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Incorporating within- and between-patch resource selection in identification of critical habitat for brood-rearing greater sage-grouse

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Abstract

Introduction: Incorporating information on animal behavior in resource-based predictive modeling (e.g., occurrence mapping) can elucidate the relationship between process and spatial pattern and depict habitat in terms of its structure as well as its function. In this paper, we assigned location data on brood-rearing greater sage-grouse (*Centrocercus urophasianus*) to either within-patch (encamped) or between-patch (traveling) behavioral modes by estimating a movement-based relative displacement index. Objectives were to estimate and validate spatially explicit models of within- versus between-patch resource selection for application in habitat management and compare these models to a non-behaviorally adjusted model.

Results: A single model, the vegetation and water resources model, was most plausible for both the encamped and traveling modes, including the non-behaviorally adjusted model. When encamped, sage-grouse selected for taller shrubs, avoided bare ground, and were closer to mesic areas. Traveling sage-grouse selected for greater litter cover and herbaceous vegetation. Preference for proximity to mesic areas was common to both encamped and traveling modes and to the non-behaviorally adjusted model. The non-behaviorally adjusted map was similar to the encamped model and validated well. However, we observed different selection patterns during traveling that could have been masked had behavioral state not been accounted for.

Conclusions: Characterizing habitat that structured between-patch movement broadens our understanding of the habitat needs of brood-rearing sage-grouse, and the combined raster surface offers a reliable habitat management tool that is readily amenable to application by GIS users in efforts to focus sustainable landscape management.

Keywords: Behavioral mode; Brood-rearing; *Centrocercus urophasianus*; Conditional logistic regression; Conservation planning; Information-theoretic approach; Relative displacement index; Species occurrence model

Introduction

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) occurs throughout shrub-steppe habitat in 11 western American states and 2 Canadian provinces. The species is endangered in Canada (COSEWIC 2008). The sage-grouse is not listed in the US as federally threatened or endangered, although it was found to be warranted (United States Fish and Wildlife Service 2010). Long-term population declines have been observed throughout much of the species distribution (Connelly and Braun 1997; Connelly et al. 2004; Fedy and Aldridge 2011). Factors associated with decline include large-scale changes in temperature and precipitation cycles, fire, predation, and human activity associated with agriculture and energy development (Connelly and Braun 1997; Connelly et al. 2000; Walker et al. 2007; Doherty et al. 2008; Harju et al. 2010; Holloran et al. 2010).

Identifying resources necessary for critical life-history phases (e.g., brood-rearing, nesting, and roosting) and survival are important for managing landscapes (Dzialak et al. 2011b), especially when landscapes are exposed to large-scale modification from climatic and anthropogenic sources. The needs of brooded hens and their chicks revolve around nutrition acquisition, protection

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from predation, water needs, and favorable thermal environments. Brood-rearing areas for sage-grouse include moderate shrub coverage with a prominent sagebrush component, proximity to mesic areas, and herbaceous vegetation such as forbs that also harbors insects (Hagen et al. 2007; Dzialak et al. 2011b; Harju et al. 2013a). However, less is known about how behavior structures the use of resources during critical seasons.

Resource-based predictive modeling of species occurrence has strong application in wildlife management because it provides information on the relationship between animals and landscape features, and it offers spatially explicit guidance in identifying critical habitat throughout large areas (Johnson et al. 2004; Guisan and Thuiller 2005). One of the most useful and prevalent applications of species occurrence modeling is spatial prioritization of management activity, wherein habitat that is identified as having a high probability of importance to wildlife is managed differently than habitat that is predicted to be used with low frequency or otherwise of less importance (Margules and Pressey 2000; Aldridge and Boyce 2007; Sawyer et al. 2009; Dzialak et al. 2011b). Efforts to identify and prioritize important wildlife habitat are particularly relevant in human-modified areas where wildlife conservation may be one of the several valued land uses or where protecting large contiguous areas of unmodified habitat is not an option (Moilanen et al. 2005). Thus, incorporating information on behavior in predictive modeling can play an important role in developing accurate predicted occurrence maps that depict habitat in terms of its composition and configuration for different behaviors (Taylor et al. 1993; Tischendorf and Fahrig 2000; Kindlmann and Burel 2008; Van Moorter et al. 2010).

Availability of spatial data has created opportunities to advance methods that link behavioral modes to processes such as population change or resource selection (Turchin 1998; Forester et al. 2009; Morales et al. 2010). From a spatial perspective, a behavioral mode can be thought of as a manner of movement characterized by parameters such as movement rate, net displacement, or tortuosity (Patterson et al. 2008). For example, in some species, behavior characterized by high directional persistence, a high rate of movement, and high displacement will reflect a between-patch mode such as traveling or migration, whereas high tortuosity, a low rate of movement, and low displacement will reflect a within-patch mode such as encampment, resting or foraging (Van Moorter et al. 2010). From a management perspective, species-specific behavioral responses to the landscape establish a mechanistic basis for understanding how particular features function ecologically (Tischendorf and Fahrig 2000). Behavioral mode is a variable that the investigator may wish to characterize before conducting further analysis (Van Moorter et al. 2010) or incorporate as a latent process into structural equation or time-series models (Patterson et al. 2008). Depending on the scale of investigation, dominant breeding season behavioral modes of sage-grouse might include pre-nesting behavior such as lek attendance, nest-site selection, nesting off-bout behavior, and between-versus within-patch movement of the brooded female (Aldridge and Brigham 2002; Aldridge and Boyce 2007; Doherty et al. 2010; Dzialak et al. 2011b). Global positioning system (GPS) data at a fine temporal scale make transitions between these modes readily observable (Dzialak et al. 2011b). Identifying behavioral mode within the context of current management establishes the opportunity to quantitatively assign observed data to a defined mode as an initial analytical step. Incorporating datum-specific information on behavior into subsequent spatial modeling enables the investigator to depict the landscape in terms of its structure (composition and configuration of patches) relative to a given behavior mode, offering richer insight for habitat management (Taylor et al. 1993; Kindlmann and Burel 2008).

The objective of this work was to identify within-patch (encamped) versus between-patch (traveling) brood-rearing habitat for the sage-grouse throughout a portion of its Wyoming, USA, distribution. Preliminary GPS data revealed a pattern observed across all sampled individuals involving movement between and within patches (Figure 1). We aimed to assign location data to encamped versus traveling behavioral modes based on movement parameters estimated from GPS data, estimate resource selection functions for these two respective modes, and compare the behavioral models to a non-behaviorally adjusted model (including all data not assigned to behavioral state). To provide spatial products for application in prioritization of management, we developed spatially explicit estimates of occurrence separately for encamped and traveling modes. We integrated encamped and traveling raster surfaces to depict (i.e., map) areas important during within-patch movement, between-patch movement, and concurrently in both behavioral modes. We validated predictions using location data withheld from model development.

