Environmental Management (2016) 58:585–596
DOI 10.1007/s00267-016-0745-8

RESEARCH

Does Wyoming's Core Area Policy Protect Winter Habitats for Greater Sage-Grouse?

Kurt T. Smith[1] · **Jeffrey L. Beck**[1] · **Aaron C. Pratt**[1]

Received: 24 September 2015 / Accepted: 23 July 2016 / Published online: 11 August 2016
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Abstract Conservation reserves established to protect important habitat for wildlife species are used world-wide as a wildlife conservation measure. Effective reserves must adequately protect year-round habitats to maintain wildlife populations. Wyoming's Sage-Grouse Core Area policy was established to protect breeding habitats for greater sage-grouse (*Centrocercus urophasianus*). Protecting only one important seasonal habitat could result in loss or degradation of other important habitats and potential declines in local populations. The purpose of our study was to identify the timing of winter habitat use, the extent which individuals breeding in Core Areas used winter habitats, and develop resource selection functions to assess effectiveness of Core Areas in conserving sage-grouse winter habitats in portions of 5 Core Areas in central and north-central Wyoming during winters 2011–2015. We found that use of winter habitats occured over a longer period than current Core Area winter timing stipulations and a substantial amount of winter habitat outside of Core Areas was used by individuals that bred in Core Areas, particularly in smaller Core Areas. Resource selection functions for each study area indicated that sage-grouse were selecting habitats in response to landscapes dominated by big sagebrush and flatter topography similar to other research on sage-grouse winter habitat selection. The substantial portion of sage-grouse locations and predicted probability of selection during winter outside small Core Areas illustrate that winter requirements for sage-grouse are not adequately met by existing Core Areas. Consequently, further considerations for identifying and managing important winter sage-grouse habitats under Wyoming's Core Area Policy are warranted.

Keywords *Centrocercus urophasianus* · Sage-grouse · Resource selection functions · Winter habitat selection · Wyoming sage-grouse core area policy

Introduction

Conservation reserves designed to protect habitats have been established to maintain viable wildlife populations and biodiversity in protected areas. Approximately 14.6 % of Earth's land surface is designated as protected areas for conservation (Butchart et al. 2015). Early advocates of conservation reserves generally regarded that reserve size would predict the reserves ability to maintain species abundance and diversity (e.g., Diamond 1975). However, regardless of size, protected areas may not sufficiently capture habitat needs of a species on a yearly basis. This is particularly the case for species with large home ranges that move between distinct seasonal habitats. Information regarding a species annual distribution and selection of habitats, within and outside of breeding seasons, is necessary when designating protection areas for conserving habitats (Johnson et al. 2004).

One analysis suggests greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) occupy approximately 56 % of their potential pre-settlement habitat in 11 states and 2 Canadian provinces and are closely linked to sagebrush (*Artemisia* spp.) habitats (Schroeder et al. 2004). Long-term declines of sage-grouse across much of the

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✉ Kurt T. Smith
ksmith94@uwyo.edu

[1] Department of Ecosystem Science and Management, College of Agriculture and Natural Resources, University of Wyoming, Dept. 3354, 1000 E University Ave, Laramie, WY 82071, USA

species range (Connelly and Braun, 1997) are largely attributed to landscape change resulting in direct loss and fragmentation of sagebrush habitats (Braun 1998; Connelly et al. 2004). Land changes including agricultural development (Swenson et al. 1987), energy development (Doherty et al. 2008, 2011; Harju et al. 2010; Gregory and Beck 2014; LeBeau et al. 2014), urban and exurban development (Braun 1998; Connelly et al. 2004), livestock grazing (Beck and Mitchell 2000; Boyd et al, 2014), and fire (Connelly et al. 2000a; Blomberg et al. 2012) have resulted in declining populations, with the effects of different disturbances acting synergistically to influence sage-grouse populations (Hess and Beck 2012).

Wyoming's Sage-Grouse Core Area Policy (hereafter, Core Area) was implemented to limit disturbance (activities that result in removal of sage-grouse habitat) in areas of high sage-grouse breeding population densities by setting disturbance limits and timing stipulations (Doherty et al. 2011; Kiesecker et al. 2011; State of Wyoming 2011). Core Areas were originally defined by Doherty et al. (2011) who delineated priority nesting areas based on proximity of surrounding leks and habitat within 6.4 km of leks. Breeding density areas were modeled by assigning an abundance-weighted density of male sage-grouse to each lek until 75 % (core75) of the population was included. The Wyoming Core Areas represent an adapted version of core75 areas defined by Doherty et al. (2011), modified to incorporate multiple land-use decisions such as leased oil and gas well sites or planned residential development. Build-out scenarios suggest that Core Areas focused on breeding habitats may reduce projected long term sage-grouse population declines (Copeland et al. 2013). However, because breeding habitats may not contain all habitats necessary for survival, protection of crucial habitats must focus on all seasonal requirements for effective sage-grouse conservation (Doherty et al. 2011; Fedy et al. 2012). Winter survival estimates for sage-grouse are generally higher (78–97 %; Beck et al. 2006; Baxter et al. 2013) than annual breeding-age survival rates (58 %; Taylor et al. 2012), but winter survival may be depressed during severe winter conditions (Moynahan et al. 2006; Anthony and Willis 2009). Adult female survival is of critical importance for sage-grouse population viability (Taylor et al, 2012; Dahlgren et al. 2016); consequently, winter survival of females may represent a significant vital rate for population persistence (Moynahan et al. 2006). The effectiveness of Core Areas hinge on their ability to not only protect high quality breeding habitats used by sage-grouse, but also habitats necessary for survival during other seasons.

