



Research Article

Approaches to Delineate Greater Sage-Grouse Winter Concentration Areas

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ABSTRACT The usefulness of protected areas as regulatory mechanisms to conserve wildlife populations relies on their ability to contain all seasonal habitats necessary for species persistence. Efficient conservation practices require understanding behavior and habitat needs of individual species and populations rather than simply relying on reserves of approximate size and configuration. Priority Areas of Conservation (PACs) have been delineated as protected areas based on known breeding habitat for greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) throughout their range. These PACs include Core Areas designated in the Wyoming Sage-grouse Executive Order; however, this order also indicated the need to identify winter concentration areas (WCAs; flocks ≥ 50 individuals) based on habitat features using validated resource selection functions (RSFs). We used aerial infrared videography to identify locations of wintering sage-grouse in south-central and southwest Wyoming, USA, to evaluate winter sage-grouse habitat selection with individual-based RSFs, RSFs based on WCAs, and relative flock size. We located 4,859 individuals comprising 132 flocks across our study area. Flocks occurred in Core Areas more than expected, but a biologically meaningful number of sage-grouse flocks were located outside of Core Areas. Individual-based RSFs contained useful predictors that were consistent with previous sage-grouse winter habitat selection studies. Flock size and WCA models produced similar predictions to individual-based RSF models. Individual-based and WCA-based RSF model predictions had a high degree of similarity, suggesting that identifying important winter habitats with individual-based RSF modeling is useful for locating potential WCAs when information on flock sizes is not available. Our results and survey technique provide a potential framework for identifying sage-grouse WCAs with implications for improving PAC protection of all seasonal habitats for sage-grouse conservation. © 2019 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, conservation policy, infrared surveys, winter concentration areas, winter habitat.

Protected areas conserve important habitats and maintain biodiversity of wildlife worldwide. Globally, protected areas encompass nearly 15% of terrestrial environments and contain higher species richness and abundance compared to unprotected areas (Butchart et al. 2015, Gray et al. 2016). The effectiveness of protected areas for conservation of mobile species depends on the size and composition of important seasonal habitats necessary for all life-history stages (Runge et al. 2014). For example, individual protected areas may be inadequate for migratory birds that travel long distances between seasonal habitats (Runge et al. 2015). Even short-distance migrants require connectivity among seasonal habitats for adequate conservation (Sawyer et al. 2009, Copeland et al. 2014). Species of concern may require a variety of seasonal

habitats to support their life-history characteristics, which suggests that conserving wildlife with protected areas requires comprehensive knowledge of the spatial distribution, arrangement, and components of seasonal habitats of focal species (Simberloff and Abele 1976, Johnson et al. 2004, Walker et al. 2016).

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are an emblematic species of the sagebrush (*Artemisia* spp.) steppe of western North America, having received considerable conservation attention as a result of long-term population declines (Connelly and Braun 1997, Western Association of Fish and Wildlife Agencies 2015) and several petitions to be listed under the Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 2015). Priority Areas for Conservation (PACs) were designated range-wide to protect high-quality sage-grouse habitats by limiting human land use and development in crucial areas for current sage-grouse populations (USFWS 2013). Boundaries of PACs in Wyoming, USA, were delineated by the Wyoming Core Area Strategy. The Core Area Strategy was developed to limit disturbance

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within 6.4 km around communal breeding grounds of sage-grouse, thereby conserving areas with the highest breeding population densities (State of Wyoming 2008, 2011; Doherty et al. 2011). Empirical studies support the effectiveness of the Core Area Strategy to maintain sage-grouse populations (Copeland et al. 2013, Gamo and Beck 2017, Spence et al. 2017, Burkhalter et al. 2018). But most sage-grouse populations in Core Areas continue to decline (Edmunds et al. 2018), though less than outside Core Areas (Spence et al. 2017), suggesting that focused conservation of other seasonal habitats may be necessary.

Conservation of sage-grouse breeding habitats through the Core Area Strategy provides protection of other seasonal habitats (e.g., winter habitat) required for sage-grouse populations (State of Wyoming 2015). Yet the Core Area Strategy acknowledges that essential seasonal habitats may occur outside of Core Areas; these areas may be necessary to fulfill seasonal habitat requirements of sage-grouse that breed in Core Areas (USFWS 2013, State of Wyoming 2015). Sage-grouse are a partially migratory species with many individuals within populations using spatially distinct breeding and winter habitats (Connelly et al. 2011, Dinkins et al. 2017, Pratt et al. 2017). During winter, sage-grouse generally require large expanses of sagebrush above snow in flatter terrain with few anthropogenic features (Doherty et al. 2008; Carpenter et al. 2010; Dzialak et al. 2012; Smith et al. 2014, 2016; Holloran et al. 2015). The Wyoming Sage-grouse Executive Order recognized a need to identify areas where sage-grouse exhibit concentrated winter use (winter concentration areas [WCAs]) because these areas may not have been adequately protected with the Core Area Strategy's focus on breeding habitat. Winter concentration areas are areas with consistent aggregation of ≥ 50 sage-grouse between 1 December and 14 March (State of Wyoming 2015). Unfortunately, information on spatially explicit abundance of sage-grouse during winter is rare, limiting the ability to relate winter habitat selection to sage-grouse densities. In the absence of clear spatial relationships between winter sage-grouse habitats and abundance, documentation of WCAs lags behind our knowledge of sage-grouse winter habitat requirements and space use during other critical periods. The Wyoming Sage-Grouse Executive Order indicated that WCAs should be identified based on habitat features using validated resource selection functions (RSFs; State of Wyoming 2015). This approach assumes that RSFs can estimate abundance of individuals in a flock, which contrasts with a more traditional design that compares used and available habitat. Resource selection functions are theoretically useful for approximating abundance or density of some species (Boyce and McDonald 1999). However, RSFs do not explicitly include information about relative abundance.

Our study was designed to detect locations of wintering sage-grouse and identify WCAs. We predicted that the majority of WCAs would be in Core Areas. We also expected that individual-based RSFs would be useful for identifying winter habitat used by sage-grouse, irrespective of flock size.

STUDY AREA

Our 44,543-km² study occurred in south-central and southwest Wyoming, USA, in portions of 8 Core Areas including Blacks Fork, Fontanelle, Greater South Pass, Sage, Salt Wells, Seedskafee, South Rawlins, and Uinta from 20 January to 5 February 2017 (Fig. 1). Wyoming big sagebrush (*A. tridentata wyomingensis*) communities dominated the area. Other species of sagebrush included black sagebrush (*A. nova*), low sagebrush (*A. arbuscula*). Mountain big sagebrush (*A.t. vaseyana*) occurred at higher elevations (Knight et al. 2014). For a more detailed description of the region, refer to Smith et al. (2014, 2016) and Dinkins et al. (2017).

