 1997, Hosmer and Lemeshow 1999). Therefore, we tested the variables in our top survival models independently and collectively (e.g., top models) for proportionality at $\alpha = 0.05$ (Le 1997, Hosmer and Lemeshow 1999). We assessed if a particular observation was disproportionately influential on a coefficient estimate for each variable by testing for inflated residuals and leverage (dfbetas; Hosmer and Lemeshow 1999, Allison 2010). No observations were removed as a result of disproportionally high influence.

We used a derivation of the AIC technique adapted specifically for survival modeling (AIC$_{SUR}$) to select the best-supported survival models (Liang and Zou 2008). In the same manner as our occurrence modeling effort, we explored all variables univariately and, for scale-dependent variables, compared the three spatial scales to determine the scale that best explained survival by comparing AIC$_{SUR}$ scores (Arnold 2010, Carpenter et al. 2010, Doherty et al. 2010) for scale-dependent variables. We retained the variable scale with the lowest

AIC_{SUR} score. After selection of the appropriate variable scale, we screened variables by removing unsupported variables having parameter estimates with an 85% CI that included 0 (Le 1997, Hosmer and Lemeshow 1999, Arnold 2010). For the remaining variables, we assessed multicollinearity with a Pearson's correlation matrix and variance inflation factor (VIF) scores combined with tolerance (T) values. We omitted variables from correlated groups when $r \geq 0.6$ or $t \leq 0.4$ (Allison 2009). Finally, we checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($0.3 \leq r \geq 0.6$). When variables were correlated, the variable with the lowest AIC_{SUR} score was retained unless findings from previous research informed 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.

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 (Boyce et al. 2002). We evaluated the variable weights of predictor variables for occurrence and survival within model subsets: anthropogenic and environmental. We used a sequential modeling approach (Arnold 2010) consisting of two steps to identify the most effective predictors of occurrence and survival. In the first level of model selection, environmental and anthropogenic model subsets were modeled separately; 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. Models with AIC_c scores effectively equivalent (<2 AIC_c or AIC_{SUR}) to the null model were not considered informative (Allison 2010, Doherty et al. 2010). To address model selection uncertainty, we used additional metrics to determine 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). We checked for models with similar 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). We also 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.

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). For example, we explored whether the final model(s) from the environmental subset had the most support by itself, or if a combination of top models from environmental plus anthropogenic subsets produced a model with greater support, as assessed through a comparison of AIC_c or AIC_{SUR} scores. If the combined model had greater support than the anthropogenic and environmental models alone, we accepted the combined model.

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). Our brood survival data contained the lowest number of events. Consequently, we modified selection of brood survival models by only fitting models with three or fewer variables to maintain acceptable model performance (Vittinghoff and McCulloch 2006) at both levels of model selection. Within the nest survival and female survival variable subsets and final set, we did not exceed four variables per model, without modification; because many uninformative predictor variables were already removed through the screening process (85% CI included 0).

Model evaluation

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). To test the predictive accuracy of our final occurrence models, we performed an area-adjusted five-fold cross-validation for each life stage, in which we folded 20% of our data, without replacement, across folds (Boyce et al. 2002). For each of the five data folds (bins), the withheld set was assessed against the model predictions of that training data set, using Spearman rank correlations between bin ranks of the RSF values. A high score corresponded to good predictive performance (Boyce et al. 2002). Because model accuracy is more complex when censoring is involved, we used the overall C statistic (C index), designed specifically for survival models, to assess the discrimination ability of our survival models (Pencina and D'Agostino 2004). Values of $C > 0.7$ have acceptable discrimination, whereas values of $C \leq 0.5$ indicates that the model predicts the outcome no better than chance (Hosmer and Lemeshow 2000). We conducted all statistical analyses with SAS version 9.2 (SAS Institute 2009). We report all K-M survival estimates as estimate $\pm$ standard error (SE).

Mapping ecological models on the ARPA landscape

We had competitive models for all of our survival periods ($n = 3$) and female life stages ($n = 5$). Therefore, to produce more robust predictive surfaces for our final RSFs and SPFs, in a GIS framework, we model-averaged over the 90% confidence set (see Aldridge et al. 2012). For each female life stage, the relative probability of occurrence estimates specific to each

model were scaled between 0 and 1, incorporating the estimated β_0. The weights for each model in the 90% confidence set were recalculated within the set to sum to 1 and the recalculated weights were then applied to the spatial predictions for each model. The weighted predictions were summed to produce a final model-averaged relative probability surface for each RSF (Aldridge et al. 2012). We followed a similar process to produce our SPFs; however, we first applied each Cox model in the 90% confidence set to spatially predict daily risk (Eq. 2) and then converted these to individual SPFs (Eq. 3). Because the predicted relative survival probabilities are inherently scaled between 0 and 1, we applied the weights (recalculated within the 90% confidence set) to each SPF. The weighted SPFs were summed to form a final model-averaged relative survival probability surface (SPF) for each demographic (e.g., nest survival, brood survival, and female survival).

Because we were concerned with the importance of habitats to population persistence, we weighted the RSF layers for each life stage based on their influence on λ before summing them into a single female summer occurrence layer. For this weighting exercise, we used sensitivity values from Taylor et al. (2012) that reflect the influence of female survival (1.70), chick survival (1.20), and nest survival (0.95) on range-wide Sage-Grouse population growth (i.e., λ). Therefore, habitats that influenced the survival of females and chicks (i.e., early-brooding and late-brooding RSFs) received a weight of (1.70 + 1.20 = 2.90) and, consequently, received the highest weight. Habitats that were only influencing female survival (i.e., early non-brooding and late non-brooding RSFs) received the lowest weight (1.70). The weighted RSFs were then summed to form a predictive surface that scored habitat importance per cell on the basis of relative probabilities of female occurrence encompassing all summer life stages. For interpretation, the final female occurrence map was rescaled between 0 and 1, where 1 represented the highest and 0 represented the lowest predicted relative probability of occurrence. All maps or layers were in a raster format with 30-m cell resolution.