The Core Area Policy suggests that the majority of winter habitat likely occurs inside Core Areas (State of Wyoming 2011). Approximately 90 % of sage-grouse yearlong habitat use was within 5 km of lek sites in the Bi-State Population in eastern California and western Nevada (Coates et al. 2013), suggesting that breeding habitats include a large portion of year-round habitats for sage-grouse in that region. Conversely, Fedy et al. (2012) found that the average movement of sage-grouse from late summer to winter areas averaged 17.3 km, with 31 to 100 % of winter locations occurring within 100 % Core Areas for 11 study populations distributed across Wyoming indicating that a substantial portion of winter habitat use by sage-grouse populations may occur outside Core Areas. Because habitat selection varies considerably across seasons (e.g., Fedy et al. 2014), Core Areas are unlikely to afford protection for sage-grouse outside of the breeding season unless winter areas are in close proximity to breeding habitats. Also, if winter habitats represent a limiting seasonal habitat within Core Areas, special conservation strategies must be implemented to create additional protection in critical wintering areas.

Seasonal use restrictions are in place to limit disturbance activities in identified winter concentration areas both in and out of Core Areas from 1 December to 15 March (State of Wyoming 2011; BLM 2012). The Wyoming Sage-grouse Executive Order (SGEO) suggests that disturbance in non-Core Areas should be minimized in mature sagebrush habitats in winter concentration areas (State of Wyoming 2011); however, no regulation has been established for these areas explicitly regulating the amount of allowable disturbance.

We used data collected from Global Positioning System (GPS)-marked female sage-grouse across two study areas that overlap portions of the Greater South Pass, Shell, Hyattville, Oregon Basin, and Washakie Core Areas to evaluate how well the Core Area policy protects sage-grouse winter habitats. Specifically, our objectives were to evaluate the effectiveness of Core Areas to protect sage-grouse winter habitats by (1) evaluating the timing of winter habitat use relative to current winter seasonal timing stipulations, (2) determining the portion of winter habitat use of individuals that use breeding habitats within Core Areas, and (3) developing winter resource selection functions (RSFs) for female sage-grouse to determine the amount and arrangement of winter habitats in relation to Core Areas.

Methods

Study Area

The Bighorn Basin study area (3834 km^2) was associated with the Hyattville, Oregon Basin, Shell, and Washakie Core Areas in eastern Big Horn and Washakie counties, and northeastern Hot Springs County, Wyoming (Figs. 1–3).

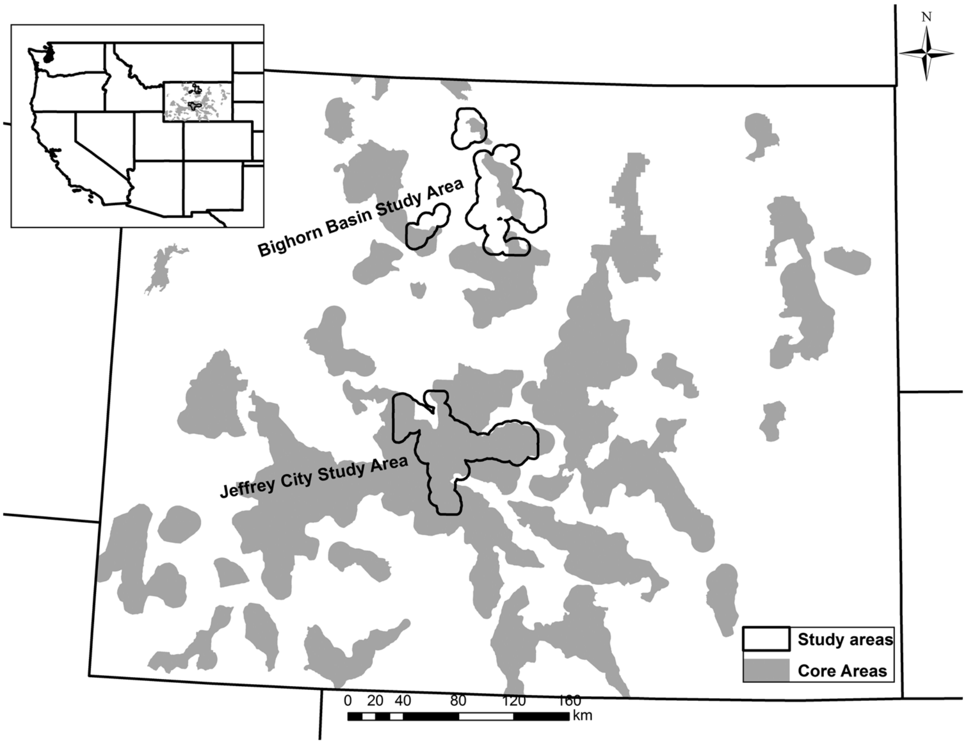

Fig. 1 Map of the two study areas based on 100 % kernel density estimates encompassing winter sage-grouse use locations in central and north-central Wyoming, USA, winters 2011–2015