Methods

Study area

The 7,948-km^2 study area encompassed portions of the Great Divide Basin in south-central Wyoming, USA. Terrain is characterized by rolling sagebrush steppe interspersed with gently sloping flats, drainages, and vegetated sand dunes; elevation is 1,933 to 2,385 m. Dominant vegetation at lower elevation included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), birdfoot sagebrush (*A. pedatifida*), black greasewood (*Sarcobatus vermiculatus*), shadscale (*Atriplex confertifolia*),

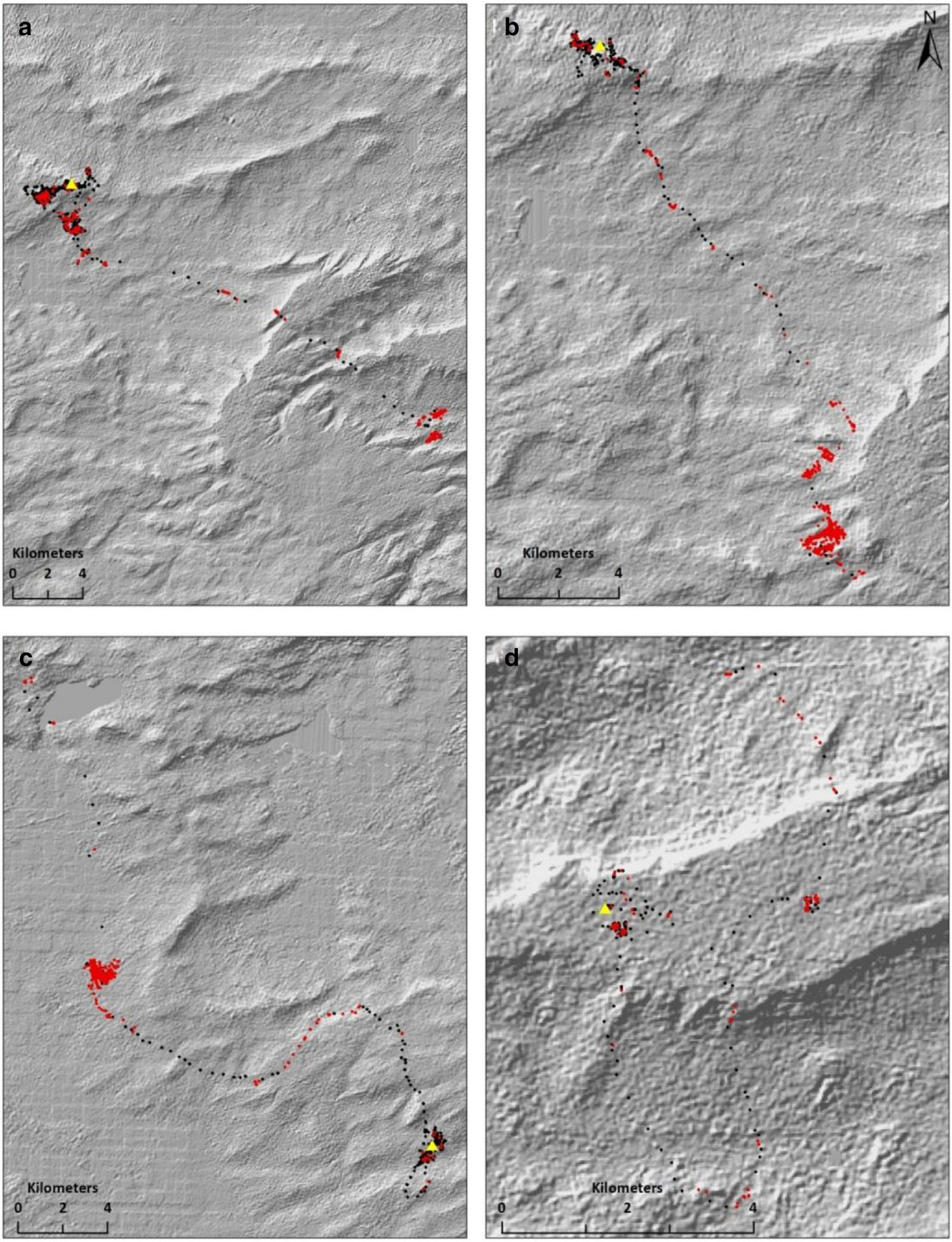

Figure 1 (See legend on next page.)

(See figure on previous page.)

Figure 1 GPS locations and movement patterns of greater sage-grouse in Wyoming. All greater sage-grouse (*Centrocercus urophasianus*) comprising the sample showed within-patch (clusters of GPS locations) and between-patch (trails between clusters) movement in south-central Wyoming, USA, during 2009 to 2012. Based on the relative displacement index, red dots indicate locations assigned to the encamped behavioral mode and black dots indicate locations assigned to the traveling mode; yellow triangles show the nest location. Panels **(a-d)** each show one unique individual for the years 2009 to 2012, respectively.

and grass species (e.g., *Pseudoroegneria spicata*, *Agropyron* spp., *Bromus* spp.). At higher elevation, mountain big sagebrush (*A. t. vaseyana*) was present; basin big sagebrush (*A. t. tridentata*) occurred in drainages. Average monthly precipitation during the study period was 2.68 cm (Western Regional Climate 2011). Predominant historic and ongoing land uses were domestic livestock grazing and development of energy resources. As of March 2012, there were 4,894 active wells within the study area (1 well/1.62 km^2).

Field procedures and location data

During 2008 to 2011, we captured female sage-grouse with nets and the aid of binoculars and spotlights (Wakkinen et al. 1992) during spring (generally March and April) on and around leks that were dispersed throughout the study area. We determined age (Crunden 1963) and fitted sage-grouse with either 22 or 30-g ARGOS/GPS Solar PTTs (PTT-100, Microwave Telemetry Inc., Columbia, MD, USA) using a rump-mount technique (Dzialak et al. 2012). GPS units had a 3-year operational life and were configured with ultra-high frequency (UHF) beacons that enabled ground tracking for field-based confirmation of events (i.e., fatality). For this analysis, we used brood-rearing data defined uniquely for each bird; brood-rearing across birds occurred from 11 May to 12 August, 2009 to 2012. Collars were programmed to record location information every 1 h from 0700 to 2200 h. The use of GPS made the transition from nesting to brood-rearing readily observable, with the initiation of brood-rearing defined for each bird as the specific GPS location at which the female moved from the nest with no subsequent return to the nest site (Dzialak et al. 2011b). Brood surveys were conducted weekly beginning when chicks were about 7 days old. An effort was made to determine presence versus absence of a brood without flushing females. The presence of chicks was determined by direct observation of chicks and based on behavior of the female (i.e., the female walking or running away from the observer rather than flying, becoming defensive or aggressive, or displaying wing-dragging or flutter-hopping behavior) (Patterson 1952). Animal capture and handling protocols were approved by the Wyoming Game and Fish Department (Chapter 33 Permit #649).