In following with our research objective to identify habitats contributing to Sage-Grouse population persistence in the ARPA, we formed a fitness metric (FM). The FM was adjusted on the basis of productivity correlated with habitat features (e.g., environmental and anthropogenic predictor variables). In forming the FM, we relied upon current knowledge of Sage-Grouse population dynamics as well as matrix population modeling (see Johnson and Braun 1999, Hagen 2003, Holloran 2005). In the FM model, we integrated our SPFs specific to nests, broods, and adult female summer survival into the following equation:

$$\text{Fitness metric} = [(\text{nest initiation} \times \text{nest survival})$$
$$\times (\text{brood survival} \times \text{♀chick})]$$
$$+ (\text{♀adult summer survival}) \qquad (4)$$

where nest initiation was a fixed value from the mean of our initiation rates from 2008 and 2009. A female was assessed as initiating a nest if tracked consistently during the pre-nesting season (e.g., 1 April to 15 May) and a nest was documented. Nest survival was a dynamic (varying) value from our nest SPF; brood survival was a dynamic 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 chicks (7.5 eggs and 94.3% hatchability; Crawford et al. 2004, Connelly et al. 2011), a brood sex ratio of 1:1 (Bush 2009), and a mean chick survival rate of 0.23 to 36 days, approximated from a chick survival curve that accounted for lack of independence of chicks (frailty model) within broods (see Aldridge and Boyce 2008); ♀adult summer survival was a dynamic value from our female summer SPF. For the vital rates that did not come directly from our research (♀chick), we were conservative in our estimation of the FM by using the lower estimates available in the Sage-Grouse literature. However, estimates were within the breadth of values found in other studies (Schroeder et al. 1999, Connelly et al. 2011). The value of the average brood size of 6.4 chicks is also supported by our mean count of hatched eggs (6.46 ± 0.16 eggs; range 5–9 eggs). When calculated, the FM model (Eq. 4) predictions fluctuated around 1. A value at or above 1 suggests productive habitat; that is, habitat where a female is more likely to replace herself during the reproductive period (i.e., female chick production offset or exceeded female mortality in the summer). A value below 1 suggests less productive habitat where female mortality is more likely to exceeded female production (i.e., the female is less likely to replace herself in these habitats; Table 2).

We mapped the FM estimates onto the ARPA landscape with Eq. 4 and termed this a productivity map. Therefore, each 30-m cell was adjusted per changing FM values that were driven by the SPFs for nest, brood, and female summer. The combination of our female summer occurrence map and productivity map formed our final ecological map, with a goal to spatially predict sink and source habitat on the ARPA landscape. The predictions were distributed into five categories based on the FM threshold of 1, ranking habitat productivity into high-productivity habitats (female chick production offset or exceeded female mortality) or low-productivity habitats (female mortality exceeded female chick production), and a three-quantile partition of the relative probabilities of occurrence predicted by our female summer occurrence map. The relative probabilities were ranked into high, moderate, and low occurrence (Table 2). The final source–sink map included the following habitat classifications: primary source, secondary source, primary sink, secondary sink, and low occurrence. The predictive surfaces were mapped on the 2009 landscape, thus reflecting the landscape conditions at the end of the study.

TABLE 2. Quantification of predicted source and sink habitats on the ARPA (Atlantic Rim Project Area) coalbed natural gas field landscape, south-central Wyoming, USA.

Occurrence	Probability of female summer selection	Fitness metric	Habitat productivity	Habitat categories
↑↑	>66%	≥1	high	primary source
↑	33–66%	≥1	high	secondary source
↑↑	>66%	<1	low	primary sink
↑	33–66%	<1	low	secondary sink
↓	<33%			low occurrence

Notes: The relative probability of female summer selection is based upon a three-quantile classification of map predictions. In high-productivity habitat, female chick production offsets or exceeds female mortality during the summer. In low-productivity habitat, female mortality in the summer exceeds female chick production.

To further assess the predictive ability of our final ecological model and corresponding source–sink map, we conducted a post hoc analysis by summarizing active leks and peak-male lek counts with lek data gathered in our study area from 2007 to 2011. We reasoned that if our model was successfully predicting high-occurrence areas with greater fitness outcomes, this should also be reflected in lek placement (i.e., the 30-m cell that contained the lek centroid) and corresponding peak-male counts (Gibson 1996). For instance, we would expect that Sage-Grouse leks and lekking numbers should be disproportionately higher within areas identified as primary source than within secondary source.

RESULTS

In spring 2007 and 2008, we radio-marked 90 female Sage-Grouse (Sage-Grouse were not monitored on the ground in 2007) and we were able to consistently monitor 76 of these in 2008. In 2009, we radio-marked an additional 60 female Sage-Grouse and were able to consistently monitor 70 radio-marked females. Our occurrence models included 93 nests, 68 early brood-rearing locations, 69 late brood-rearing locations, 134 early non-brooding locations, and 158 late non-brooding locations. Of the females monitored each year, only 16 were monitored in both 2008 and 2009; of these, five had the same status across years (e.g., hatched nest and with brood for the early and late periods). To ensure equal representation of individuals in our occurrence models, subsamples per individual per year were equal. For our early brood-rearing and early non-brooding models, each individual contributed two observations. Each individual contributed three observations for our late brood-rearing models and each individual contributed two observations for our late non-brooding models. All relocations were used in our survival analyses. The average recorded nest initiation across years was 59%. We recorded minimal nest abandonment ($n = 1$ in 2008 and $n = 5$ in 2009). Eighty-three nests (47 events), 35 broods (11 events), and 129 females (17 events) had sufficient observation history (at least two observations for broods and females) to assess in the nest, brood, and adult female summer survival analyses.

Nest occurrence

The predictor variables that formed the best approximating models and were model-averaged over the 90% confidence set for nest occurrence represented three spatial scales (Table 3). Model support increased with the inclusion of the anthropogenic variables (environmental plus anthropogenic model; Appendix: Table A1). At the patch scale (0.25 km², 0.282 km radius), big sagebrush canopy cover (Bsage) and litter (Litter) were positively correlated with nest occurrence; at the largest landscape scale (5 km²), the likelihood of nest occurrence decreased as the standard deviation in NDVI ($NDVI_{SD}$) increased. At the 1-km² scale, as terrain roughness (VRM) increased, the likelihood of nest occurrence decreased. The final model contained the anthropogenic variable visible well count (Vwell) at the 1-km² scale. The addition of one visible well within a 1-km² area reduced the odds of nest occurrence by ~52%. Available locations averaged 0.29 ± 0.04 visible wells/km² while nest locations averaged 0.06 ± 0.03 visible wells per km². The environmental and anthropogenic predictor variables, Bsage_0.25, Litter_0.25, $NDVI_{SD}$_5.0, and Vwell_1.0, formed the nest RSF model. The likelihood ratio χ² test statistic suggested that the full nest RSF model (i.e., model containing all of the variables in the 90% confidence set) had good fit ($\chi^2_4 = 33.80$, $P < 0.001$). Based on five-fold cross-validation, the predictive ability of the full nest RSF model was excellent ($r_S = 0.96$, $P < 0.001$, $n = 10$).