The area included approximately 78.9 % Federal, 5.2 % State, and 15.9 % privately administered lands. The 30 year normal monthly precipitation averaged from November through March was 8.1 cm and ranged from 8.2 to 10.8 cm during 2011 to 2015 (Prism Climate Group 2016). Elevation ranged from 1157 to 2976 m. Major land uses in this area included bentonite mining, livestock grazing, and a variety of recreational activities. The 4144-km^2 Jeffrey City study area occurred in portions of Fremont, Natrona, and Sweetwater counties, Wyoming, within the Greater South Pass Core Area (Figs. 1 and 4). The area included approximately 82.4 % Federal, 7.3 % State, and 10.3 % privately administered lands. The 30 year normal monthly precipitation averaged from November through March was 6.6 cm and ranged from 5.1 to 7.8 cm during the study period (Prism Climate Group 2016). Elevation ranged from 1529 to 2524 m. Major land uses during the study included livestock grazing. There is interest to resume uranium ore mining that historically occurred in this area. Dominant shrub species that composed the shrub-steppe in both areas include Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), with communities of mountain big sagebrush (*A.t. vaseyana*) at higher elevations. Other shrub species occurring in each area included black sagebrush (*A. nova*), silver sagebrush (*A. cana*), rabbitbrush (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*), Gardner's saltbush (*Atriplex gardneri*), shadscale saltbush (*Atriplex confertifolia*), and greasewood (*Sarcobatus vermiculatus*).

Field Procedures and Monitoring

We captured and radio-marked female sage-grouse around leks during spring or at roost sites during summer in 2011–2014 by spot-lighting and hoop-netting (Giesen et al, 1982; Wakkinen et al., 1992). We attached GPS transmitters (22-g PTT-100 Solar Argos/GPS PTT [Microwave Telemetry, Columbia, MD, USA] or Model 22 GPS PTT [North Star Science and Technology, King George, VA, USA]) via rump mount. GPS transmitters were solar-powered and uploaded their GPS locations (±~20-m error) to satellites used by the Argos system (CLS America, Largo, MD, USA) every 3 days. Transmitters were programmed to acquire 3 locations per day from 1 November to 14 March (at 0900, 1200, and 1500 local time ignoring Daylight Savings Time), 4 locations per day from 15 March to 30 April and 25 August to 30 October (at 0700, 1000, 1300, 1600), 5 locations per day from 1 May to 24 August (at 0600, 0900, 1200, 1500, 1800), and included an additional location every night at midnight (2400). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Sage-grouse were captured, marked, processed, and monitored in adherence with approved protocols (Bighorn Basin study [Wyoming Game and Fish Department Chapter 33–800 permit and University of Wyoming Institutional Animal Care and Use Committee protocols 03142011 and 20140228JB00065]; Jeffrey City study [Wyoming Game and Fish Department