Assigning location data to behavioral mode

We developed a relative displacement index to assign location data to encamped versus traveling behavioral modes. The index is based on net displacement or the straight-line distance between the starting location for an individual and each subsequent location along the movement path of that individual (Turchin 1998). Net displacement was calculated for each location within each individual's movement path as:

$$\text{Net displacement}_1 = \sqrt{\begin{array}{l}\{(\text{UTMe}_l - \text{UTMe}_1)^2 \\ +(\text{UTMn}_l - \text{UTMn}_1)^2\}\end{array}} \quad (1)$$

where UTMe and UTMn are respective easting and northing coordinates of location data (datum and projection were North American Datum of 1983 and Universal Transverse Mercator zone 13 north), 1 is the first GPS location in an individual's path, and l is each subsequent location in the individual's path from 1 to l locations. We calculated the relative displacement index as:

$$|\{(\text{net displacement}_l - \text{net displacement}_{l+1}) \div \text{net displacement}_l\} \times 100| \quad (2)$$

which quantifies the relative change in amplitude of net displacement between location l and location $l+1$. We assigned a cut-off associated with the relative displacement index of 5% based on visual inspection and preliminary analysis of the location data. Locations considered as encamped did not vary substantially in amplitude, and the frequency of locations with a relative displacement index of ≤5% was much greater compared to the frequency of locations with a relative displacement index >5%; these locations also corresponded with much longer movement distances. Specifically, for any instance in which the relative change in amplitude of net displacement from location l to location $l+1$ was ≤ 5%, we assigned the behavioral mode as encamped; otherwise, we assigned the behavioral mode as traveling (relative displacement index > 5%; Figures 1 and 2).

Predictor variables

Using a geographic information system (GIS; ArcGIS 10, ESRI, Redlands, CA, USA), we calculated predictor variables depicting landscape features that influence resource selection behavior of sage-grouse (Table 1). This suite of variables has provided a basis for accurate prediction of occurrence and demographic responses among sage-grouse as part of companion studies (Dzialak et al. 2011b; 2012; 2013a; 2013b; Webb et al.

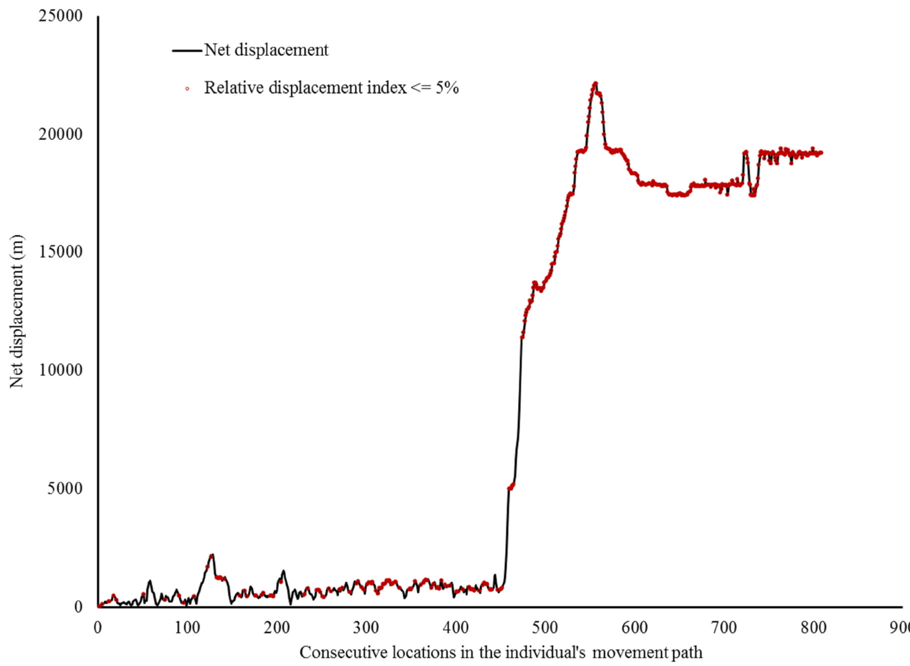

Figure 2 Relationship between net displacement and relative displacement index for assigning behavioral state to greater sage-grouse. General relationship between net displacement and the relative displacement index for greater sage-grouse (*Centrocercus urophasianus*) in south-central Wyoming, USA, from 2009 to 2012. The black line illustrates net displacement or the straight-line distance between the starting location for an individual and subsequent locations along the movement path of that individual. Red dots highlight those locations for which the relative displacement index (%), or relative change in amplitude of net displacement between location *l* and location *l* + 1, is ≤5%, which identifies the encamped behavioral mode.

2012). Raster images of oil and natural gas wells were updated annually so that we could analyze sage-grouse location data against the most up-to-date information on the location of wells. Raster images of all other human modification of the landscape were developed based on 2006 aerial imagery and updated using 2009 imagery (Table 1). These images were developed via heads-up-digitizing, a process whereby linear and areal features displayed in remotely sensed imagery are identified, interpreted, delineated, and attributed manually in a GIS by an investigator and then converted to raster data. We used spatial analyst in ArcGIS to develop all raster images and to extract cell values from raster images to location data (i.e., used and non-used points) for all predictor variables. All raster data were calculated at a resolution of 30 m (Table 1). We natural log-transformed distance variables (after adding 0.1 to all values; Table 1) to allow a functional form of the relationship between resource selection and distance that depicted a decreasing magnitude of influence with increasing distance. We also developed quadratic terms for vegetation and topographic variables because sage-grouse have been shown to avoid the lowest and highest values associated with some landscape features (Aldridge and Boyce 2007; Dzialak et al. 2011b; 2012) and to assess potential thresholds.

Modeling resource selection

We estimated resource selection using conditional logistic regression within an information-theoretic framework (Burnham and Anderson 2004). To identify potentially informative versus uninformative predictor variables (*sensu* Arnold 2010), we conducted univariate conditional logistic regression using the PHREG procedure in SAS. For each variable, we assessed the difference in Akaike's information criterion (AIC) between the null model and each univariate model. If the univariate model was within 4 AIC units of the null model, then it was considered uninformative and was dropped from further consideration. **We then checked for correlation among retained variables using the correlation procedure (PROC CORR) in SAS;** if correlation was very high (Pearson product-moment correlation ≥ |0.8|), we eliminated the variable that was thought to be less relevant biologically (Drut et al. 1994; Sveum et al. 1998; Connelly et al. 2000; Thompson et al. 2006). Retained variables were then structured into a candidate set of models that depicted 15 competing hypotheses on how landscape features structured occurrence (Table 2; Walker et al. 2007; Doherty et al. 2008; Dzialak et al. 2011b); we also assessed a null and global model for a total of 17 candidate models (i.e., competing hypotheses).