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 the same temporal period. Consequently, we formed RSF models specific to each of these life stages.

The best-supported models, model-averaged over the 90% confidence set, for early-brooding female occur-

Table 3. Final resource selection function (RSF) 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.

Model and variable	Scale (km^2)	Coefficient	95% CI Lower	95% CI Upper	Odds ratio	Variable weight
Nest RSF						
Environmental model						
NDVI$_{SD}$†	5.0	−0.244	−0.370	−0.127	0.783	1.000
Bsage	0.25	0.197	0.098	0.3073	1.217	0.766
Litter	0.25	*0.047*	*−0.034*	*0.129*	1.048	0.407
VRM‡	1.0	*−0.218*	*−0.796*	*0.333*	0.804	0.256
Anthropogenic model						
Vwell	1.0	−0.656	−1.459	−0.081	0.519	0.852
Early-brooding RSF						
Environmental model						
Herb$_{SD}$	1.0	−0.388	−0.661	−0.139	0.678	1.000
Sage	1.0	1.536	0.350	3.000	4.648	0.849
(Sage^2)	1.0	−0.054	−0.107	−0.013	0.947	0.849
Anthropogenic model						
Two-track	5.0	0.121	0.001	0.248	1.129	0.750
Vwell	1.0	*−0.742*	*−2.001*	*0.062*	0.476	0.658
Two-trackdist (km)		*−2.355*	*−5.360*	*0.483*	0.095	0.606
Early non-brooding RSF						
Environmental model						
Litter	0.25	0.075	0.018	0.134	1.078	1.000
NDVI$_{SD}$†	1.0	−0.131	−0.206	−0.646	0.877	0.789
VRM‡	1.0	−0.536	−1.087	−0.006	0.585	0.770
Wysage	1.0	*0.057*	*−0.173*	*0.291*	1.058	0.278
Anthropogenic model						
Welldist (km)		*0.106*	*−0.300*	*0.565*	1.112	1.000
(Welldist^2) (km)		−0.034	−0.087	−0.004	0.966	1.000
Vwell	5.0	−1.055	−2.083	−0.303	0.348	1.000
Late-brooding RSF						
Environmental model						
Sage	1.0	2.453	0.656	4.751	11.627	1.000
(Sage^2)	1.0	−0.097	−0.187	−0.029	0.907	1.000
Herb$_{SD}$	5.0	−0.148	−0.375	0.071	0.863	0.423
Shrbhgt$_{SD}$	0.25	*0.071*	*−0.076*	*0.222*	1.073	0.290
Anthropogenic model						
Two-track	0.25	1.060	0.243	1.934	2.886	0.964
Hauldist (km)		−0.385	−0.754	−0.034	0.681	0.532
Dstbarea†	5.0	2.19	0.201	4.360	8.935	0.359
(Dstbarea)^2†	5.0	*−0.008*	*−0.019*	*0.002*	0.992	0.359
Late non-brooding RSF						
Environmental model						
Sage	0.25	0.090	0.025	0.161	1.095	1.000
Forestdist (km)		−0.132	−0.291	0.021	0.877	0.691
Anthropogenic model						
Two-trackdist (km)		*1.266*	*−0.037*	*2.621*	3.546	0.676
Vwell	5.0	*−0.377*	*−0.984*	*0.119*	0.686	0.576

Notes: Parameter coefficients, 95% confidence intervals (CI), and odds ratios come from the top models (90% confidence set used to map our predictive surfaces) in which that variable first occurs. Variable weights are derived from the 90% confidence set. The parameter coefficient and corresponding CI are shown in italic when the 95% CI overlaps zero.

† For interpretation, estimates for a 100 unit change in variable.

‡ For interpretation, estimates for a 1000 unit change in variable.

rence contained the quadratic form of percent sagebrush canopy cover (Sage + Sage^2) and the variability in herbaceous cover (Herb$_{SD}$) from the 1-km^2 landscape scale (Appendix: Table A2). The variability in percent herbaceous cover within a 1-km^2 area (0.564 km radius)

was negatively correlated with selection during the early brood-rearing period, suggesting selection for habitats with more homogenous herbaceous cover. Unlike the variable Bsage (big sagebrush species), predictive in the nest occurrence model, the variable Sage included all

sagebrush regardless of the species or subspecies. The quadratic form of Sage_1.0 suggested that the association with sagebrush was positive, but the densest sagebrush was avoided at this scale. The anthropogenic model combined with the environmental model substantially increased model support (Appendix: Table A2). The final anthropogenic model for early brooding included Vwell at the 1-km^2 scale, total linear distance of unimproved road (Two-track_5.0) within 5 km^2, and distance (km) to nearest unimproved road (Two-trackdist). Female early brood-rearing locations were negatively correlated with the number of visible wells within 0.564 km, with the model predicting a 47% decrease in occurrence with the addition of one visible well. Early brood-rearing locations were positively associated with unimproved road density at the 5-km^2 scale, and as the distance from the nearest unimproved road (e.g., two-track) increased, the likelihood of occurrence decreased (Table 3).

Female Sage-Grouse without broods early in the season (early non-brooding) were selecting habitats with greater litter within 0.282 km (Litter_0.25), less variability in NDVI values (NDVI$_{SD}$_1.0), higher Wyoming sagebrush cover (Wysage_1.0), and lower terrain roughness values (VRM_1.0) within 0.564 km. The inclusion of the anthropogenic variables with the environmental model produced a model with substantially more support (Appendix: Table A3). In the 90% confidence set, the variable Wysage_1.0 had the least support (variable weight = 0.28) and the 95% CI overlapped 0. The quadratic form of distance to well (Welldist + Welldist^2) were predictive of occurrence. But the 95% CI for the linear term of the quadratic variable Welldist also overlapped 0 (Table 3). In accordance with nesting and early brood-rearing, visual well count (Vwell_5.0) was negatively related to occurrence of females without broods early in the season. The quadratic term for distance to a well suggests that the relative probability of early non-brooding female occurrence initially increased as the distance from wells increased then started to decrease as the distance from wells increased.