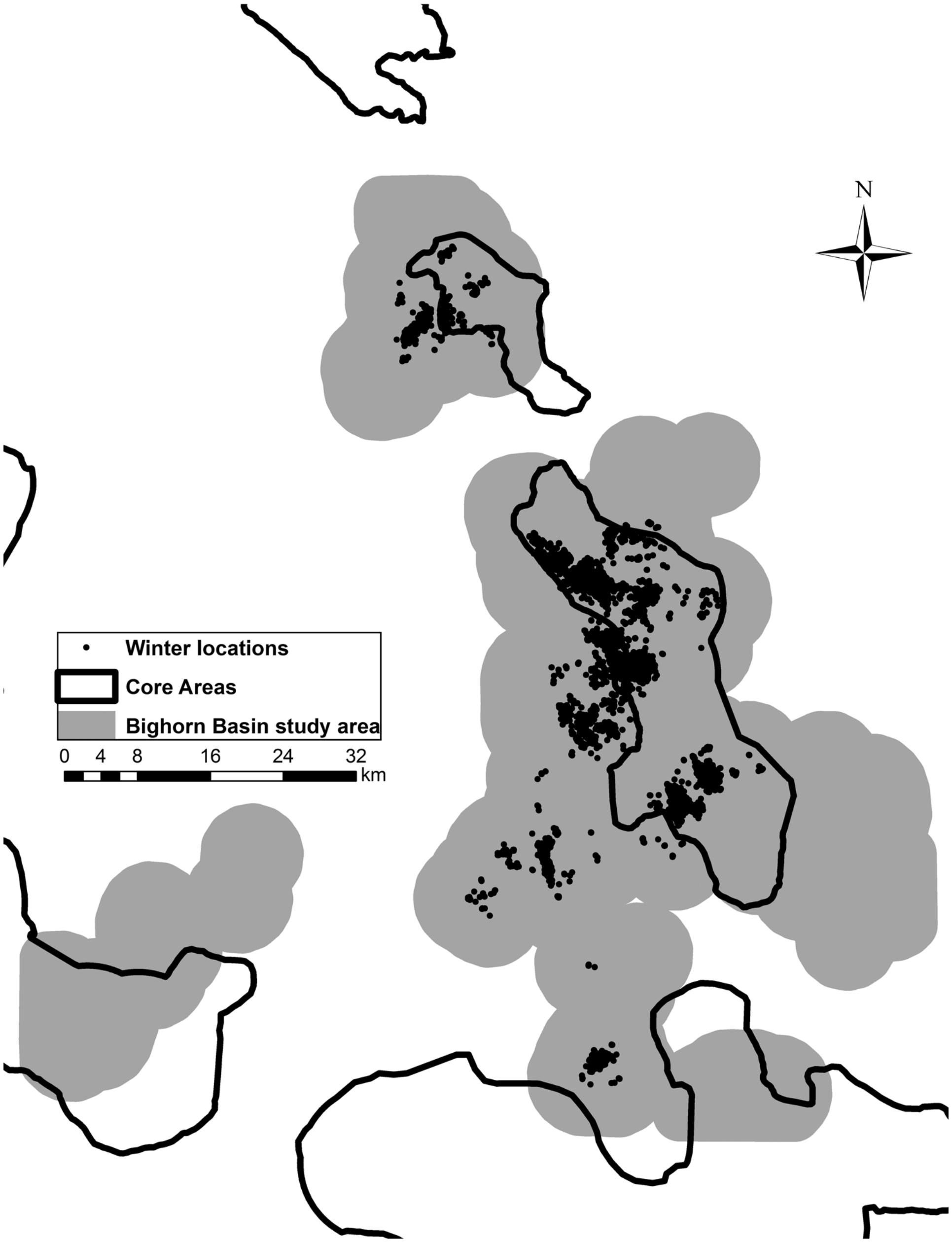

Fig. 2 Winter locations for 17 female greater sage-grouse that nested in Core Areas in the Bighorn Basin study area (3834-km^2), Wyoming, 2011–2015. Winter use locations were based on seasonal movement timing (26 Oct to 21 Mar; $n = 24{,}311$)

Chapter 33–801 permit and University of Wyoming Institutional Animal Care and Use Committee protocols 03132011 and 20140128JB0059]).

Timing of Winter Habitat Use and Proportion of Winter Use in Core Areas

We defined the winter season based on distinct movements of migratory individuals (≥10 km; Connelly et al. 2000b) between fall and winter, and winter and spring ranges. If individuals did not exhibit distinct movement to winter ranges, we used the average movement timing of migratory sage-grouse in each study area to delineate winter locations for that individual. We defined a female as a Core Area inhabitant if it nested within a Core Area. For those individuals, we determined the proportion of their locations in Core Areas during the winter season.

Sage-Grouse Resource Selection

Landscape Predictor Variables

We used a suite of remotely sensed vegetation, topography, and anthropogenic predictor variables that have been shown

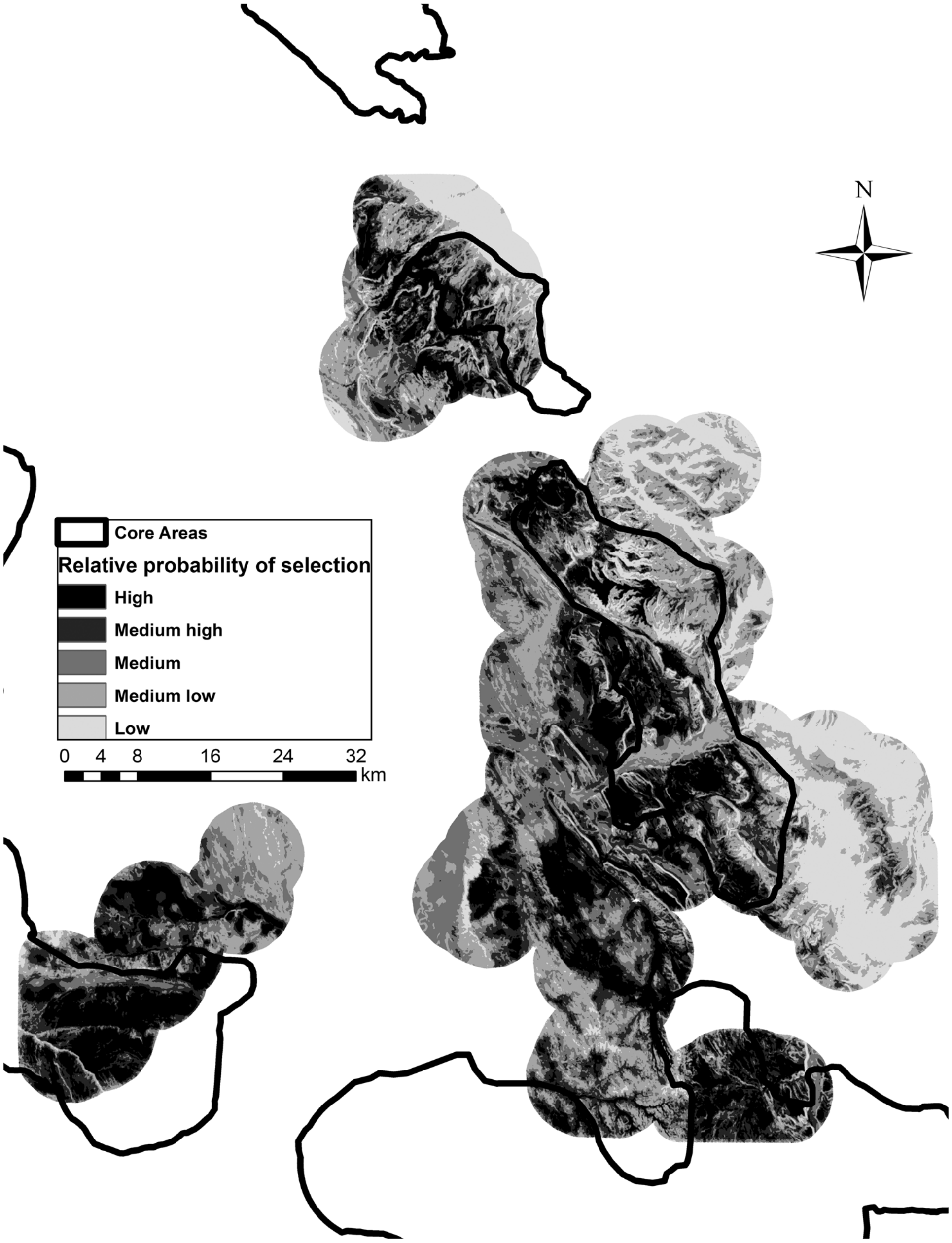

Fig. 3 Predicted probability of sage-grouse winter habitat selection in the 3834-km^2 Bighorn Basin study area during winters 2011–2015. This map spatially depicts a resource selection function that was binned into five quantiles of predicted relative probability of occurrence