Table 1 Predictor variables important to resource selection by greater sage-grouse in Wyoming

Variable	Description
Predominant human modifications of the landscape	
Distance to nearest well	Distance (m) to the nearest oil or natural gas well. Data on the location of wells, as of March 2012, were obtained from the Wyoming Oil and Gas Conservation Commission. All distance covariates were calculated using the Spatial Analyst\Euclidean Distance tool in ArcMap
Distance to nearest road	Distance (m) to paved, improved un-paved, or maintained dirt roads. Two-track roads were not included. Roads were heads-up-digitized at a scale of 1:2,000 from 2006 and 2009 National Agriculture Imagery Program aerial imagery at 1-m resolution
Distance to nearest residential or agricultural structure	Distance (m) to the nearest residential or agricultural structure including houses, sheds, and barns. Structures were heads-up-digitized as described above
Distance to nearest energy-related ancillary feature	Distance (m) to the nearest infrastructure associated with energy development other than wells. Such ancillary features included compressor stations, settling ponds, and buildings. Ancillary features were heads-up-digitized as described above
Predominant vegetation in the study area	
Percent shrub	Estimated percent of each pixel comprising the raster surface for which the vegetation type is shrub species. The data source was the Provisional Remote Sensing Sagebrush Habitat Quantification Products for Wyoming developed by the US Geological Survey. Detailed information on development and accuracy of all vegetation layers is in (Homer et al. 2012)
Percent sagebrush	Estimated percent of each pixel comprising the raster surface for which the vegetation type is sagebrush (*Artemisia* spp.). See Homer et al. (2012)
Percent herbaceous	Estimated percent of each pixel comprising the raster surface that is herbaceous cover. See Homer et al. (2012)
Percent bare ground	Estimated percent of each pixel comprising the raster surface that is bare ground. See Homer et al. (2012)
Percent litter	Estimated percent of each pixel comprising the raster surface that is herbaceous litter. See Homer et al. (2012)
Estimated shrub height	Estimated pixel-wide height (cm) of shrub vegetation. See Homer et al. (2012)
Topographic and other natural features of the landscape	
Convexity 90 m	Using a digital elevation model (DEM; 1 arc-second National Elevation Dataset [NED] re-sampled to 30 m; available at http://nationalmap.gov/viewer.html), convexity was calculated as the DEM pixel value minus the average elevation within a 90 × 90 m moving window (3 × 3 pixels). The average value of elevation within the moving window was calculated using the Spatial Analyst\Local\Cell Statistics tool selecting mean as the overlay statistic
Heat load index (HLI)	Rescaling of aspect (θ; radians calculated from the NED using Spatial Analyst in GIS) from 0 to 1 oriented northeast to southwest depicting the gradient from coolest to warmest aspect using the equation of McCune and Keon (2002): HLI = 1 to cosine(θ − 45)/2
Slope	Steepness (degrees) calculated from the NED using Spatial Analyst
Terrain roughness 90 m	An index of terrain roughness calculated as the standard deviation (SD) of elevation from a DEM within a 90 × 90 m moving window (3 × 3 pixels). This covariate was calculated using the Spatial Analyst\Local\Cell Statistics tool selecting SD as the overlay statistic
Distance to nearest mesic area	Distance (m) to the nearest permanent or intermittent stream, seep, spring, impoundment, irrigation, or water discharge area. The raster image was developed from 0.3-m true-color and CIR aerial photography (2009) using Feature Analyst® 4.2 (Visual Learning Systems 2008) for ArcGIS® 10

Predictor variables calculated in a Geographic Information System (GIS; Esri ArcMap10) for potential inclusion in models of resource selection by greater sage-grouse (*Centrocercus urophasianus*) tracked during 2009 to 2012 in south-central Wyoming, USA. A description of each variable is provided in the right-hand column. All data (raster images) were calculated at a resolution of 30 m.

To define resource availability, we calculated the distance (D) between successive grouse locations l_t and l_{t+1}. The spatial domain from which alternative choices to l_{t+1} (non-used locations) could be drawn was defined as a circular buffer centered on l_t with a radius equal to D between l_t and l_{t+1} plus 20% of that distance. We enforced a minimum buffer distance (i.e., 56 m) that was equal to the median distance between successive locations (i.e., D) observed across all individuals to acknowledge there was a minimum area available even if an individual did not move during that time period on a given day. We matched each used location with a set of five non-used locations drawn from within the circular buffer and considered each used location with its associated five non-used locations as a single stratum. This discrete-choice design (Cooper and Millspaugh 1999; Compton et al. 2002; McDonald et al. 2006) quantifies a choice made by an individual female sage-grouse (i.e., used location) relative to five alternative choices that also were available temporally and spatially but were not

Table 2 Candidate models and variables used to assess resource selection in greater sage-grouse

Model	Parameters[a]	K
Null	None[b]	0
Sagebrush	Percent sagebrush (linear and quadratic terms)	2
Water resources	Percent sagebrush (linear and quadratic terms), distance to the nearest mesic area, and convexity 90 m	4
Sagebrush and non-energy-related anthropogenic features	Percent sagebrush (linear and quadratic terms), distance to the nearest mesic area, and distance to nearest residential or agricultural structure	4
Sagebrush and energy-related anthropogenic features	Percent sagebrush (linear and quadratic terms), distance to the nearest road, distance to nearest energy-related ancillary feature, and distance to nearest well	5
Terrain/topography	Percent sagebrush (linear and quadratic terms), slope (linear and quadratic terms), terrain roughness 90 m, and convexity 90 m	6
Movement facilitation	Percent sagebrush (linear and quadratic terms), percent bare ground (linear and quadratic terms), terrain roughness 90 m, and distance to the nearest road	6
Foraging	Percent sagebrush (linear and quadratic terms), percent herbaceous (linear and quadratic terms), distance to the nearest mesic area, and distance to the nearest residential or agricultural structure	6
Agriculture	Percent sagebrush (linear and quadratic terms), percent litter (linear and quadratic terms), distance to the nearest mesic area, and distance to the nearest residential or agricultural structure	6
Thermal environment	Percent sagebrush (linear and quadratic terms), percent shrub (linear and quadratic terms), slope (linear and quadratic terms), and heat load index	7
Local concealment	Percent sagebrush (linear and quadratic terms), percent shrub (linear and quadratic terms), percent bare ground (linear and quadratic terms), and percent litter (linear and quadratic terms)	8
Terrain/topography and foraging	Percent sagebrush (linear and quadratic terms), percent herbaceous (linear and quadratic terms), distance to the nearest mesic area, and distance to the nearest residential or agricultural structure, slope (linear and quadratic terms), terrain roughness 90 m, and convexity 90 m	10
Vegetation	Percent sagebrush (linear and quadratic terms), percent shrub (linear and quadratic terms), percent herbaceous (linear and quadratic terms), percent litter (linear and quadratic terms), percent bare ground (linear and quadratic terms), and estimated shrub height (linear and quadratic terms)	12
Foraging/perceived risk	Percent sagebrush (linear and quadratic terms), percent herbaceous (linear and quadratic terms), percent bare ground (linear and quadratic terms), estimated shrub height (linear and quadratic terms), distance to the nearest mesic area, distance to the nearest road, distance to the nearest energy-related ancillary feature, and distance to the nearest well	13
Vegetation and water resources	Percent sagebrush (linear and quadratic terms), percent shrub (linear and quadratic terms), percent herbaceous (linear and quadratic terms), percent litter (linear and quadratic terms), percent bare ground (linear and quadratic terms), estimated shrub height (linear and quadratic terms), and distance to the nearest mesic area	13
Vegetation and terrain/ topography	Percent sagebrush (linear and quadratic terms), percent shrub (linear and quadratic terms), percent herbaceous (linear and quadratic terms), percent litter (linear and quadratic terms), percent bare ground (linear and quadratic terms), estimated shrub height (linear and quadratic terms), slope (linear and quadratic terms), terrain roughness 90 m, and convexity 90 m	16
Global	All parameters	22