For the early brooding and early non-brooding full RSF models, the χ^2 likelihood ratio indicated good model fit: $\chi^2_6 = 29.30$, $P < 0.001$ and $\chi^2_6 = 63.07$, $P < 0.001$, respectively. Predictive ability of the full models, assessed by five-fold cross-validation, for the early brood ($r_S = 0.95$, $P < 0.001$, $n = 10$) and early non-brood ($r_S = 0.97$, $P < 0.001$, $n = 10$) was excellent.

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 diverged; therefore, 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.

The addition of the anthropogenic model only slightly increased model support for late-brooding female occurrence (Appendix: Table A4), but we believe that the increase was sufficient to justify including these anthropogenic variables in the final RSF model because, individually, these variables had support (95% CIs; Table 3) and the full model, which included the anthropogenic variables, had excellent predictive ability. Occurrence was negatively correlated with the variability in percent herbaceous cover within 1.260 km (Herb$_{SD}$_5.0) and positively correlated with variability in shrub heights at a smaller scale (0.25 km^2). Shrbhgt$_{SD}$_0.25 was the least supported variable in the 90% confidence set (variable weight = 0.29) and the 95% CI overlapped 0 (Table 3). As with early brood-rearing selection, sagebrush cover was an important predictor of occurrence in the quadratic form (Sage = 2.45 + Sage^2 = −0.10) at the 1.0-km^2 scale. The anthropogenic variables in the 90% confidence set included the quadratic form of the percent surface disturbance area (Dstbarea_5.0), the distance to the nearest haul road (Hauldist), and the linear distance of unimproved road (Two-track_0.25). Similar to early-brooding females, late-brooding females were positively associated with unimproved road density. 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 some surface disturbance (e.g., well pads and haul roads), but as disturbance reached ~2%, the relationship gradually became negative, suggesting reduced use beyond this disturbance level. No late-brooding females in our sample used habitats with disturbance that exceeded 8%. The association between late-brooding female occurrence and haul roads suggests that as the distance from haul roads increased, the probability of occurrence decreased; thus, late brood-rearing females were using habitats adjacent to haul roads. This relationship does not necessarily indicate that habitats immediately adjacent to haul roads were being selected because late-brooding locations averaged 1.11 ± 0.12 km vs. available locations that averaged 1.38 ± 0.06 km from the nearest haul road.

Environmental predictor variables supported in our late non-brooding modeling included Forestdist and Sage_0.25. The percent sagebrush canopy cover was positively correlated with female late non-brooding occurrence at the patch scale, and as the distance to forest edge decreased, the probability of selection by late non-brooding females increased. The positive association with forest edge was not supported in any of the other models (nesting, early brood-rearing, early non-brooding, and late brood-rearing), again suggesting different habitat use for females without broods later in the summer (Table 3). The inclusion of the final late non-brooding anthropogenic model improved model fit when compared with the environmental model alone (Appendix: Table A5). The late non-brooding anthropogenic model contained the variables Two-trackdist

TABLE 4. Final models and associated spatial variables predictive of survival for nest, brood, and adult female in south-central Wyoming, USA.

Model and variable	Scale (km^2)	Coefficient	95% CI Lower	95% CI Upper	Risk ratio	Variable weight
Nest survival						
Environmental model						
TWI	0.25	0.257	0.109	0.406	1.294	0.774
Wysage	5.0	−0.311	−0.442	−0.179	0.733	0.552
Shrbhgt$_{SD}$	1.0	−0.095	−0.163	−0.025	0.910	0.483
Brood survival†						
Environmental model						
Shrbhgt$_{SD}$	1.0	−0.488	−0.707	−0.269	0.614	0.908
Herb	1.0	0.104	0.049	0.159	1.111	0.680
Anthropogenic model						
Dstbarea	1.0	−0.118	−0.216	−0.019	0.889	0.606
(Dstbarea)^2	1.0	0.002	0.001	0.003	1.002	0.606
Female summer survival†						
Environmental model						
Shrbhgt$_{SD}$	1.0	−0.168	−0.293	−0.043	0.845	0.580
VRM‡	5.0	*0.312*	*−0.131*	*0.754*	1.365	0.324
Anthropogenic model						
Edgedist (km)		0.717	0.506	0.927	2.048	1.000

Notes: Parameter coefficients, 95% confidence intervals (CI), and risk ratios come from the top models (90% confidence set used to map our predictive surfaces) in which that variable first occurs. A risk ratio greater than 1 indicates increased risk with an increase in the variable. The variable weights are derived from the 90% confidence set. The parameter coefficient and corresponding CI are highlighted in italics when the 95% CI overlaps zero (for VRM).

† Contains time-dependent variables that represent average cumulative exposure to the corresponding habitat characteristics over the entire survival time and specific to each individual.

‡ For interpretation, estimates for a 1000 unit change in variable.

and Vwell_5.0. Vwell density was negatively correlated with late non-brooding female occurrence at the largest scale (5 km^2). As the distance to the nearest unimproved road (Two-trackdist) increased, late non-brooding female occurrence increased (i.e., females later in the summer without broods were selecting habitats farther from two-track roads).

The likelihood ratio χ^2 test suggested that the full late-brooding and late non-brooding models had good fit: $\chi^2_6 = 20.83$, $P < 0.002$ and $\chi^2_4 = 23.23$, $P < 0.001$, respectively. Predictive ability measured by five-fold cross-validation for the full late-brooding RSF model ($r_S = 0.93$, $P < 0.001$, $n = 10$) was excellent. Yet, five-fold cross-validation for the full late non-brooding RSF model ($r_S = 0.70$, $P < 0.033$, $n = 10$) indicated only moderate performance.