to influence sage-grouse winter habitat selection in other studies (Homer et al. 1993; Doherty et al. 2008; Carpenter et al. 2010; Fedy et al. 2014; Smith et al. 2014; Table 1). We evaluated variables at six analysis scales: 0.1-km radii (0.03 km^2), 0.25-km radii (0.20 km^2), 0.5-km radii (0.79 km^2), 1.0-km radii (3.14 km^2), 2.0-km radii (12.56 km^2), and 3.2-km radii (32.15 km^2). Scales were similar to other studies evaluating sage-grouse winter habitat selection (Doherty et al. 2008; Carpenter et al. 2010; Dzialak et al. 2013; Smith et al. 2014; Walker et al. 2016), and are relevant to sage-grouse management (*sensu* Walker et al. 2016).

We derived land cover and vegetation variables from the U.S. Department of Agriculture Forest Service LANDFIRE Existing Vegetation Type raster dataset to estimate land cover type for big sagebrush, shrub, and forest land cover (i.e., dominant land cover within a 30 × 30 m pixel; LANDFIRE 2013). We used LANDFIRE products because they were readily available and spatial coverage included both study areas as well as most western range land systems. We used a 30-m digital elevation map (DEM; U.S. Geological Survey 2011) to calculate slope, a Topographic Ruggedness Index (TRI), and a Topographic Wetness Index (TWI). TRI is a measure of the difference between local elevation and the mean of the elevation at the surrounding 8 raster cells; higher values correspond to increasing ruggedness (Riley et al. 1999). TWI measured wetness

Table 1 Variables used for model selection evaluating greater sage-grouse winter habitat selection in central and north-central Wyoming, USA, winters 2011–2015

Variable name	Description
Environmental	
Bsage	Proportion of big sagebrush land cover (*Artemisia* spp.; LANDFIRE 2013)
Shrub	Proportion of shrub land cover (LANDFIRE 2013)
Forest	Proportion of forest land cover (LANDFIRE 2013)
Slope	Mean slope (%) derived from 30-m digital elevation map (DEM; USGS 2011)
NDVI	Mean normalized difference vegetation index derived from NAIP imagery (USDA 2012)
TWI	Mean topographic wetness index (TWI; high values = increased soil moisture; Theobald 2007)
TRI	Mean topographic ruggedness (TRI; high values = increased ruggedness; Riley et al. 1999).
Anthropogenic	
TDstbarea	Total surface disturbance (ha); any bare ground resulting from vegetation removal
MajRd	Surface disturbance (ha); bare ground resulting from vegetation removal for improved roads
MinRd	Surface disturbance (ha); bare ground resulting from vegetation removal for minor roads
GenD	Surface disturbance (ha); bare ground resulting from vegetation removal, excluding major and minor roads
DistTDstbarea	Average Euclidean distance (km) to TDstbarea
DistMajRd	Average Euclidean distance (km) to MajRd
DistMinRd	Average Euclidean distance (km) to MinRd
DistGenD	Average Euclidean distance (km) to GenD

potential based on drainage of the local slope and upslope (integration of slope and aspect; Sorensen et al. 2006; Theobald 2007). TWI incorporates solar insulation to identify differences in north- and south-facing aspects to predict soil moisture (Zinko et al. 2005).

We followed the Wyoming Density Disturbance Calculation Tool (DDCT) protocol to create time-stamped disturbance layers that quantified areas of bare ground resulting from removal of vegetation (Wyoming Geographic Information Science Center 2016). Disturbances included energy infrastructure, roads, and non-energy related disturbance such as human structures. We obtained road data for Wyoming from the U.S. Geological Survey (O'Donnell et al. 2014). We separated roads into major roads (i.e., improved gravel or paved roads) and minor roads (i.e., high-clearance four-wheel drive or two tracks). Major and minor roads were buffered by 10 m and 3 m, respectively. We inspected the accuracy, validated, and manually digitized remaining disturbances using 2012 and 2015 NAIP imagery (USDA 2012; USDA 2015).

Experimental Design and Statistical Analysis

We evaluated sage-grouse winter resource selection with a use-availability framework in each study area at the population level by pooling locations across individuals (Manley et al. 2002) and estimated the RSF with an exponential link function (Johnson et al. 2006, McDonald 2013). We identified use as locations of marked individuals during the winter season (defined above). Habitat availability was defined at the population level for each study area where we generated random locations at a rate of 20X grouse use locations within 100 % fixed kernels of GPS-marked sage-grouse winter locations using "adehabitat" package in R (default bivariate kernel smoothing parameter; Worton 1989). We modeled relative probability of selection using generalized estimating equations (GEE) with PROC GENMOD in SAS software 9.4 (SAS Institute Inc. 2012). GEE models provide robust standard error estimates, account for repeated observations of the same individual, and are appropriate for unbalanced designs while providing population averaged inference (Fieberg et al. 2009, 2010; Koper and Manseau 2009). Individuals and randomly assigned available locations in proportion to the number of used locations for each individual were assigned to clusters. We selected between independent and compound-symmetric correlation structures by comparing the ratio of empirical and model based standard error estimates and selected the working correlation structure with the lowest ratio (Koper and Manseau 2009). We used quasi-likelihood criteria (QIC) to assess model support (Pan 2001).