[a]Listed in Table 1. [b]The PHREG procedure in SAS does not estimate an intercept. Candidate model set that includes competing hypotheses (null model, global model, and 15 competing hypotheses) on how landscape features structure occurrence of greater sage-grouse (*Centrocercus urophasianus*) during 2009 to 2012 in south-central Wyoming, USA. Each model (i.e., competing hypothesis) lists the number of parameters (*K*) and their description. Models are sorted in ascending order from least to most parameters.

chosen (i.e., non-used locations). One benefit of discrete-choice models is that inference is conditional on individual strata (e.g., a single used location and the paired non-used locations), thus accounting for potential spatiotemporal or within-individual autocorrelation among used locations (Pendergast et al. 1996; Johnson et al. 2004; Baasch et al. 2010; Cushman and Lewis 2010). We estimated resource selection models across all individuals and years to make population-level inference using conditional logistic regression for encamped and traveling behavioral modes separately, and then combined all behavior-specific data back into a non-behaviorally adjusted model for comparison. For the non-behaviorally adjusted model, we included a weight statement to adjust for the greater number of locations assigned to the encamped state. Locations assigned to the encamped mode were given a weight of 0.5138 whereas the traveling locations were given a weight of 1.0. AIC adjusted for small sample size difference (ΔAIC_c) and Akaike weights (w) were used to assess and select the most parsimonious models (Burnham and Anderson 2004) of occurrence during encamped and traveling modes and for the non-behaviorally adjusted model.

Mapping the response and model validation

Using the raster calculator tool in Spatial Analyst, we created natural log-transformed grids for distance variables, as well as grids depicting a quadratic form for terrain and vegetation variables. Models were made spatial using the raster calculator tool to invoke the equation:

$$w(x) = \exp\left(\sum_{k=1}^{K} \beta_k^* x_k\right) \quad (3)$$

where $w(x)$ is the relative probability of use, β_k^* is the parameter estimate for covariate k ($k = 1 \ldots K$), and raster data have values x (Manly et al. 2002). Separate raster surfaces were generated for predicted occurrence during encamped and traveling behavioral modes and for the non-behaviorally adjusted model. Using SAS (rank and means procedures) and GIS, we partitioned cells comprising raster surfaces into deciles based on cell value, resulting in ten ranks for the relative probability of occurrence (1 = lowest, 10 = highest).

We withheld seven sage-grouse (20% of the total sample) from the model development as an independent validation sample; the validation sample was selected using a random number generator. We validated encamped and traveling raster surfaces by plotting 2,752 and 1,804 validation locations from the withheld sage-grouse on each surface, respectively, and testing whether the number of locations increased monotonically with bin rank (bins 1 to 10) using Spearman rank correlation (ρ) implemented by the CORR procedure in SAS. We used another independent set of sage-grouse ($n = 7$) with 4,174 locations to validate the non-behaviorally adjusted raster surface. To generate a final map of predicted occurrence, we combined encamped and traveling raster layers using Spatial Analyst\Local\Combine, which provided an output raster in which a unique output value was assigned to each unique combination of input values. We reclassified the combined surface into the occurrence probability classes: high-priority encamped habitat; high-priority traveling habitat; high-priority encamped and traveling habitat; and low priority habitat.

Results

Fix success rate during the brood-rearing season was high, averaging 94.0% (±1.7% SD). For model development, we used 19,557 GPS locations across 28 female sage-grouse; all locations were used for estimating resource selection of the non-behaviorally adjusted model. The relative displacement index assigned 12,919 locations to the encamped behavioral mode, and 6,638 locations to the traveling behavioral mode. Assignment to behavioral mode provided the basis for modeling resource selection during encamped and traveling modes (*sensu* Figures 1 and 2).

A single model was most plausible for each of the behavioral modes (Table 3), as well as for the combined, non-behaviorally adjusted model (Table 4). For both encamped and traveling modes and the non-behaviorally adjusted model, there was strong evidence in favor of the hypothesis that vegetation and water resources underpinned occurrence patterns of brooded females compared to all other hypotheses tested (Table 4). The vegetation and water resources model for encamped had 95% of model support and was 5.75 AIC_c units better than the next best model, which only had a model weight (w) of 0.05 (Table 3). During the traveling mode, the vegetation and water resources model had overwhelming model support ($w = 0.97$) compared to the next best model ($w = 0.03$; $\Delta AIC_c = 7.22$) (Table 3). Compared to the behavioral models, the vegetation and water resources model for the non-behaviorally adjusted data (Table 4) still had strong support ($w = 0.88$) but not as much support as the individual behavioral models.

When encamped, sage-grouse selected for taller shrubs and proximity to mesic areas, but avoided bare ground (Table 5). When traveling, sage-grouse selected for greater litter cover, herbaceous vegetation, and proximity to mesic areas. Sage-grouse during the encamped mode showed an affinity to greater shrub coverage, including sagebrush; during traveling, sage-grouse preferred taller shrubs but at a lower percentage of shrub coverage (Table 5). Resource selection patterns of sage-grouse in the non-behaviorally adjusted model had the same patterns of selection as the encamped model, albeit the magnitude of coefficient estimates was different (Table 6).

The map depicting the encamped behavioral mode validated well ($\rho = 0.99$, $df = 9$, $P < 0.001$) with 9.3% of validation locations occurring in the lowest four bins and 70.6% in the highest four bins. Likewise, the map depicting the traveling behavioral mode validated well ($\rho = 0.99$, $df = 9$, $P < 0.001$) with 21.8% of validation locations occurring in the lowest four bins and 61.3% in the highest four bins. The non-behaviorally adjusted map validated well ($\rho = 0.988$, $df = 9$, $P < 0.001$); 69.5% of locations were in the highest four bins and 13.1% were in the lowest four bins. The final map in which encamped and traveling raster surfaces were combined depicts high-priority habitat for brood-rearing sage-grouse (Table 7, Figure 3).