METHODS

Aerial Infrared Flights

We used aerial infrared videography to identify locations of wintering sage-grouse in south-central and southwest Wyoming, USA. We contracted Owyhee Air Research, Nampa, Idaho, USA, to count sage-grouse with aerial infrared flights (cooled thermal imager positioned in a fixed-wing aircraft) from 20 January to 5 February 2017. We developed a standardized survey protocol for pilots to detect WCAs, which consisted of maximizing area surveyed per flight time. We designed survey units to contain 14, 30.6-km survey transects that were spaced 1,600 m apart (Fig. 1). We designed each transect to have an approximately 0.8-km wide view centered on the transect; thus, each survey unit had infrared videography of approximately 50% of the 685-km² survey area. Most (57%) of the area surveyed occurred in Core Areas. We surveyed in predominantly sagebrush areas (Landscape Fire and Resource Management Planning Tools Project; LANDFIRE 2013) that were $< 2,700$ m in elevation to avoid surveying areas that were unlikely to be winter habitats based on previous winter habitat selection studies in Wyoming (Smith et al. 2014, 2016; Dinkins et al. 2017). The altitude of surveys ensured that sage-grouse were not disturbed by the aircraft.

Pilots conducted surveys during daylight hours because test flights before those included in our study suggested higher detection of individuals compared to flights conducted at night. In addition, behavioral differences between night and day (e.g., snow burrowing at night) could reduce the availability of sage-grouse to be detected (Back et al. 1987; J. Romero, Owyhee Air Research, personal communication). When pilots located individual grouse, the aircraft left the transect line to obtain accurate counts and global positioning system (GPS) locations of individuals within flocks prior to resuming the survey. We assumed that detection was similar across survey transects. We feel this was a reasonable assumption during the day given the ability of infrared to accurately count prairie grouse at leks (Gillette et al. 2013, 2015). There is a paucity of information on the makeup of winter sage-grouse flocks, but available information suggests that individuals in winter flocks are often located within 200 m of each other (Beck 1977). Without additional information to assign flock membership based

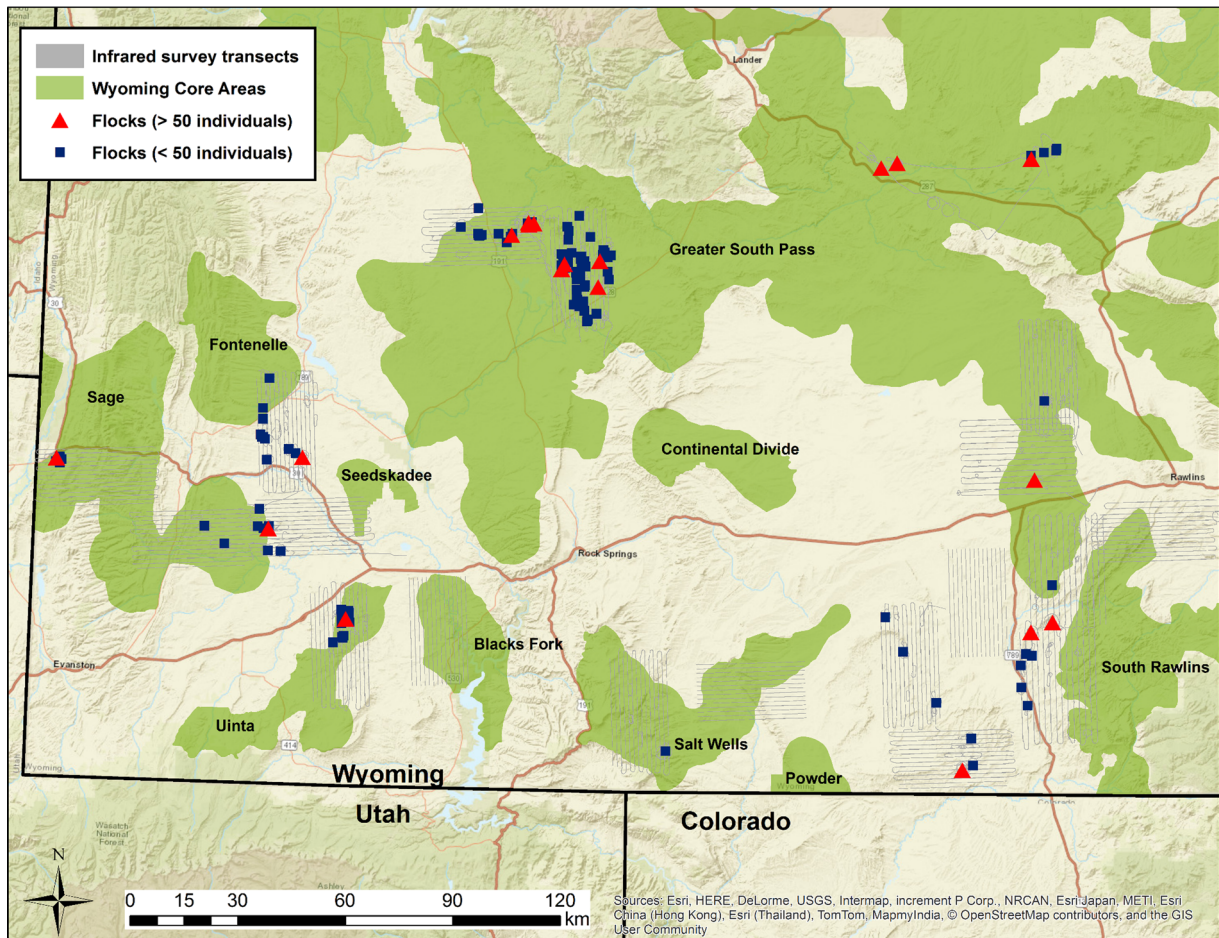


Figure 1. Study area depicting locations of infrared flight surveys of identified sage-grouse flocks greater than (red triangles) and less than (blue squares) 50 individuals in relation to Wyoming's Core Areas. Flights occurred in south-central and southwest, Wyoming, USA, between 20 January and 5 February 2017.

upon spacing of individuals, we used a simple procedure to identify flock membership by assigning individuals to a flock when they were located within 200 m of any other individual.

Predictor Variables

We evaluated all models using predictor variables describing grouse breeding densities, vegetation, topography, and anthropogenic landscape features. Breeding density variables included distance to occupied leks (Wyoming Game and Fish Department 2012) and the maximum male count from 2012 to 2016. We used maximum male lek count data obtained from the Wyoming Game and Fish Department annual sage-grouse lek survey database (Christiansen 2012). We summed maximum male counts across occupied leks within an 11.1-km circular region around individual sage-grouse within a flock. The 11.1-km region represented the maximum distance from an identified flock to a known lek and was designed to assess whether flock size was related to proximate breeding densities. We generated the proportion of sagebrush-dominated landscape from the LANDFIRE Existing Vegetation Type raster dataset (LANDFIRE 2013). Sagebrush landscapes were restricted to Great Basin xeric mixed sagebrush shrubland, Intermountain basins big

sagebrush shrubland, Columbia Plateau low sagebrush steppe, Intermountain basins big sagebrush steppe, and Intermountain basins montane sagebrush steppe identified from LANDFIRE (Donnelly et al. 2017). We estimated shrub height for all shrub species, and percent canopy cover of big sagebrush from remotely sensed products developed by Homer et al. (2012). We also assessed quadratic relationships for sagebrush and shrub height predictors because sage-grouse have demonstrated selection for intermediate values of sagebrush cover and shrub height during winter (Smith et al. 2014).