We performed a series of variable screening procedures to remove non-informative variables. We removed individual variables when 85 % confidence intervals for coefficients overlapped 0 (Arnold 2010). We determined the most predictive of the six analysis scales by comparing each variable scale individually and retained the scale with the lowest QIC value. We tested remaining predictor variables for collinearity ($|r| > 0.6$) and did not allow correlated variables to be included in the same model. We also checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($0.3 \leq |r| \leq 0.6$). If coefficient sign switching occurred, we did not permit these variables to compete in the same model.

We used a sequential modeling approach (Arnold 2010) by evaluating predictor variables within environmental and anthropogenic subsets. In the first level of model selection, we explored all variable combinations within the environmental and anthropogenic variable subsets separately (Burnham and Anderson 2002). The model with the lowest QIC value was identified as being the best fit model; however, models within 4 QIC of the best fit model were considered competitive (Arnold 2010). Competitive models within each variable subset were then allowed to compete across the environmental and anthropogenic variable subsets to assess model improvement. We assessed model fit by the weight of evidence (w_i) and differences between QIC (ΔQIC; Burnham and Anderson 2002) for the top model and candidate models.

We evaluated the performance of our top RSF for each study area using 5-fold cross validation. We randomly retained locations from approximately 80 % of the individuals to develop five RSF models from the most supportive GEE model and tested each RSF with the withheld data. We binned RSF predictions from each fold into 5 quantile intervals and performed linear regression on the number of observed locations from the test dataset vs. the expected test locations generated from each RSF bin adjusted by the midpoint of the raw RSF values and area of each bin (Johnson et al. 2006).

We mapped our final models with 30-m pixel resolution across each study area. We distributed relative probabilities into 5 RSF bins based on quantile breaks in probabilities to classify areas as low, medium to low, medium, medium high, and high probability of selection (Sawyer et al. 2006) representing increasing relative probability of selection.

Results

We obtained 24,311 locations from 38 female sage-grouse during 4 winters (2011–2015) in the Bighorn Basin study area and 19,689 winter locations from 34 female sage-grouse across 3 winters (2012–2015) in the Jeffrey City study area. The mean winter season, based on population averaged movements by individual grouse to and from winter range, was delineated as 26 October to 21 March for Bighorn Basin and 7 October to 21 March for Jeffrey City. Average movement distance from fall to winter range was 8.2 ± 1.7 km (range: 0–80.3 km) and 5.1 ± 1.3 km (range: 0–37.4 km) in the Bighorn Basin and Jeffrey City, respectively.

Of the individuals with nesting location data, 17 of 30 (56.7 %) nested in Core Areas in the Bighorn Basin study area. The portion of winter locations in Core Areas for those individuals was 62.5 ± 9.5 % (SE; Fig. 2). Three individuals (17.6 %) wintered entirely outside and 2 (11.7 %) wintered entirely inside Core Areas. In the Jeffrey City study area, all individuals nested in Core and 98.0 ± 1.4 % (SE) of winter locations were in Core Areas. Only 6 (17.6 %) of 34 individuals occupied a portion of any seasonal range outside of Core Area in Jeffrey City.

Sage-Grouse Resource Selection

Bighorn Basin Study Area

The top model explaining sage-grouse winter habitat use in the Bighorn Basin study area included 6 predictor variables across 4 analysis scales (Table 2). Sage-grouse selected areas with lower slope and less total surface disturbance at the 0.1-km radii scale, greater proportion of big sagebrush habitats and closer to minor roads within 0.5-km, lower surface area of major roads within 1.0-km, and lower proportion of forest habitats within 2.0-km (Table 3). Variables with 95 % confidence intervals of coefficients overlapping 0 included proportion of forest habitats, surface area of major roads, total surface disturbance, and distance to minor roads. We considered these variables to be marginal predictors, but they were retained to develop the RSF

Table 2 Top and competing models best explaining sage-grouse winter habitat selection in the Bighorn Basin and Jeffrey City study areas, Wyoming, winters 2011–2015

	Model fit statistics		
Model	K	ΔQIC	w_i
Bighorn Basin study area			
$[\mathrm{Bsage}_{0.5} + \mathrm{Forest}_{2.0} + \mathrm{Slope}_{0.1}]^{\mathrm{env}} + [\mathrm{DistMinRd}_{0.5} + \mathrm{MajRd}_{1.0} + \mathrm{TDstbarea}_{0.1}]^{\mathrm{anthro}}$	7	0.0	1.0
$[\mathrm{Bsage}_{0.5} + \mathrm{Forest}_{2.0} + \mathrm{Slope}_{0.1}]^{\mathrm{env}}$	4	660.0	0.0
$[\mathrm{DistMinRd}_{0.5} + \mathrm{MajRd}_{1.0} + \mathrm{TDstbarea}_{0.1}]^{\mathrm{anthro}}$	4	25458.8	0.0
Jeffrey City study area			
$[\mathrm{Bsage}_{0.25} + \mathrm{Slope}_{0.25}]^{\mathrm{env}}$	3	0.0	1.0
$[\mathrm{Bsage}_{0.25} + \mathrm{Slope}_{0.25}]^{\mathrm{env}} + [\mathrm{MajRd}_{3.2}]^{\mathrm{anthro}}$	4	833.8	0.0
$[\mathrm{MajRd}_{3.2}]^{\mathrm{anthro}}$	2	10584.1	0.0

surface because they influenced other variables in the model informing our RSF (e.g., Aldridge et al. 2012). Predicted high and medium-high areas of winter selection encompassed 37.7 % of the study area (1445 km^2; Fig. 3); 30.4 % of those areas were in Core Areas. Cross-validation indicated that the top model performed well at predicting winter habitat selection within the study area with high r^2 values from linear regression models of observed vs. expected locations in each RSF bin (average $r^2 = 0.92 \pm 0.04$ SE), intercept coefficients did not differ from 0, slope coefficients differed from 0 in all but 1 fold, and slope coefficients did not differ from 1.