We note an area in question associated with these raster surfaces (Figure 3). Based on first-hand experience of the site, habitat in this area is best described as vegetated sand dunes and is comprised of dunes interspersed with vegetated hummocks that include species such as shadscale, spiny hopsage (*Grayia spinosa*), greasewood, Gardner's saltbush (*Atriplex gardneri*), and grasses. Although sage-grouse under observation have occurred in this area, its inclusion here as high-priority brood-rearing

Table 3 Ranking of candidate models for encamped and traveling modes of greater sage-grouse

Modes	*K*	AIC_c	Δ	*w*
Encamped				
Model				
Vegetation and water resources	13	33,663.78	0.00	0.95
Global	22	33,669.52	5.75	0.05
Foraging/perceived risk	13	33,769.51	105.73	0.00
Agriculture	6	33,835.05	171.28	0.00
Vegetation	12	33,895.72	231.95	0.00
Vegetation and terrain/topography	16	33,901.36	237.58	0.00
Local concealment	8	33,987.29	323.51	0.00
Sagebrush and non-energy-related anthropogenic features	4	33,988.50	324.72	0.00
Water resources	4	33,989.64	325.86	0.00
Foraging	6	33,990.89	327.11	0.00
Terrain/topography and foraging	10	33,994.76	330.99	0.00
Movement facilitation	6	34,050.88	387.10	0.00
Thermal environment	7	34,244.93	581.15	0.00
Sagebrush and energy-related anthropogenic features	5	34,321.29	657.52	0.00
Sagebrush	2	34,328.50	664.72	0.00
Terrain/topography	6	34,330.78	667.00	0.00
Null	0	34,671.67	1 007.90	0.00
Traveling				
Model				
Vegetation and water resources	13	17,540.62	0.00	0.97
Vegetation	12	17,547.84	7.22	0.03
Global	22	17,552.09	11.48	0.00
Vegetation and terrain/topography	16	17,554.23	13.61	0.00
Agriculture	6	17,557.83	17.21	0.00
Local concealment	8	17,562.81	22.20	0.00
Foraging/perceived risk	13	17,575.16	34.54	0.00
Movement facilitation	6	17,582.81	42.20	0.00
Foraging	6	17,605.54	64.93	0.00
Thermal environment	7	17,607.75	67.13	0.00
Sagebrush and non-energy-related anthropogenic features	4	17,609.30	68.69	0.00
Terrain/topography and foraging	10	17,610.45	69.83	0.00
Water resources	4	17,611.45	70.84	0.00
Sagebrush	2	17,624.95	84.34	0.00
Sagebrush and energy-related anthropogenic features	5	17,625.16	84.55	0.00
Terrain/topography	6	17,628.74	88.13	0.00
Null	0	17,733.84	193.23	0.00

List of candidate models (i.e., competing hypotheses) for encamped and traveling modes of greater sage-grouse (*Centrocercus urophasianus*) in south-central Wyoming, USA, from 2009 to 2012. Models are ranked in order of most plausible, including number of parameters (*K*), Akiake information scores corrected for small sample size (AIC_c), difference in AIC_c scores (Δ), and AIC_c weights (*w*).

habitat may be erroneous, reflecting relatively high values for percent shrub in the covariate raster set (Table 1; Homer et al. 2012).

Lastly, upon undertaking this investigation, we intended to analyze fatality among brooded females relative to landscape features and behavioral mode (*sensu* Dzialak et al.

Table 4 Ranking of candidate models for the non-behaviorally adjusted model of greater sage-grouse

Model	K	AIC_c	Δ	w
Vegetation and water resources	13	28,266.89	0.00	0.88
Foraging/perceived risk	13	28,270.86	3.97	0.12
Global	22	28,279.22	12.33	0.00
Agriculture	6	28,362.19	95.31	0.00
Vegetation	12	28,384.96	118.07	0.00
Vegetation and terrain/topography	16	28,391.44	124.55	0.00
Local concealment	8	28,446.15	179.26	0.00
Movement facilitation	6	28,480.97	214.08	0.00
Sagebrush and non-energy-related anthropogenic features	4	28,483.76	216.88	0.00
Foraging	6	28,484.18	217.29	0.00
Water resources	4	28,484.72	217.83	0.00
Terrain/topography and foraging	10	28,488.96	222.07	0.00
Thermal environment	7	28,593.09	326.20	0.00
Sagebrush and energy-related anthropogenic features	5	28,656.49	389.60	0.00
Sagebrush	2	28,659.07	392.18	0.00
Terrain/topography	6	28,662.48	395.59	0.00
Null	0	28,928.05	661.17	0.00

List of candidate models (i.e., competing hypotheses) for the non-behaviorally adjusted model of resource selection for greater sage-grouse (*Centrocercus urophasianus*) in south-central Wyoming, USA, from 2009 to 2012. Models are ranked in order of most plausible, including number of parameters (*K*), Akiake information scores corrected for small sample size (AIC_c), difference in AIC_c scores (Δ), and AIC_c weights (*w*).

2011b); however, only six fatalities occurred during the investigation. Notably, the GPS location immediately preceding fatality (and in some cases, many locations preceding fatality) in all six instances was assigned to the encamped behavioral mode.

Discussion

From these data, it appears that resource selection by sage-grouse is structured, at least partially, during the brood-rearing season, by different movement behaviors. Only one model (i.e., vegetation and water resources) was identified as the most plausible model across all scenarios. We also found that the non-behaviorally adjusted model validated well. Despite these findings, there were differences in selection for some resources in the two different behavioral modes, which highlights the importance of considering behavioral mode when investigating sage-grouse brood-rearing habitat selection. Generally, the non-behaviorally adjusted model was similar to the encamped model but had a lower weight of evidence as being the best model in the candidate set. The similarity between the encamped and non-behaviorally adjusted model could have been an artifact of the larger sample size for encamped locations; however, we accounted for this fact by weighting the data prior to analysis. We found that resource selection during traveling exhibits a much different pattern of selection because these landscape features serve a different purpose compared to the general selection patterns of sage-grouse that occur for a wide-range of behaviors (e.g., resting, encamped, foraging, etc.). Therefore, prioritization of habitat for brood-rearing sage-grouse not only needs to consider general selection patterns and demographics but also should incorporate behavior-specific patterns of selection, which may disproportionately influence population persistence or connectivity because these landscape features may not be as predominant as other features that are typically viewed as important to general resource selection of the species.

Brood-rearing in sage-grouse has been investigated in terms of days post-hatching, with the brood-rearing phase and accompanying analyses partitioned into early- and late-summer periods (Connelly et al. 2000; Thompson et al. 2006), and the landscape context within which these resources occur establish a reasonable basis for investigating temporal patterns of selection (Mysterud and Ims 1998; Sveum et al. 1998; Thompson et al. 2006; Dzialak et al. 2011b) yet do not describe how resources are used during different behaviors. Another way to look at brood-rearing involves the behavioral mode underpinning observed movement and occurrence patterns. At a fundamental level, within- versus between-patch movements are dominant behavioral modes among female sage-grouse during brood-rearing. The fine-scale temporal data provided by GPS units made this apparent (Figure 1). Behavioral mode, as a latent process influencing occurrence patterns, reflects spatial and temporal attributes of variation in local conditions driving

Table 5 Covariate parameter estimates of the most plausible model during encamped and traveling modes for greater sage-grouse