We used a 10-m digital elevation map (U.S. Geological Survey 2011) to calculate elevation, slope, and standard deviation of slope within a 5 × 5-pixel moving window. We used standard deviation of slope as an index of topographic ruggedness (Grohmann et al. 2011). We used the Geomorphometry and Gradient Metrics toolbox in ArcGIS (Environmental Systems Research Institute Redlands, CA, USA; Evans et al. 2014) to calculate a heat load index and compound topographic index. The heat load index approximated an index of coolest to warmest aspects (0–1; McCune and Keon 2002) and the compound topographic index was a steady state soil moisture index (higher values represent greater wetness; Gessler et al. 1995). We used

products generated for the Wyoming Basins Ecoregional Assessment to estimate distance to perennial and intermittent water to approximate mesic areas (Hanser et al. 2011). We assumed that more mesic areas would have taller sagebrush and potentially different sagebrush subspecies (Barker and McKell 1983), which may influence winter habitat selection by sage-grouse. We generated daily snow depth from validated meteorological distribution and snow-evolution models (Liston and Elder 2006a,b). Anthropogenic predictors included distance to roads and count of active and producing oil and coalbed natural gas wells. We calculated the Euclidean distance to state, county, United States, or interstate roads (O'Donnell et al. 2014), excluding minor 2-track roads because they likely receive little use in winter. We obtained producing oil and coalbed methane well data from the Wyoming Oil and Gas Conservation Commission (2017). We estimated the number of well pads by merging well heads within 60 m of each other and considered them to be a single well pad (Gamo and Beck 2017).

We assessed non-distance-based predictors across 5 circular regions and 4 concentric annuli: 0.4-km radii (0.5 km²), 0.8-km radii (2.0 km²), 1.6-km radii (8.0 km²), 3.2-km radii (32.2 km²), 6.4-km radii (128.7 km²), 0.4–0.8-km annuli (1.5 km²), 0.8–1.6-km annuli (6.0 km²), 1.6–3.2 km annuli (24.1 km²), and 3.2–6.4 km annuli (96.5 km²). Researchers have identified the importance of scale for winter sage-grouse habitat selection, and the circular regions we assessed have relevance to existing management stipulations (Doherty et al. 2008; Carpenter et al. 2010; Dzialak et al. 2013; Smith et al. 2014, 2016; Walker et al. 2016). We also included annuli to assess potential relationships between sage-grouse winter locations and surrounding areas, rather than mean values within circular regions. For example, 0.4–0.8-km annuli estimated mean values of habitat predictors between 0.4 and 0.8 km from a grouse location, excluding areas between 0.0 and 0.4 km.

Data Analyses

We first used a chi-squared goodness-of-fit test to evaluate whether flocks occurred in Core Areas in proportion to expectations based on the proportion of area surveyed by aerial infrared in Core and non-Core Areas. We used 3 approaches to predict sage-grouse winter habitat selection based on habitat features and population indices. First, we used locations of individuals identified from infrared surveys to develop sage-grouse winter habitat selection models as individual-based RSFs. Second, we developed an RSF comparing infrared-identified WCAs to available locations. Finally, we evaluated habitat differences related to flock sizes. We used second-order Akaike's Information Criterion (AIC_c) to assess model support for all models described below (Burnham and Anderson 2002). We employed initial variable screening by removing unsupported predictor variables when single-variable models had AIC_c scores that were less informative than null models. For variables that we considered across multiple circular regions and annuli, we retained the variable scale that had the lowest

AIC_c score if it was more informative than null models. We evaluated multicollinearity of remaining variables and did not allow variables to compete in the same model when $|r| > 0.6$. We assessed variable combinations to generate a set of competitive models (described for each model below). We considered models within 4 AIC_c of the best model to be competitive (Arnold 2010). To avoid potential shortcomings of model averaging when addressing model uncertainty across competitive models (Cade 2015), we present all competitive models in each modeling effort. We calculated the interpretation of change in relative selection probabilities per unit change in variables as the median change bound by the range of values for that variable using unstandardized model coefficients from the most parsimonious models. We only interpreted variables that had parameter estimates with 95% confidence intervals that excluded 0. We performed all statistical analyses in R version 3.3.2 (R Core Team 2016).

Winter resource selection.—We evaluated sage-grouse winter resource selection with a use–availability framework. We defined habitat availability for each individual by generating 35 times the number of available locations for each individual, constrained to a minimum convex polygon (MCP) surrounding all located individuals and extracted predictor variables at each individual and available location. We used 35 available locations per used location to ensure that the number of available locations adequately characterized the distribution of used locations (Northrup et al. 2013). This approach followed a Type 1 population-level design (Manly et al. 2002, Thomas and Taylor 2006) and allowed us to make predictions across a large landscape. An assumption of this analysis was that areas within the MCP were available to all individuals. We excluded available locations if they fell in land cover types such as exposed rock, open water, and major roads. We used this MCP to demarcate the study area. We used binomial generalized mixed models to estimate an individual-based RSF with package lme4 in R (exponential link function; McDonald 2013, Bates et al. 2015). We used flock membership for each individual as a random factor. We centered and scaled variables to ensure model convergence prior to modeling (Becker et al. 1988). We retained nearly all single-variable models following variable screening procedures; to circumvent excessive computation times and potential model overfitting, we did not assess all variable combinations. Instead, we used a sequential approach by subsetting predictors into categories (Arnold 2010). We explored all variable combinations of ≤ 3 variables within each subset and brought forward competitive models within each variable subset. We evaluated all combinations of variables within competitive model subsets to generate final models.

Winter concentration areas.—We used binomial generalized linear models to evaluate WCAs (flocks ≥ 50 individuals) and estimate a WCA-based RSF with the same procedure as the individual-based RSF. We compared used habitat at WCAs to available habitat by generating 35 available locations for each WCA. Available habitat was constrained to an MCP surrounding all located flocks. We extracted

predictor variables within each circular region and annuli positioned over the centroid of each flock to approximate the used habitat around each flock. This was a reasonable estimation of habitat around flocks because our predictor variables were calculated at spatial extents larger than the area occupied by flocks. We assessed all variable combinations to generate a set of competitive models.

Relative flock size.—We used zero-truncated negative binomial regression to model the number of individuals in each flock as a function of predictor variables described above using package VGAM in R (Yee and Wild 1996, Yee 2015). Zero-truncated negative binomial regression is appropriate for non-zero count data, particularly when the data exhibit overdispersion (variance in the response greater than the mean; Hilbe 2007). We extracted predictor variables within each circular region and annuli positioned over the centroid of each flock to generate a single value for each predictor for the flock. We assessed all variable combinations to generate a set of competitive models.

Mapping.—We mapped our most parsimonious individual and WCA-based RSFs, and relative flock size models across the study area with 90-m pixel resolution. Models took the form: $w(x) = \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_k X_k)$, where $w(x)$ were relative probabilities of selection, and $\beta_1, \beta_2, \beta_k$ were regression coefficients of X_1, X_2, \dots, X_k predictors. We distributed predictions into 4 bins based on quantile breaks (equal area) in predicted values for comparison. We estimated the percent agreement between individual-based and WCA-based RSFs, and individual-based RSF and flock size predictions by redistributing predictions into 2 bins that represented the top 2 and bottom 2 prediction bins. We then compared prediction surfaces by calculating the proportion of similar pixels to total pixels for respective bins.