Table 3 Estimated variable coefficients, standard errors (SE), and 95 % confidence intervals (CI) for variables that were included in top models depicting population-level sage-grouse winter habitat selection in Jeffrey City and Bighorn Basin study areas, Wyoming, winters 2011–2015

			95 % CI	
Parameter	Estimate	SE	Lower	Upper
Bighorn Basin study area				
Bsage$_{0.5}$	0.0037	0.0006	0.0025	0.0049
Forest$_{2.0}$	−0.0002	0.0002	−0.0005	0.0001
Slope$_{0.1}$	−0.2264	0.0287	−0.2827	−0.1701
DistMinRd$_{0.5}$	−0.0002	0.0001	−0.0005	0.0000
MajRd$_{1.0}$	−0.0000	0.0000	−0.0001	0.0000
TDstbarea$_{0.1}$	−0.0000	0.0000	−0.0000	0.0000
Jeffrey City study area				
Bsage$_{0.25}$	0.0115	0.0036	0.0044	0.0186
Slope$_{0.25}$	−0.3090	0.0593	−0.4253	−0.1927

Jeffrey City Study Area

The model that best explained sage-grouse winter habitat selection in the Jeffrey City study area included 2 predictor variables at the 0.25-km radii scale (Table 2); greater proportion of big sagebrush and lower slopes within 0.25-km (Table 3). We predicted high or medium-high winter habitat selection across 39.6 % of the Jeffrey City study area (1643 km^2; Fig. 4). Our top model was a strong predictor of selection. Linear regressions of observed vs. expected winter locations produced high r^2 values (average $r^2 = 0.94 \pm 0.03$ SE). Intercept coefficients did not differ from 0, and slope coefficients differed from 0 and did not differ from 1 with the exception of 1 fold.

Discussion

The ability of a conservation area to maintain wildlife populations is a function of the reserves ability to meet seasonal habitat requirements. We found a meaningful portion of female sage-grouse occupying areas in winter

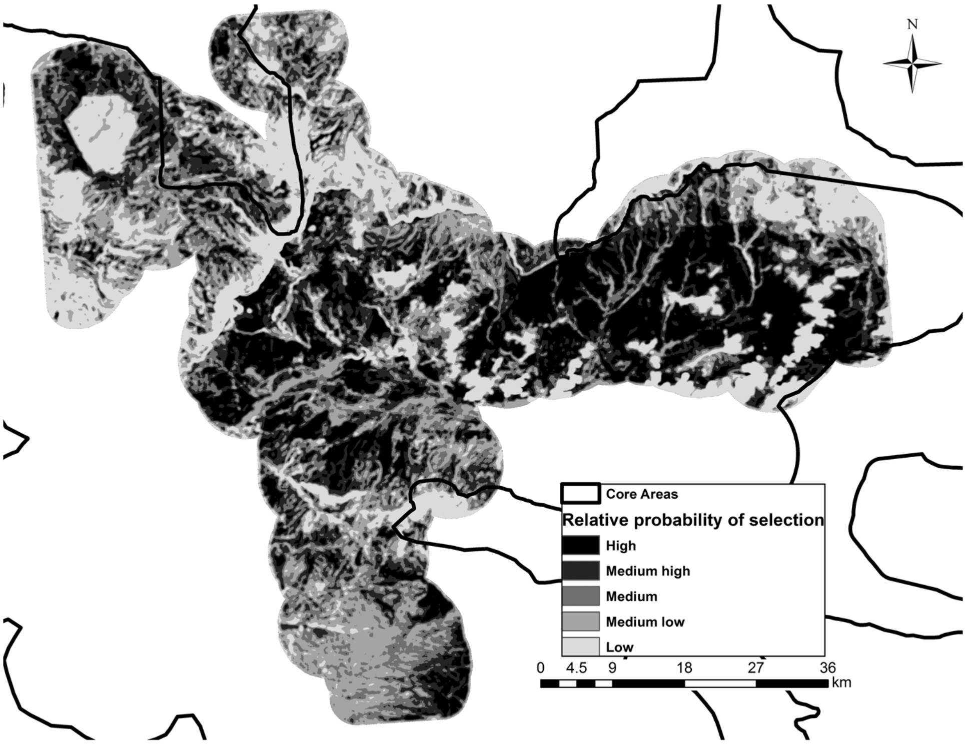

Fig. 4 Predicted probability of sage-grouse winter habitat selection in the 4144-km^2 Jeffrey City study area during winters 2012–2015. This map spatially depicts a resource selection function that was binned into five quantiles of predicted relative probability of occurrence

entirely outside of designated Core Areas in the Bighorn Basin. Because sage-grouse have a high fidelity to wintering areas (Connelly et al. 2004), highly used winter habitats that are compromised by development activities could negatively influence sage-grouse populations. This is supported by studies that documented sage-grouse avoidance of energy development and associated infrastructure during winter (Doherty et al, 2008; Carpenter et al. 2010; Smith et al. 2014; Holloran et al. 2015) and could result in indirect loss of otherwise suitable habitats (functional habitat loss; Aldridge and Boyce 2007; Smith et al. 2014).