Modes	Estimate	SE	95% CL
Encamped			
Parameter			
Percent sagebrush (linear)	0.04	0.05	−0.06 to 0.15
Percent sagebrush (quadratic)	−0.003	0.003	−0.009 to 0.003
Percent shrub (linear)	0.13	0.07	−0.01 to 0.26
Percent shrub (quadratic)	−0.004	0.003	−0.01 to 0.001
Estimated shrub height (linear)	0.04	0.01	*0.02 to 0.07*
Estimated shrub height (quadratic)	−0.0004	0.001	−0.001 to 0.0002
Percent bare ground (linear)	−0.05	0.02	*−0.09 to -0.02*
Percent bare ground (quadratic)	0.0003	0.0002	*1.8 E−5 to 0.0007*
Percent litter (linear)	0.003	0.02	−0.03 to 0.04
Percent litter (quadratic)	−0.0001	0.0004	−0.0009 to 0.0008
Percent herbaceous (linear)	0.02	0.02	−0.02 to 0.06
Percent herbaceous (quadratic)	−0.0003	0.0007	−0.002 to 0.001
Distance to nearest mesic area	−0.10	0.01	*−0.13 to −0.08*
Traveling			
Parameter			
Percent sagebrush (linear)	−0.001	0.04	−0.09 to 0.09
Percent sagebrush (quadratic)	0.0001	0.002	−0.004 to 0.005
Percent shrub (linear)	−0.06	0.06	−0.18 to 0.07
Percent shrub (quadratic)	0.002	0.002	−0.003 to 0.007
Estimated shrub height (linear)	0.01	0.009	−0.005 to 0.03
Estimated shrub height (quadratic)	5.0 E−5	0.0002	−0.0003 to 0.0004
Percent bare ground (linear)	−0.02	0.02	−0.06 to 0.02
Percent bare ground (quadratic)	0.0001	0.0002	−0.0002 to 0.0005
Percent litter (linear)	0.07	0.02	*0.03 to 0.10*
Percent litter (quadratic)	−0.001	0.0005	*−0.002 to −0.0004*
Percent herbaceous (linear)	0.007	0.02	−0.04 to 0.05
Percent herbaceous (quadratic)	2.0 E−5	0.0008	−0.002 to 0.002
Distance to nearest mesic area	−0.04	0.02	*−0.08 to −0.005*

Coefficient estimates, standard error (SE), and 95% confidence limits (CL) for covariates from the most plausible model (vegetation and water resources; see Table 3) of resource selection by greater sage-grouse (*Centrocercus urophasianus*) during encamped and traveling behavioral modes in south-central Wyoming, USA from 2009 to 2012. Confidence limits in italics did not include zero.

Table 6 Covariate parameter estimates of the most plausible model of the non-behaviorally adjusted model for greater sage-grouse

Parameter	Estimate	SE	95% CL
Percent sagebrush (linear)	0.03	0.038	−0.04 to 0.11
Percent sagebrush (quadratic)	−0.002	0.002	−0.01 to 2.5 E−3
Percent shrub (linear)	0.053	0.057	−0.06 to 0.16
Percent shrub (quadratic)	−0.002	0.002	−0.01 to 2.2 E−3
Estimated shrub height (linear)	0.029	0.009	*0.01 to 0.05*
Estimated shrub height (quadratic)	2.0 E−4	2.0 E−4	−6.0 E−4 to 2.0 E−4
Percent bare ground (linear)	−0.037	0.014	*−0.06 to −0.01*
Percent bare ground (quadratic)	3.0 E−4	1.0 E−4	*1.0 E−5 to 5.0 E−4*
Percent litter (linear)	0.029	0.012	*4.6 E−3 to 0.05*
Percent litter (quadratic)	−0.001	3.0^{e-4}	−1.2 E−3 to 1.0 E−4
Percent herbaceous (linear)	0.013	0.014	−0.01 to 0.04
Percent herbaceous (quadratic)	3.0 E−4	0.001	−1.4 E−3 to 8.0 E−4
Distance to nearest mesic area	−0.084	0.017	*−0.12 to −0.05*

Coefficient estimates, standard error (SE), and 95% confidence limits (CL) for covariates from the non-behaviorally adjusted model (vegetation and water resources; see Table 4) of resource selection by greater sage-grouse (*Centrocercus urophasianus*) in south-central Wyoming, USA, from 2009 to 2012. Confidence limits in italics did not include zero.

resource availability independently of days post-hatching. The estimated relative displacement index was one approach to incorporating information on behavior to strengthen inference on resource needs (Figures 1 and 2). Other approaches to identify behavioral modes or to assign data to defined modes have involved random walk models (Wu et al. 2000), cluster analysis (Van Moorter et al. 2010), state-space models (Jonsen et al. 2005), fractals (Etzenhouser et al. 1998; Webb et al. 2009), and generalized additive models (Dzialak et al. 2011a). Results of the resource

Table 7 Reclassification of relative probability bins into broad designations that prioritized habitat based on behavioral mode

Bin rank				
Encamped	Traveling	Designation	Number of cells	Percentage of landscape
1 to 7	8 to 10	High-priority traveling habitat	406,624	4.6
8 to 10	1 to 7	High priority encamped habitat	406,624	4.6
8 to 10	8 to 10	High priority encamped and traveling habitat	2,240,132	25.4
1 to 7	1 to 7	Lower priority habitat	5,769,140	65.4
Total			8,822,520	

Raster surfaces depicting encamped and traveling behavior of greater sage-grouse (*Centrocercus urophasianus*) in south-central Wyoming, USA, during 2009 to 2012 were developed with the predicted probability of occurrence classified into ten relative probability bins (1 = lowest, 10 = highest) that included 10% of the landscape area. The encamped and traveling surfaces were combined to provide an output raster in which a unique output value (designation) was assigned to each of four combinations of input values.