Validation of RSF and relative flock size models.—We used cross validation to evaluate the most-supported model for each analysis type, where we estimated predictions from 4 of the 5 groups (training data) and compared them to the withheld group (Johnson et al. 2006). We used the most parsimonious model from competitive models for validation. We binned predictions into 4 equal-area (quartile) intervals (Wiens et al. 2008). For individual-based RSF validations, we ran simple linear regression models on the number of observed locations from test data compared to expected locations generated from each RSF bin, adjusted by area (Johnson et al. 2006). We performed the first 5-fold validation by randomly partitioning data by individuals and performed the second set by partitioning data by flock. We considered RSFs to be good predictions when linear regression models were characterized by high coefficients of determination ($r^2 \geq 0.9$), and 95% confidence intervals of slope estimates that excluded zero and included 1. Acceptable RSF models were characterized by slope estimates that excluded zero and 1 (Howlin et al. 2004). In addition, we validated the individual-based RSF model by calculating the proportion of locations occurring within each bin from independent sage-grouse locations collected to assess winter sage-grouse habitat use in other studies (Smith et al. 2014, Dinkins et al. 2017). These studies collected locations of

winter use by radio-marked female sage-grouse with aerial telemetry during 2007–2010 (Smith et al. 2014) and 2008–2011 (Dinkins et al. 2017), respectively. For WCA and relative flock size models, we considered models predictive when more large flocks (WCAs) from test data were in the top 2 prediction bins from training data.

RESULTS

We located 4,878 individual sage-grouse with 4,859 individuals comprising 132 flocks (flock size: $\bar{x} = 37$; median = 21; range = 2–607) during infrared surveys (Fig. 1). We located 104 flocks in Core Areas and 28 flocks in non-Core Areas. Mean flock size was 36 (median = 19) in Core Areas and 38 (median = 23) in non-Core Areas. We found 14 WCAs in Core Areas and 5 WCAs in non-Core Areas. Flocks occurred in Core Areas more than expected based on the proportion of area searched within Core Areas ($\chi^2 = 25.57, P < 0.001$).

Winter Habitat Selection

The model best explaining sage-grouse winter habitat selection based on individual locations included 5 predictor variables across 3 circular regions (Table 1). No other models were within 4.6 AIC_c points of this model. Sage-grouse selected for intermediate shrub height (quadratic term) at the 0.4-km scale. Relative probability of selection increased by approximately 28% for every 5-cm increase in shrub height within 0.4 km up to 20 cm; for every 5-cm increase in shrub height >20 cm, we predicted a decrease in relative selection by 65%. At the 0.8-km scale, proportion of sagebrush was positively associated with winter habitat selection. For every 5% increase in the proportion of the landscape dominated by sagebrush within 0.8 km, relative probability of selection increased by approximately 17%. Sage-grouse selected winter habitats closer to leks and with greater breeding population densities (max. male count). Relative probability of selection increased by approximately 17% for each 1-km decrease in distance to leks and increased 64% for each increase of 100 males within 11.1 km. Sage-grouse selected areas with greater oil or coalbed-methane wells within 1.6 km. Our models

Table 1. Parameter estimates with 95% confidence intervals for predictor variables describing winter sage-grouse resource selection. Analysis was based on individual grouse located in south-central and southwest Wyoming, USA, by aerial infrared flights during winter 2017.

Parameter ^a	Estimate	95% CI	
		Lower	Upper
Shrub height _{0.4}	−0.29	−0.35	−0.23
Shrub height _{0.4} ²	−0.19	−0.23	−0.15
Sage _{0.8}	0.84	0.78	0.90
Wells _{1.6}	0.04	0.01	0.07
Distance to lek	−0.53	−0.59	−0.46
Males	0.95	0.92	0.98

^a Parameter estimates obtained from models with centered and scaled variables. Parameters include mean shrub height (cm) and quadratic term within 0.4 km, proportion of sagebrush land cover within 0.8 km, count of active and producing wells within 1.6 km, distance to occupied leks (km), and sum of the maximum male counts at leks (2012–2016) within 11.1 km.

Table 2. Five-fold cross validation results from sage-grouse winter resource selection function (RSF) models across south-central and southwest Wyoming, USA, winter 2017. We considered models (K) good predictors of winter habitat selection when they had a high coefficient of determination ($r^2 \geq 0.9$) and 95% confidence intervals (CI) surrounding slope estimates (B_1) that excluded zero and included 1. We considered RSF models to be acceptable when slope estimates (B_1) excluded both zero and 1.

K	r^2	B_0^a	CI	B_1	CI
Individual					
1	0.95	-56.17	(-352.53, 240.19)	1.23	(0.37, 2.09)
2	0.95	-65.60	(-379.79, 248.58)	1.27	(0.36, 2.18)
3	0.94	-58.22	(-378.12, 261.67)	1.24	(0.31, 2.16)
4	0.96	-48.62	(-295.82, 198.58)	1.20	(0.49, 1.91)
5	0.96	-55.20	(-335.72, 225.33)	1.23	(0.42, 2.03)
Flock					
1	0.84	34.33	(-355.57, 424.23)	0.85	(-0.28, 1.98) ^b
2	0.94	-102.53	(-489.57, 284.50)	1.40	(0.32, 2.47)
3	0.90	-151.42	(-789.00, 486.16)	1.50	(0.01, 2.98)
4	0.90	-10.55	(-321.63, 300.52)	1.05	(-0.01, 2.11) ^b
5	0.98	-30.19	(-165.56, 105.18)	1.14	(0.69, 1.58)

^a Intercept.

^b Slope estimate included zero.

predicted a 3% increase in relative probability of selection with an addition of 5 wells within 1.6 km.

Overall, the individual-based RSF was a good predictor of winter habitat selection (Table 2; Fig. 2). When we partitioned validation folds by individual, average r^2 equaled 0.95 ± 0.003 (SE), and confidence intervals of slope included 1 and excluded zero in all folds. When partitioned

by flock, average r^2 equaled 0.91 ± 0.02 , but confidence intervals of slope estimates included zero in 2 of 5 cases. Validation with independent locations also indicated good model performance with approximately 84% of 806 locations of marked sage-grouse located in the highest 2 predicted RSF bins. Approximately 59% of independent locations were in the highest predicted RSF bin. Overall,