Seasonal use restrictions in known winter concentration areas afford some level of protection during winter months. However, allowing disturbance outside of this period in known wintering areas may result in loss or subsequent avoidance of winter habitats. The timing of seasonal restrictions in winter concentration areas (1 Dec to 15 Mar; State of Wyoming 2011) must also align with the duration that sage-grouse spend on winter range. We found that the date of average movement from fall to winter habitat was earlier and that movement from winter to breeding habitat was later than current seasonal restrictions in both study areas. Minimal differences in the distribution of winter locations relative to our definition of the winter season and the Wyoming Core Area Policy stipulation of a 1 December to 15 March seasonal use restriction suggest that the distribution of winter locations (and presumably habitat use) was similar under these two definitions, yet winter habitats were used for considerably longer than the SGEO designation of the winter season. The Greater South Pass Core Area is the largest Core Area in Wyoming (~18,588 km^2) and likely contains a significant proportion of winter habitat for sage-grouse that occupy that region during breeding seasons. In the Jeffrey City study area, only 17.6 % of radio-marked individuals spent a portion of time in habitats outside of Core Areas. Individuals occupying smaller Core Areas likely relied on seasonal habitats outside of Core Areas to meet their annual life history requirements. Over one-third of the winter locations of GPS-marked females that nested in Core Areas in the Bighorn Basin study area occurred outside of Core Areas.

In both study areas, sage-grouse selected areas dominated by big sagebrush habitats and gentle slopes. Selection for landscapes dominated by big sagebrush is consistent with other studies that report sage-grouse selection of continuous sagebrush cover in winter. For example, Doherty et al. (2008) found that sage-grouse were more likely to occur in areas of greater sagebrush cover within 4-km^2 of winter grouse locations in northeast Wyoming. Sage-grouse selected less rugged areas with lower slopes in both study areas. Selection of areas with low topographic relief is consistent with findings of other studies evaluating sage-grouse winter habitat selection (Doherty et al. 2008; Carpenter et al. 2010, Dzialak et al. 2012, Walker et al. 2016).

Our models showed little support for anthropogenic variables being predictive of winter habitat selection. This was generally expected given the relatively low levels of disturbance in areas occupied by sage-grouse during winter in both study areas. We caution that while even low levels of disturbance may lead to habitat avoidance by sage-grouse, our estimates represent total surface disturbance that may not result in avoidance behaviors during the winter. For example, minor roads contributed to a significant portion of estimated surface disturbance across both study areas. However, minor roads are not counted in Wyoming's DDCT process. We found that grouse were selecting areas closer to minor roads in the Bighorn Basin study area, although this was considered a marginal predictor. Carpenter et al. (2010) found the opposite relationship for sage-grouse wintering in Alberta. However, the relative probability of selection did not increase greatly after habitat was greater than 1.2 km from a two track truck trail (Fig. 2 in Carpenter et al. 2010). Aldridge and Boyce (2007) and Kirol et al. (2015) found that brood-rearing females also selected areas closer to two track roads. Minor roads in both of our winter study areas were generally located in gentle topography and likely received little traffic volume, particularly in winter when snow precludes vehicle use in many areas.

We estimated that only one-third of predicted high and medium-high use winter habitat in the Bighorn Basin study area was in Core Areas, leaving a significant portion of predicted high and medium-high selected habitats outside of Core Area protection. We did not collect information regarding flock sizes of female sage-grouse in winter. Therefore, we did not explicitly model numbers of birds using areas in winter with our RSF models. However, sage-grouse generally exhibit flocking behaviors during winter (e.g. Beck 1977) and we assume that radio-marked individuals were representative of each population. It is likely that many more individual grouse were exhibiting similar patterns of winter habitat use and occupying these areas. Significant use by sage-grouse outside of Core Areas warrants further consideration for managing winter sage-grouse habitats in relation to Wyoming's Core Area Policy.

Land-use decisions that influenced Core Area boundaries resulted in removing some areas used by female sage-grouse from Core Area protection. Many areas outside of Core Areas identified as winter habitats contain breeding habitats, but were not included in Core Area designations to avoid existing development. The size and shape of constrained Core Areas relative to available sage-grouse breeding habitat in these areas resulted in more grouse locations falling outside Core Area protection during the breeding (15 Mar to 30 Jun) and winter (1 Dec to 15 Mar) seasons. This suggests seasonal use restrictions and potentially other means to avoid impacts should be afforded to winter habitats outside designated Core Areas, particularly in the Bighorn Basin where 17.6 % of sage-grouse did not winter in designated Core Areas and only 62.5 % of their winter locations fell within Core Areas. The amount and arrangement of winter habitats that fall outside of Core Areas dictates a need to assess Wyoming's Core Area Policy for future sage-grouse conservation. While Core Areas function as protection areas across a significant portion of sage-grouse breeding and nesting habitats throughout Wyoming, limited protection during other seasons does not support comprehensive sage-grouse conservation.

Acknowledgments The authors thank the American Colloid Company, the Wyoming Sage-Grouse Conservation Fund of the Wyoming Game and Fish Department; Bates Hole, Big Horn Basin, Southwest, South-Central and Wind River/Sweetwater River Local Sage-Grouse Working Groups; the Margaret and Sam Kelly Ornithological Research Fund; and the Wyoming Wildlife and Natural Resource Trust for supporting other facets of this research. We thank K. Lawson for assistance with spatial analyses. This work would not have been possible without the help of many research technicians who assisted with captures. We thank three anonymous reviewers for providing comments and improving earlier versions of our paper.

Funding Funding for this analysis was provided by the State of Wyoming Legislature through the Wyoming Wildlife and Natural Resource Trust on behalf of the Wyoming Sage-Grouse Implementation Team.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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