Nest survival

Nest survival was similar from year to year, with an average K-M nest survival estimate over a 28-day incubation period of 43.4% ± 5.4%. Nest survival modeling identified three environmental variables at three different scales that were correlated with 28-day nest survival (Table 4). The predictive variables included variability in shrub height at the 1-km^2 scale (Shrbhgt$_{SD}$_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). Daily nest survival increased with an increase in Shrbhgt$_{SD}$_1.0. Thus, habitats at the 1-km^2 scale with less variability in shrub heights were riskier habitats for nesting. A 5-cm increase in the variability in shrub height corresponded to about a 41% increase in the relative probability of daily nest survival (mean 7.74 ± 2.35 cm, range 3.91–13.83 cm). The percent Wysage_5.0 was positively correlated with nest success. With a 1% increase in Wyoming big sagebrush canopy cover within a 1.260 km radius surrounding a nest, the likelihood of success increased by ~26% (mean 9.57% ± 1.13%, range 5.67–12.58%). At the patch scale, topographic wetness index (TWI) was negatively related to nest success. None of the anthropogenic models in the model subset were better than the null model ($\Delta AIC_{SUR} \geq 2$). Thus, the 90% confidence set contained only environmental predictor variables. The full nest survival model provided a good fit to the data: $\chi^2_3 = 8.72$, $P < 0.033$, with a C index value of 0.79, indicating that the discrimination ability of the model was acceptable.

Brood survival

The K-M brood survival estimated to 36 days post-hatch was 76.2% ± 8.0%. Variables included in the brood survival models represent average cumulative exposure over the duration preceding a mortality event or to approximately 36 days. Brood survival to 36 days was correlated with both environmental and anthropo-
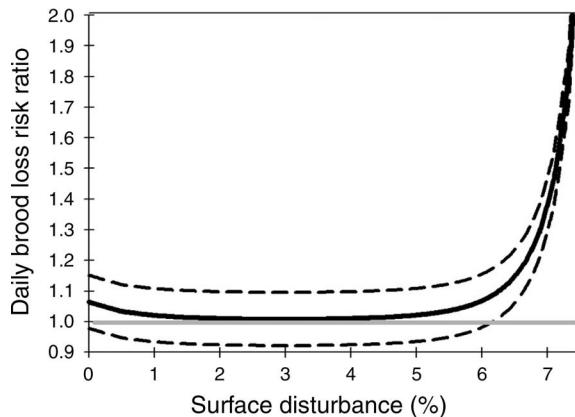
FIG. 2. Daily risk of brood loss over successive brood locations as a function of the percentage of surface disturbance at the 1-km^2 scale, south-central Wyoming, USA. The solid line represents mean brood loss risk ratio, and the dashed lines define the 95% CI.

genic variables at the 1-km^2 scale (Table 4). The cumulative environmental variables relating to daily brood survival included percent herbaceous cover (Herb) and Shrbhgt$_{SD}$. Greater herbaceous cover within a 0.564 km radius of successive brood locations was negatively related to daily brood survival. With a 1% increase in herbaceous cover, the odds of 36-day brood survival decreased by ~11% (mean 11.34% ± 5.29%, range 5.01–24.11%). Average cumulative Shrubhgt$_{SD}$_1.0 was positively correlated with daily brood survival. A 5-cm increase in the variability of shrub height over successive brood locations corresponded with an approximate 80% increase in the relative probability of daily survival (mean 28.08 ± 4.29 cm, range 18.07–41.98 cm). The combination of the final anthropogenic model and final environmental model improved model fit (Appendix: Table A6).

The top anthropogenic model included the quadratic term for total surface disturbance area at the 1-km^2 scale (Dstbarea + Dstbarea^2). The quadratic term suggests that cumulative exposure to Dstbarea^2_1.0 initially had little effect on 36-day brood survival, but at a threshold of ~4% surface disturbance, the risk of daily brood loss began to increase and increased more dramatically at 6% disturbance (Fig. 2). For example, an increase in surface disturbance from 6% to 7% equated to approximately a 29% increase in the relative probability of daily brood loss (mean 0.61% ± 1.16%, range 0–7.96%). The full 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.

Female survival

The K-M female summer survival estimate to 110 days was 93.0% ± 2.6% (2008–2009). Environmental variables that were predictive of Sage-Grouse female

summer survival ($t = 110$) included Shrbhgt$_{SD}$_1.0 and VRM_5.0. Like brood survival, variables represent average cumulative exposure over the duration preceding a mortality event or to 110 days if the female survived. The variability in shrub height within a 0.564 km radius of successive female locations was positively correlated with female survival. As terrain roughness (VRM_5.0) increased, female risk increased.

Model support improved with the inclusion of the anthropogenic variables when compared to the full environmental model only ($w_i = 0.40$ vs. $w_i = 0.18$). The full anthropogenic model included the distance to nearest anthropogenic edge (Edgedist). Edgedist suggested that as the distance from anthropogenic edge increased, the relative probability of 110-day female survival decreased. 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 was 1.04 ± 0.03 km vs. that of females that did not survive, 1.70 ± 0.10 km. The final female survival model provided a good fit to the data: $\chi^2_3 = 12.80$, $P < 0.005$; the C index value of 0.74 indicated acceptable model discrimination ability.

Ecological maps and validation

The nesting, early brood-rearing, early non-brooding, late brood-rearing, and late non-brooding maps (Appendix: Fig. A1) spatially demonstrated differences in habitat selection across life stages, but also identified habitats that were consistently important (high relative probability of occurrence scores) across life stages. The female summer occurrence map implicated the northern ARPA as having the greatest amount of high relative probabilities of occurrence habitat for females during the summer and predicted lower relative probabilities of occurrence around energy development areas (Fig. 3). Similar to the occurrence maps, when mapped, the relative probability of survival predictions for nest, brood, and female survival show areas that consistently had higher predicted survival across these vital rates (Appendix: Fig. A2). The productivity map (Fig. 4) predicted much of the northern ARPA as having high-productivity habitat, and predicted that areas with the greatest density of development (central ARPA), centered within high-productivity habitats, were lower-productivity habitats. Our source–sink map implicated ~30% of the ARPA landscape as primary source, 29% as secondary source, 4% as primary sink, 6% as secondary sink, and 31% as low occurrence (Fig. 5).