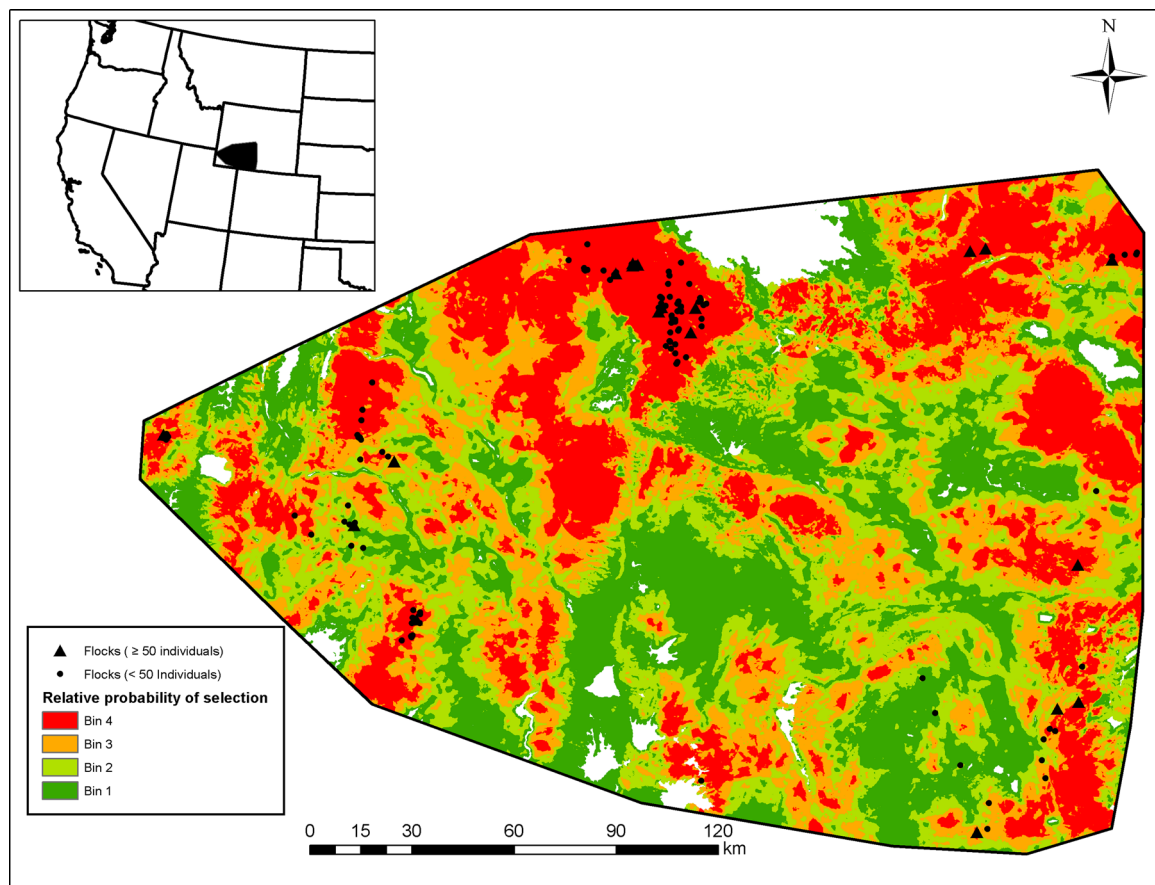


Figure 2. Predicted relative probability of sage-grouse winter habitat selection in south-central and southwest Wyoming, USA, 2017. This map spatially depicts an individual-based resource selection function that was binned into 4 quantiles increasing from low (bin 1) to high bin (4) relative probability of selection.

flock size was generally unrelated to relative probability of selection; however, larger flocks tended to occur in higher predicted RSF bins (Fig. 3). Approximately 95% of WCAs were in the highest 2 predicted RSF bins.

Winter Concentration Areas

We considered 3 models including combinations of 4 predictor variables competitive for explaining WCAs (Table 3). Winter concentration areas were correlated with greater big sagebrush cover and lower slopes within 0.4 km (Table 4). Relative selection by WCAs increased by 19% for each 1% increase in big sagebrush cover within 0.4 km. Our models predicted that a 1% increase in slope within 0.4 km resulted in an approximate 25% decrease in relative probability of selection. Winter concentration areas were also correlated with habitats closer to leks and with greater breeding population densities (max. male count). Relative probability of selection increased by 40% for each increase in 100 males within 11.1 km.

Comparison of the final mapped WCA prediction with located WCAs indicated that 89% of WCAs (17 of 19) were in the top 2 predictions bins and 63% of WCAs were located in the top prediction bin (Fig. 4). Validation indicated that, on average, 90% of withheld WCAs were in the top 2 bins when compared to predictions from training data (range = 50–100%). The top 2 prediction bins from WCA models were similar to the top 2 RSF prediction bins across 70.5% of pixels. Similarly, the lower 2 prediction bins were similar to respective RSF bins across 70.7% of pixels.

Relative Flock Size

We considered 5 competitive models including combinations of 5 predictor variables for explaining relative sage-grouse flock size (Table 5). Flock size was positively correlated with the quadratic form of big sagebrush cover within 0.4 km and lower shrub heights within 3.2 km (Table 6). Larger flocks were also associated with more rugged terrain (SD of slope) within 6.4 km, on warmer aspects within 0.8 km (heat load index), and farther from

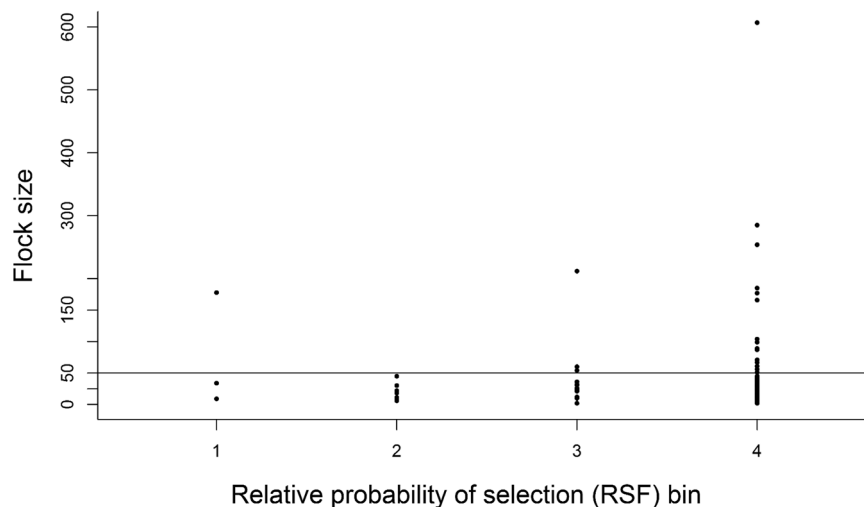


Figure 3. Relationship between flock size and resource selection function (RSF) bins generated from the mixed effects binomial generalized model. We obtained sage-grouse observations from infrared flights in south-central and southwest, Wyoming, USA, 20 January–5 February 2017. The horizontal line demarcates 50 individuals in a flock. Bin 4 has the highest relative probability of selection.

Table 3. Top and competitive models best explaining sage-grouse winter concentration areas (WCAs) in south-central and southwest Wyoming, USA, using locations of flocks with ≥ 50 individuals obtained with aerial infrared survey flights, winter 2017.

Model ^b	Model fit statistics ^a		
	<i>K</i>	ΔAIC_c	w_i
B _{sage} _{0.4} + slope _{0.4} + males	4	0.00	0.57
B _{sage} _{0.4} + slope _{0.4} + males + distance to lek	5	0.99	0.35
Slope _{0.4} + males + distance to lek	4	3.90	0.08
Null	1	34.35	0.00

^a Number of parameters (*K*), change in Akaike's Information Criterion score from the top model (ΔAIC_c), and Akaike weights (w_i).

^b Parameters include mean big sagebrush cover (B_{sage}; %) within 0.4 km, mean slope (%) within 0.4 km, sum of the maximum male counts at leks (2012–2016) within 11.1 km, and distance to occupied leks (km).

roads. Comparison of the final mapped relative flock size predictions indicated that 14 of 19 flocks were in the top 2 bins of predicted relative flock size (Fig. 5). Fifty-eight percent of WCAs were located in the top bin of predicted relative flock size. Validation indicated that on average, 73% of withheld WCAs were in the top 2 predicted flock size bins when compared to predictions from training data (range = 50–100%). The top 2 and bottom 2 relative flock size prediction bins were similar to RSF model predictions in 51.5% and 51.6% of pixels, respectively.

DISCUSSION

Like other conservation policies that designate protected areas, PACs throughout sage-grouse habitat rely on adequate protections of seasonal habitats for all life-history stages. Wyoming's Core Area Strategy used best available science to regulate disturbance in important sage-grouse breeding habitats and assumed that protection of breeding habitats also protected other important seasonal habitats, specifically winter habitat (State of Wyoming 2015). Protected areas are only effective when size and

Table 4. Parameter estimates and 95% confidence intervals in parentheses (LCL, UCL) from competitive models estimating sage-grouse winter concentration areas (WCAs) obtained from aerial infrared survey flights during winter 2017 across south-central and southwest Wyoming, USA.

Model	Parameter ^a			
	B _{sage} _{0.4}	Slope _{0.4}	Males	Distance to lek
1	0.67 (0.16, 1.19)	-1.12 (-2.26, -0.27)	0.62 (0.27, 0.97)	
2	0.60 (0.07, 1.14)	-1.05 (-2.18, -0.20)	0.58 (0.22, 0.94)	-0.43 (-1.37, 0.37)
3		-1.06 (-2.15, -0.25)	0.76 (0.44, 1.09)	-0.66 (-1.58, 0.11)

^a Parameter estimates obtained from models with centered and scaled variables. Parameters include mean big sagebrush cover (B_{sage}; %) within 0.4 km, mean slope (%) within 0.4 km, sum of the maximum male counts at leks (2012–2016) within 11.1 km, and distance to occupied leks (km).

configuration align with seasonal needs of sensitive wildlife (Jones et al. 2018). Mismatch of wildlife use of protected areas among seasons might be problematic at local scales, leaving wildlife vulnerable to disturbance regardless of having protections during some life-history stages (Runge et al. 2014). Although our findings indicated most wintering sage-grouse were located in Core Areas, 28 flocks comprising 5 WCAs were located outside of Core Areas. The majority of flocks located in non-Core Areas were adjacent to relatively smaller Core Areas in south-central and southwest Wyoming (e.g., the 3,754-km² South Rawlins and 1,030-km² Fontenelle Core Areas), which suggests smaller Core Areas are more likely to have mismatches in protection of different seasonal habitats

compared to larger Core Areas (e.g., 19,093-km² Greater South Pass Core Area). This was consistent with patterns of sage-grouse winter habitat use adjacent to small and large Core Areas in other Wyoming studies (Smith et al. 2016, Dinkins et al. 2017) and the mismatch of Core Area protections for summer compared to winter seasons (Dinkins et al. 2017). Therefore, in-depth assessment of seasonal habitat inclusion will be necessary when designating relatively smaller protected areas.

Sage-grouse generally have high overwinter survival (Beck et al. 2006, Baxter et al. 2013, Dinkins et al. 2017), except during severe winters (Moynahan et al. 2006, Anthony and Willis 2009). In addition, Dinkins et al. (2017) reported that survival of female sage-grouse was higher in Core Areas

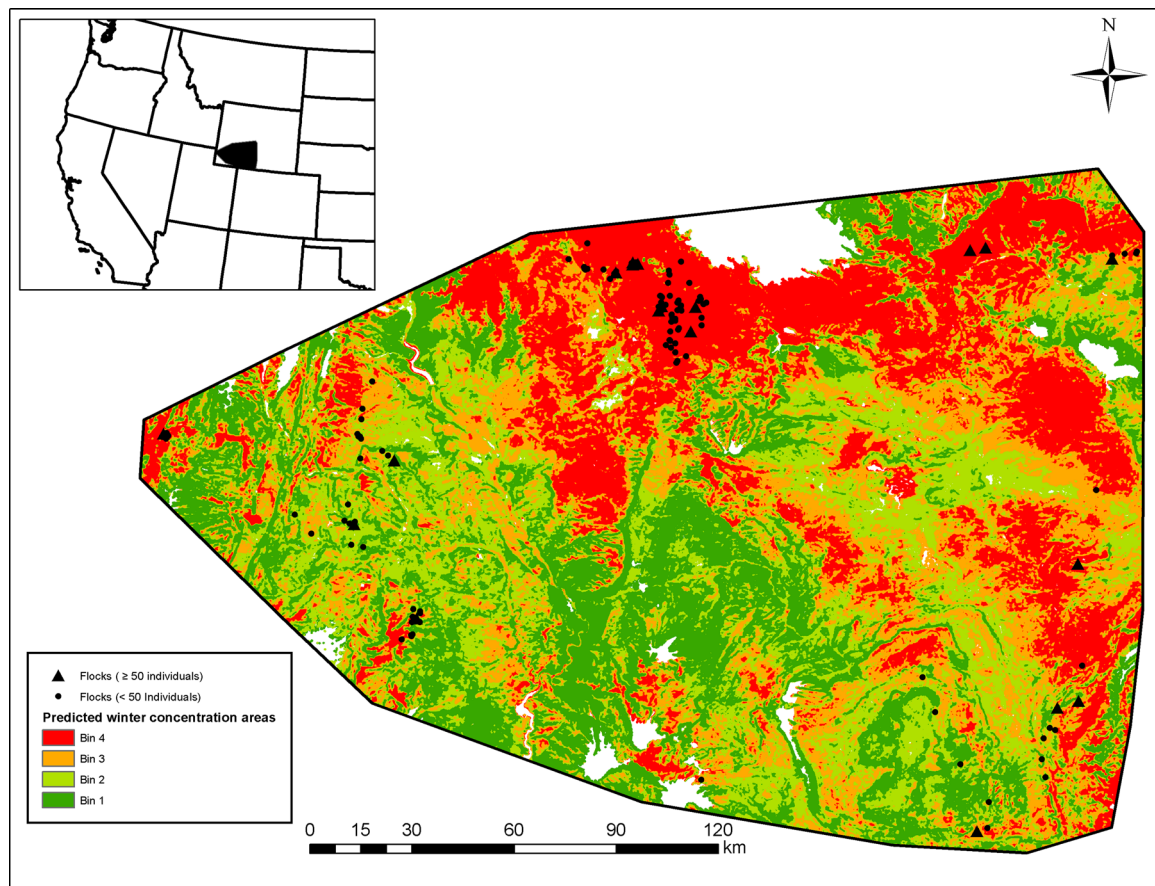


Figure 4. Predicted winter concentration areas (WCAs) in south-central and southwest Wyoming, USA, 2017. This map spatially depicts the WCAs that were binned into 4 prediction quantiles increasing from low (bin 1) to high (bin 4) predicted WCAs.

Table 5. Top and competitive models best explaining relative sage-grouse winter flock size in south-central and southwest Wyoming, USA, using flock locations and size obtained with aerial infrared survey flights, winter 2017.