Based on lek count data (WGFD 2012), 53% of $n = 25$ active leks (with ≥2 males observed during any lek count between 2008 and 2011; Stiver et al. 2010) occurred in primary source habitats (Fig. 1). Of active leks, 17% ($n = 16$) were in habitats identified as secondary source, 10% ($n = 3$) were in primary sink, and 20% ($n = 6$) were in low-occurrence habitats. We summed all of the peak-male counts in 2009 to see if there was a relationship
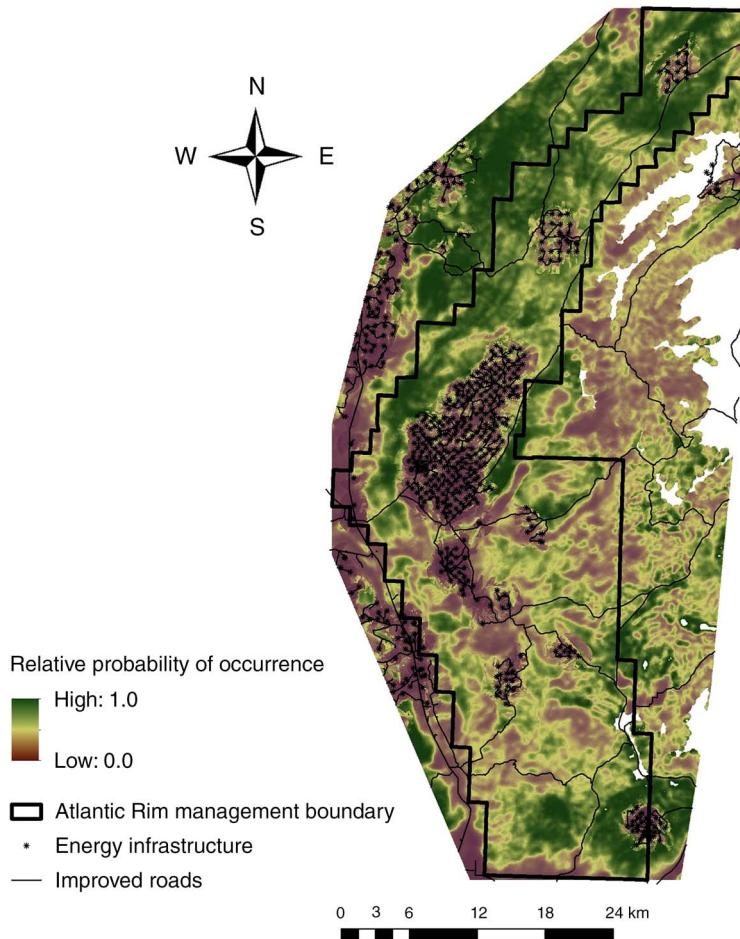
Fig. 3. Predicted relative probability of female Sage-Grouse occurrence throughout the summer (resource selection functions for all life stages were weighted based on their importance to λ, summed and rescaled; see Appendix: Fig. A1) in south-central Wyoming, USA. The map displays the relative probability of occurrence by females with 1 (green) being the highest and 0 (brown) being the lowest probability.

between male numbers and predicted source habitats. Of the total number of males counted in 2009 ($n = 678$), 51% were lekking in primary source habitat and an additional 26% were lekking in secondary source. Further, one lek that contained another 15% of the lekking males was located in low-occurrence habitat, but was immediately adjacent to (74 m from) contiguous primary source habitat. Therefore, 92% of all of the males counted in 2009 were within or immediately adjacent to predicted source habitat. Lek data suggest that our source–sink designation corresponded well with lek locations and lekking activity.

DISCUSSION

Successful management and conservation of wildlife requires that habitat suitability as well as habitat quality (demographic metrics of reproduction and survival; Hall et al. 1997) be incorporated within conservation prioritizations. Our predictions of land-scape-level habitat use and fitness outcomes presented in terms of source and sink habitat quantifications offer a means of prioritizing Sage-Grouse habitat as it relates to population-level dynamics at the scale of an energy development project. Through the spatial identification of high-value (i.e., primary source) as well as subop-timal (i.e., primary sink) habitats, we can inform energy infrastructure siting to minimize the effects of energy development to Sage-Grouse on-site as well as informing potential mitigation actions. Research on Sage-Grouse and other avian species has also shown variations in occurrence and fitness at multiple scales (Robinson et al. 1995, Chalfoun and Martin 2007, Doherty et al. 2010). We found predictive variables for Sage-Grouse occurrence during the nesting, early and late brood-rearing, and non-brooding life stages, as well as demographic responses related to nest and female survival, that spanned multiple spatial scales (Tables 3 and 4).

Anthropogenic variables related to coalbed natural gas (CBNG) development were ubiquitous in all of the
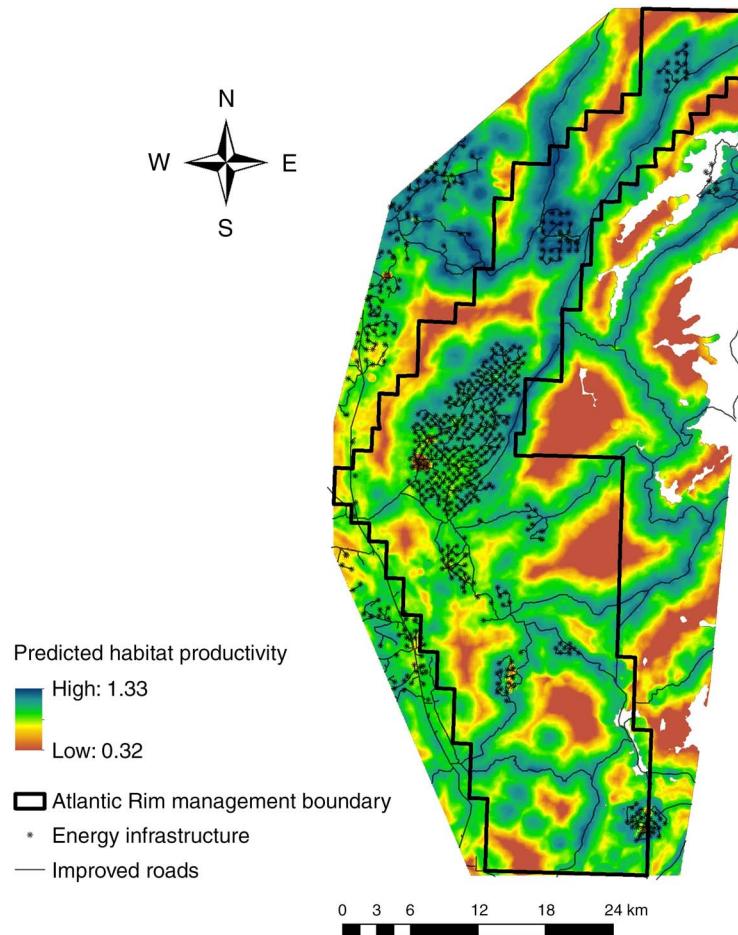
FIG. 4. Predicted habitat productivity based on variable adjusted survival probability functions specific to Sage-Grouse nest, brood, and summer female (brooding or non-brooding) survival, as well as fixed vital rates incorporated into a fitness metric model, in south-central Wyoming, USA. The map displays a continuum from the highest predicted productivity value (dark blue) to the lowest (brown).