Model ^b	Model fit statistics ^a		
	<i>K</i>	ΔAIC_c	w_i
Bsage _{0.4} ² + shrub height _{3.2} + HLI _{0.8}	6	0.00	0.40
Bsage _{0.4} ² + shrub height _{3.2} + HLI _{0.8} + slope SD _{6.4}	7	1.07	0.23
Bsage _{0.4} ² + shrub height _{3.2} + HLI _{0.8} + distance to roads	7	1.37	0.20
Bsage _{0.4} ² + shrub height _{3.2} + HLI _{0.8} + slope SD _{6.4} + distance to roads	8	2.54	0.11
Bsage _{0.4} ² + shrub height _{3.2} + distance to roads	6	3.89	0.06
Null	2	15.26	0.00

^a Number of parameters (*K*), change in Akaike's Information Criterion score from the top model (ΔAIC_c), and Akaike weights (w_i).

^b Parameters include mean big sagebrush cover (Bsage; %) and its quadratic term within 0.4 km, mean shrub height (cm) within 3.2 km, mean heat load index (HLI) within 0.8 km, mean surface roughness index (slope SD_{6.4}) within 6.4 km, and distance (km) from state, county, US, or Interstate roads.

compared to non-Core Areas during winter. Areas where sage-grouse WCAs are consistently located in non-Core Areas during winter may represent shortfalls in current protections, especially when those individuals are connected to smaller Core Areas during other seasons. These WCAs should be candidates for additional protection to conserve yearlong sage-grouse habitats connected to existing Core Areas that do not have adequate annual protections. The WCAs outside of Core Areas may be designated once areas persistently used by large flocks (≥ 50 individuals) have been identified (State of Wyoming 2015), but reproducible methods are needed to ensure that regulatory mechanisms are afforded to sage-grouse in these areas. Although our study represented a very short duration of time, our infrared-based surveys produced good predictions of habitat selection that corresponded with sage-grouse locations from marked individuals from previous studies. Studies with marked individuals have been the standard approach for assessing habitat selection of wildlife species (Manly et al. 2002). However, these studies are costly and rely on relatively small samples of individuals to be representative of population-level habitat use. Our infrared survey

alleviates the assumption that a small sample of marked animals is representative of an area or population. Furthermore, our infrared survey allows conservation and management planning the opportunity to assess habitat and flock size across large spatial expanses. For these reasons, we suggest further assessment of our methodology as an ideal protocol to balance area covered for assessment of winter habitat use and abundance.

Some pitfalls of our survey were a lack of repetition within a season and the inability to add a structured design component for detection into our surveys (e.g., distance sampling or double-observer sampling techniques) for use in habitat selection analyses. Prevailing conditions, primarily changes in snow coverage and potential snow burrowing by sage-grouse at night, led to some deviations in standard flight protocols (J. P. Romero, personal communication), which precluded us from adding a detection component to our study design. The infrared flights produced similar counts of sage-grouse during spring lek surveys compared to ground-based observers (Gillette et al. 2013); however, spring lek surveys occurred at known sage-grouse leks, allowing the pilot to home in on a specific location where grouse were likely to occur. Although not incorporating detection likely added some bias to our analyses, we standardized the data within our analyses as best as possible by including only daytime detections during conditions verified to work during our study. The most likely form of bias would be failure to detect small flocks. Yet, we located flocks as small as 2 individuals, and infrared detected several individual sage-grouse during surveys. With further refinement, identification of individuals with infrared flights would be ideal for assessment of habitat selection, relative abundance, and delineation of protected areas for sage-grouse and other species, especially with additional surveys in the same area more than once per winter.

Resource selection modeling produced a predictive individual-based RSF surface that validated well with infrared flight locations and independent data. Sage-grouse selected landscapes that were less rugged with warmer aspects dominated by sagebrush. These findings were generally consistent with previous winter sage-grouse research (Carpenter et al. 2010; Smith et al. 2014, 2016; Holloran et al. 2015; Walker et al. 2016). Sage-grouse also selected winter habitats closer to leks and in areas with

Table 6. Parameter estimates and 95% confidence intervals in parentheses (LCL, UCL) from competitive zero-truncated negative binomial models estimating relative sage-grouse winter flock size obtained from aerial infrared survey flights across south-central and southwest Wyoming, USA, during winter 2017.

Model	Parameter ^a					
	Bsage _{0.4}	Bsage _{0.4} ²	Shrub height _{3.2}	HLI _{0.8}	Slope SD _{6.4}	Distance to roads
1	0.35 (0.09, 0.61)	0.10 (-0.07, 0.26)	-0.36 (-0.63, -0.10)	0.25 (0.05, 0.45)		
2	0.35 (0.08, 0.61)	0.10 (-0.07, 0.27)	-0.36 (-0.63, -0.10)	0.26 (0.06, 0.45)	0.12 (-0.08, 0.32)	
3	0.34 (0.07, 0.60)	0.10 (-0.07, 0.27)	-0.33 (-0.60, -0.06)	0.23 (0.02, 0.43)		0.09 (-0.11, 0.30)
4	0.33 (0.07, 0.60)	0.10 (-0.07, 0.27)	-0.33 (-0.60, -0.06)	0.23 (0.03, 0.44)	0.11 (-0.08, 0.31)	0.09 (-0.11, 0.30)
5	0.37 (0.10, 0.64)	0.15 (-0.02, 0.33)	-0.29 (-0.56, -0.02)			0.15 (-0.05, 0.35)

^a Parameter estimates obtained from models with centered and scaled variables. Parameters include mean big sagebrush cover (Bsage; %) and its quadratic term within 0.4 km, mean shrub height (cm) within 3.2 km, mean heat load index (HLI) within 0.8 km, mean surface roughness index (slope SD_{6.4}) within 6.4 km, and distance (km) from state, county, US, or Interstate roads.