final occurrence models; for each life stage, there was at least one energy feature (e.g., visual wells or surface disturbance) that was negatively associated with habitat selection. Avoidance responses of Sage-Grouse and other species to energy infrastructure have been extensively documented (see Johnson et al. 2005, Sawyer et al. 2006, Doherty et al. 2008, Gilbert and Chalfoun 2011, Smith et al. 2014). Visual well density was negatively correlated with female Sage-Grouse occurrence during nesting and early brood-rearing as well as early and late non-brooding. For example, the addition of one visible well within 0.564 km of a nest decreased the relative probability of occurrence by ~52%. Researchers studying Sage-Grouse in other areas being influenced by oil and gas development also have identified negative relationships between well or visible well densities and occurrence during different life stages (Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008, Carpenter et al. 2010). However, our results suggested that anthropogenic features were not always

avoided and this depended on the female life stage. For example, during the late brood-rearing period, brooding females seemed to be tolerant of haul roads; however, on average, they were using habitats ~1 km away.

Our source–sink map suggests that primary and secondary source habitats in our study area, although still relatively abundant (59% of the landscape), were becoming low-occurrence areas because of female Sage-Grouse avoidance of energy features and disturbance across female summer life stages. Thus, avoidance appears to be resulting in what has been described as functional habitat loss (Aldridge and Boyce 2007). Our results provide strong evidence that population-level impacts to Sage-Grouse from energy development are at least initially largely driven by avoidance or displacement due to anthropogenic disturbance and not fitness consequences. This is in contrast to other research reporting that short-term consequences of human development are driven more by infrastructure impacts to demographics rather than distributions (Holloran
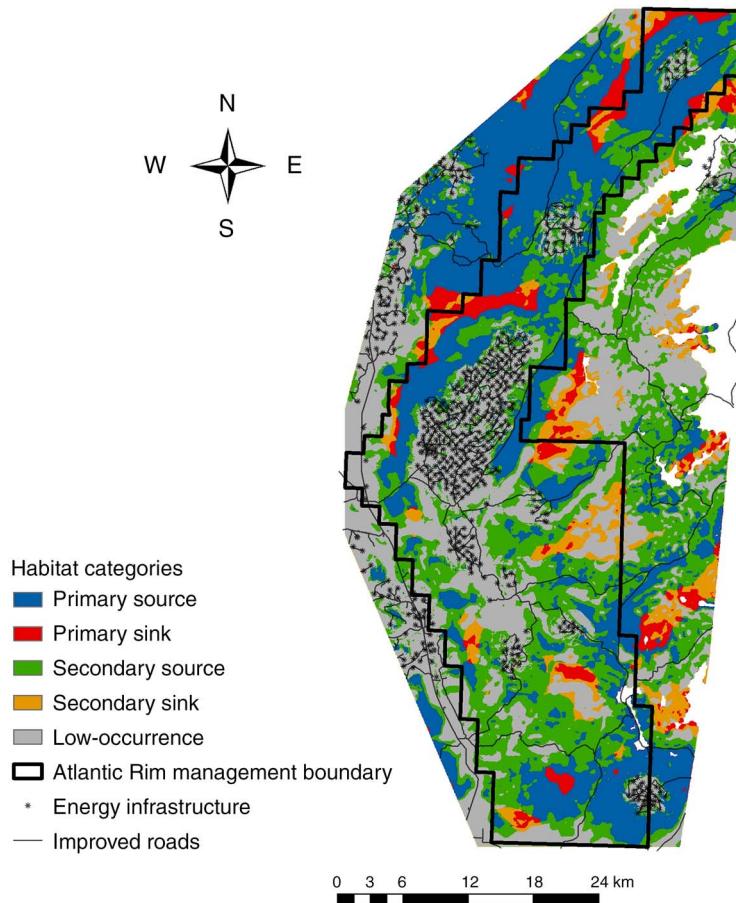
FIG. 5.   Predicted sink and source habitats for Sage-Grouse in south-central Wyoming, USA. The habitat categories are based on the fitness metric threshold of 1 (ranking habitats into high and low productivity habitats) and a three-quantile partition of the relative probabilities of occurrence predicted by our female summer occurrence map. The quantification of source–sink categories is described in Table 2.

2005, LeBeau et al. 2014) or studies finding that human development can result in ecological traps for Sage-Grouse (Aldridge and Boyce 2007). This dichotomy may be due to differences in the amount of undisturbed habitat available to the local population or to differences in the type of infrastructure and intensity of development.

Similar to other landscape-scale research (Aldridge and Boyce 2007, Doherty et al. 2010) as well as local-scale research (Holloran et al. 2005, Hagen et al. 2007, Doherty et al. 2010), nest occurrence in the ARPA was strongly correlated with big sagebrush canopy cover. In addition, 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 females. During nesting, Sage-Grouse in the ARPA appeared to be selecting for high sagebrush cover and then selecting for moderate sagebrush cover during early and late brood-rearing. This is in contrast to other studies reporting that at a landscape scale, Sage-Grouse select for moderate sagebrush cover during nesting (Aldridge and Boyce

2007, Doherty et al. 2008). Further, our results suggest that during nesting, selection for greater sagebrush cover, specifically Wyoming sagebrush cover, resulted in increased nest survival. This finding is supported by other research showing that shrub cover has a positive relationship to nest success (Kolada et al. 2009) and reduces the likelihood that avian nest predators, such as the Common Raven (*Corvus corax*), will locate nests (Coates and Delehanty 2010).

Our findings suggest a positive association between shrub height variability and survival throughout the summer: the predictor, variability in shrub height at a 1-km^2 scale, was omnipresent in nest, brood, and adult female SPFs. Thus, stands with homogenous vertical cover of sagebrush and other shrub species appeared to be riskier habitats for females in every summer life stage. We are unaware of any other studies that 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.

PLATE 1. A female Sage-Grouse with chicks (the head of another chick is visible in the background) shown in the Atlantic Rim study area, south-central Wyoming, USA, in mid-summer. Photo credit: C. P. Kirol.

Adult female summer survival was negatively correlated with terrain roughness at the largest landscape scale (5 km^2). This finding suggests that habitats with greater amounts of topographic relief were riskier habitats for female Sage-Grouse during summer. In the ARPA, this would include several prominent drainage basins and ridgelines that may have provided perching and nesting substrates for avian Sage-Grouse predators such as Golden Eagles (*Aquila chrysaetos*). Unexpectedly, we also found that habitats farther from anthropogenic edge were riskier for adult females. Dinkins et al. (2014) found a very similar relationship for female survival (e.g., higher female survival with greater haul road densities and lower terrain roughness) and oil and gas development. We suspect that this relationship is largely explained by the fact that energy infrastructure and haul roads were disproportionately located in less rugged topography (i.e., lower terrain roughness with higher female survival) that is more conducive to energy development.

With the exception of brood survival, anthropogenic features did not broadly influence fitness throughout female summer life stages. That is, our findings suggest that avoidance of anthropogenic features by female Sage-Grouse was the primary mechanism at work. This makes sense because our survival findings are dictated by the female's habitat choices. Because energy development habitats were primarily being avoided by female Sage-Grouse, potential fitness outcomes related to infrastructure probably were not realized. This is reflected in our source–sink map suggesting that many of the infrastructure areas fell in the low-occurrence category but were surrounded by source habitat. Further, our source–sink map predicted a minimal amount of sink habitat (10%; Fig. 4), which has been shown to be detrimental to Sage-Grouse and other avian species in human-altered landscapes (Misenhelter and Rotenberry 2000, Aldridge and Boyce 2007, Pearson and Fraterrigo 2011). Yet, chick survival is a critical parameter for Sage-Grouse population growth (Taylor et al. 2012). Our results suggest that brood survival was influenced by the level of surface disturbance associated with energy development. To a point, surface disturbance in habitats being used by brooding females

appeared to have little influence on brood survival; however, once disturbance reached 4–5%, the risk of brood loss began to increase. At the same spatial scale, Aldridge and Boyce (2007) found that daily Sage-Grouse chick survival (56 days) decreased with greater well densities. Similar relationships have been found in other species, such as the grizzly bear (*Ursus arctos horribilis*), which showed an increase in survival risk strongly correlated with anthropogenic habitats in general (Johnson et al. 2004).

The predicted FM values (productivity map) and corresponding source–sink predictions have limitations. A principal limitation is that our sink and source designations were based on vital rates estimated from two years of data collected during the initial stages of development on the ARPA. Although our demographic rate estimates were consistent with the literature, demographic rates may vary more on an annual basis than we documented (see Connelly et al. 2011). Further, effects on productivity and survival related to energy development may lag behind additions of infrastructure to the landscape (Harju et al. 2010), and extensive energy infrastructure in the ARPA was fairly new to the landscape (<5 years). Our study focused on identifying immediate and direct effects of anthropogenic features to use in predicting the importance of habitat that remained. In an attempt to prevent overestimating productivity and thus source habitats, we took a conservative approach in our FM model by incorporating fixed demographics from the lower range of values reported in the Sage-Grouse literature. Density dependence could be a factor if functional habitats are being avoided and this probably would manifest over a longer period of time. Ideally, we would have monitored nesting females daily; however, due to financial restraints and the size of our study area, we did not have the resources to maintain this relocation frequency. Therefore, our relocation frequency (6.21 ± 0.16 days) may explain our low nest initiation rate (59%; see Schroeder et al. 1999). Because this initiation rate is a component of our FM model, the FM estimates probably are also biased slightly low. Finally, we acknowledge that as habitat conditions change due to environmental and anthropogenic factors, source–sink dynamics may change; thus, in the context of expanding infrastructure, periodic updates to the model that incorporate Sage-Grouse monitoring data may be warranted.

Our research represents management-oriented science that is especially important for conservation of the Sage-Grouse because the majority of sagebrush habitats are managed by public agencies with multiple-use mandates (USFWS 2010). Thus, balancing land and resource use with Sage-Grouse conservation is a complex challenge. To date, leks have been the main focus of Sage-Grouse conservation and management (Harju et al. 2010). Our post hoc analysis of lekking activity in the ARPA and our source–sink model provided greater confidence in our approach because primary and secondary source habitats correlated well with active leks and peak counts of males on those leks. The correlation between lek activity and primary and secondary source habitats is suggestive of modeling or accurately designating habitats that are a source of Sage-Grouse; it does not suggest that protection at the scale of individual leks is sufficient to conserve Sage-Grouse in an energy development field (Naugle et al. 2011). Given the spatial juxtaposition of source and low-occurrence habitats (see Fig. 5), future energy development in the ARPA could potentially further restrict source habitat by resulting in habitats becoming low-occurrence habitats due to expanding infrastructure. Our results suggest that there is an increased likelihood of Sage-Grouse population persistence if the identified primary and secondary source habitats are left intact. Further, because local population dynamics depend on a balance between mortality and fecundity as well as demographic subsides from adjacent sources (Pearson and Fraterrigo 2011), primary source habitats may provide a surplus of dispersers to recolonize development areas as oil and gas resources are exhausted and energy fields are reclaimed. We believe that the analytical framework we present provides a means for wildlife conservation in areas where species conservation and human energy demands collide. Consequently, our approach to link occurrence and fitness within a source–sink framework should be useful to others developing conservation plans for species that inhabit anthropogenic landscapes.

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SUPPLEMENTAL MATERIAL

Appendix

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