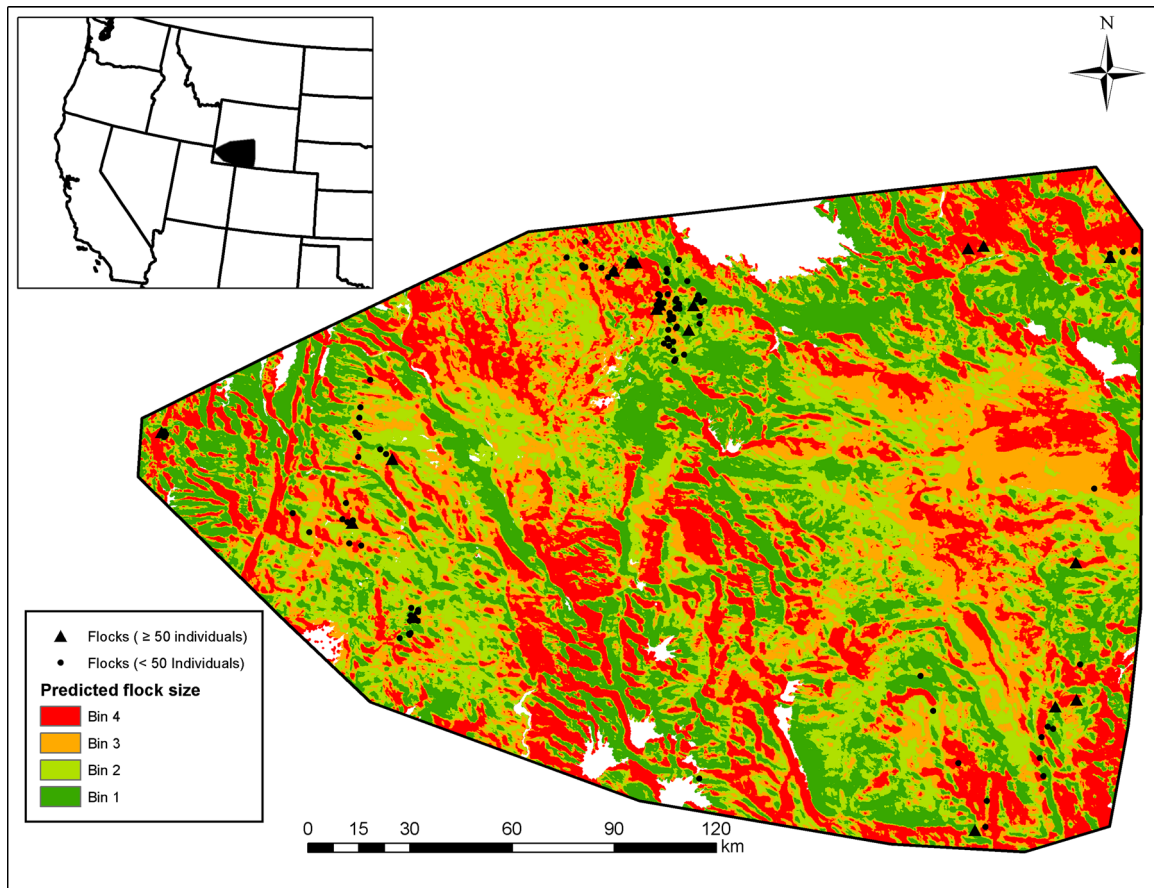


Figure 5. Predicted winter sage-grouse flock size in south-central and southwest Wyoming, USA, 2017. This map spatially depicts predicted flock size that was binned into 4 quantiles from low (bin 1) to high (bin 4) predicted flock size.

greater breeding densities (as indexed by male lek counts) within 11.1 km of known leks. Approximately 89% of flocks were located within 6.4 km of a known occupied sage-grouse lek. These findings provide additional support that most seasonal habitats are likely located near breeding areas, which were used to create Core Areas. Dinkins et al. (2017) reported theoretical core regions as designated by Doherty et al. (2010) were good indicators of sage-grouse habitat use year-round; thus, mismatches with lower winter habitat protection were introduced with the process of designating protected areas within the Core Area Strategy. Designation of this strategy was contingent on eliminating existing developments from the protected areas, which in effect reduced winter protections near small Core Areas because developed areas were related to flatter easier to access landscapes. Our finding that sage-grouse were selecting areas with greater well pad densities contradicted previous research (Doherty et al. 2008, Holloran et al. 2015), but these studies evaluated more fine-scale habitat selection. Our findings were likely due to generating available habitats across the entire extent of our study area, representing a more coarse analysis that does not infer selection for greater well pad densities at finer scales. In support, the mean number of wells within 1.6 km of an individual sage-grouse location was low (mean = 1.0, median = 0.0).

Resource selection functions are theoretically useful for approximating abundance or density of sedentary species (Boyce and McDonald 1999). However, the relationship between habitat selection and abundance is less clear when species exhibit cyclic population trends, move to seasonally distinct habitats, or congregate in groups during all or parts of a year (Boyce et al. 2016). When populations are obligate migrants, because breeding habitats become inhospitable during winter (Newton et al. 2017), the disparity between breeding densities and winter habitat selection may be exacerbated. Winter resource selection generally occurred irrespective of flock size, but RSFs were still useful in identifying potential WCAs because they occurred in areas that we predicted to have high relative probability of selection. Methods that integrate breeding population indices and resource selection have been successfully used to identify priority areas for sage-grouse conservation (Coates et al. 2015, Doherty et al. 2016). These methods largely relied on spatial relationships between female habitat use during nesting and distance to known occupied leks (Holloran and Anderson 2005, Coates et al. 2013). The relationship between population indices and habitat use, however, remains unclear during winter, particularly when individuals and populations display unique movements to wintering areas that are disjunct from breeding habitats

(Fedy et al. 2012, Smith et al. 2016, Pratt et al. 2017). In cases where winter habitats are close to leks, we still lack a clear relationship between relative size of winter flocks and winter resource selection in the absence of intensive telemetry studies. Our WCA-based RSF and flock size models produced similar findings to our individual-based RSF analysis. Specifically, WCAs or larger flocks selected flatter sagebrush-dominated areas closer to leks and with greater breeding densities. The level of agreement between individual-based RSF and WCA-based RSF predictions was generally high, suggesting that identifying areas of high predicted probability of selection with RSF modeling may be useful for identifying additional WCAs when information on flock sizes are unavailable.

Refining our understanding of persistent WCAs will require repeated flights within and across years to determine the extent where WCAs are located with changing environmental conditions. It may also be necessary to modify conservation policy to define WCA persistence as areas where large flocks are likely to be located rather than actually residing during numerous days. This would account for differences in environmental conditions across years and fluctuations in population size. Our findings also illustrate that understanding the size of flocks occurring in winter habitat may be less important than ensuring an adequate amount of adjoining winter habitat is contained in protected areas, especially for small protected areas. The mean flock size within and outside Core Areas was similar (~36 to 38 birds/flock) but lower than a WCA (≥ 50 birds). Our mean flock size results indicate biologically relevant flock size may be smaller than the current definition of WCAs. The potential WCAs that we located likely represent important areas for wintering sage-grouse and should be explored further. Sage-grouse exhibit philopatry to winter habitat areas (Connelly et al. 1988) and use a potentially small portion of the landscape depending on sagebrush cover and landscape configuration (Beck 1977). The size of sage-grouse winter ranges appear to vary regionally (~31–1,480 km²; Eng and Schladweiler 1972, Bruce et al. 2011), but repeated flights within and across years could be used to determine the extent and persistence of WCAs. Repeated sampling would also help to determine the stability of flock sizes and association within an area, which may vary daily (Eng and Schladweiler 1972, Beck 1977). Coupling flights with radio-marked individuals would help determine the extent with which flock mixing occurs and help develop a basis for the number of individuals in a flock that constitute a biologically relevant WCA.

MANAGEMENT IMPLICATIONS

A meaningful portion of wintering sage-grouse may not be receiving adequate protection through Wyoming's Core Area strategy. Managers should focus on identifying important winter habitats outside of Core Areas to provide protection for WCAs when they do not overlap with existing Core Areas. Areas predicted to have high probability of winter habitat selection were informative in identifying WCAs, and WCA-based RSF models produced similar predictions to individual-based RSF

models. This lends credence to the Wyoming Sage-grouse Executive Order protocol for identifying WCAs, particularly when information on sage-grouse flock sizes is unknown during winter. Managers should focus on conserving an adequate amount of winter habitat for sage-grouse regardless of whether winter flock sizes are known.

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