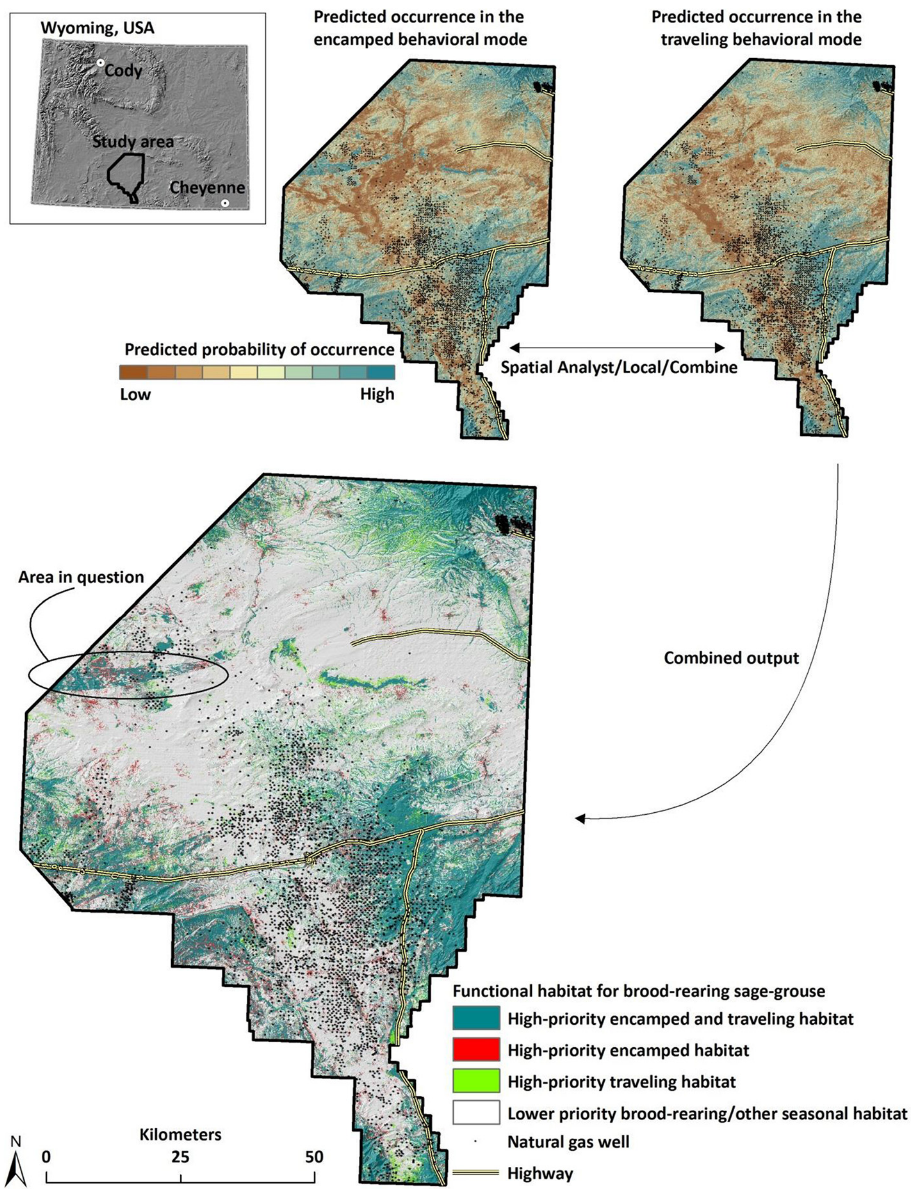

Figure 3 Study area and spatial depiction of occurrence by greater sage-grouse in Wyoming. Spatial depiction of occurrence of greater sage-grouse (*Centrocercus urophasianus*) in south-central Wyoming, USA, from 2009 to 2012 estimated from discrete-choice models of encamped and traveling behavioral modes. The combined output depicts landscapes that serve concurrently in high-priority encamped and traveling modes (25.4%; see Table 7), as well as landscapes that are used for either encampment (4.6%) or traveling (4.6%), but not both (65.4%). The 'area in question' is characterized by sand dunes and shrub brush species and is discussed in the 'Results' section.

selection models, including their validation metrics, indicate that the relative displacement index assigned data to the respective behavioral modes in a biologically meaningful way.

For both encamped and traveling modes and the non-behaviorally adjusted model, the importance of vegetation attributes and proximity to mesic areas was the best model among the candidate models. This suggests that all three models shared key attributes, perhaps most notably the importance of mesic conditions. Such overlap also can be seen in the extensive area that was used concurrently in high-priority encamped and traveling modes (Table 7, Figure 3). Nonetheless, the sign and magnitude of effect of key parameters differed between modes, and compared to the non-behaviorally adjusted model, in ways that may broaden our view of what important brood-rearing habitat looks like. The selection patterns during the traveling mode changed for 6 of 13 (46.2%) variables included in the model compared to the encamped and non-behaviorally adjusted model, which both had similar patterns of selection. The analysis also identified some areas that were suitable for either encampment or traveling modes, but not both (Table 7, Figure 3), suggesting some degree of divergence between the habitats. Assuming the encamped mode involved within-patch foraging, habitat used for forage resources was characterized by features that have become familiar to managers including areas with taller shrubs, proximity to mesic areas, and avoidance of bare ground (Figure 4a; Wallestad 1971; Dunn and Braun 1986; Drut et al. 1994; Connelly et al. 2000; Aldridge and Boyce 2007; Dzialak et al. 2011b).

Characterizing attributes of the landscape that were important during between-patch movement was a novel addition to our understanding of brood-rearing sage-grouse. While traveling, sage-grouse selected for proximity to mesic areas, but the strength of selection was diminished relative to encamped behavior. Notably, there was no apparent selection for sagebrush and shrubs among traveling sage-grouse (Table 5). From a management perspective, habitat used during between-patch movement can be described as mesic stopover sites interspersed throughout areas characterized by a high proportion of grasses or herbaceous litter (Figure 4b). Compared to encampment areas, which likely provided available forage and cover, traveling sage-grouse tended to be influenced more by the amount of litter and herbaceous vegetation. The use of open areas (i.e., less shrub coverage) in close proximity to mesic areas also could be an advantage to reduce predation whereby sage-grouse can visually detect potential predators (Webb et al. 2012). The link between behavioral modes and the reason why a given area was selected during both encamped and traveling modes is the importance of mesic areas to brooded females, chicks, and the survival of both. Although we could not link mortality with selection of resources because of limited sample size, it is noteworthy that all fatalities were classified to an encamped location. Although speculative, this finding also supports the selection of resources during traveling that may minimize predation by using open areas (i.e., for visual detection of predators) in close proximity to mesic areas that could provide hiding cover.

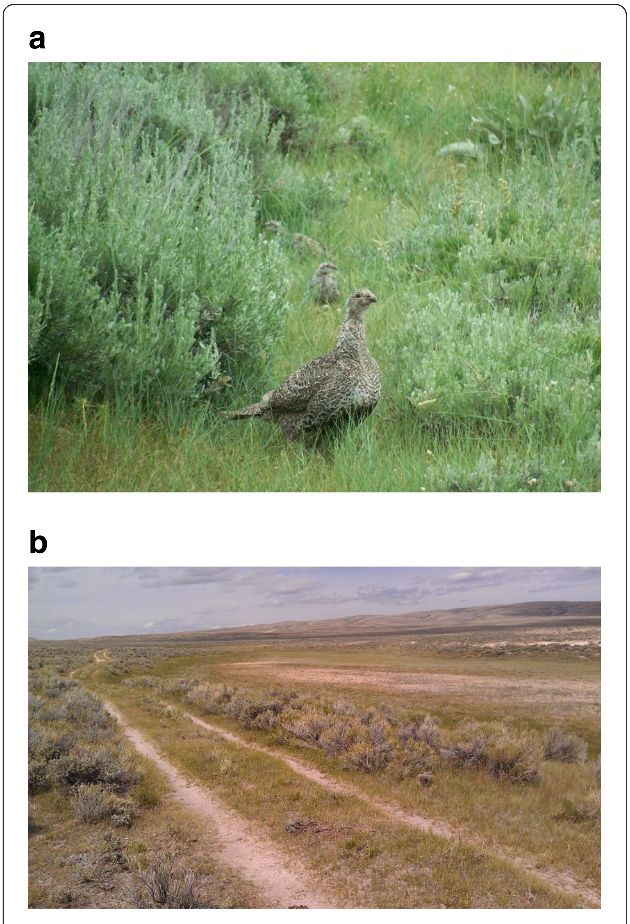

Figure 4 Representative habitat for greater sage-grouse during encamped and traveling phases in Wyoming. Encamped habitat for greater sage-grouse (*Centrocercus urophasianus*) in south-central Wyoming, USA, is shown in panel **(a)**, and traveling habitat is shown in panel **(b)**. Landscape features used for encampment behaviors included shrub coverage with a prominent sagebrush component, tall shrubs, limited bare ground, and proximity to mesic areas. Traveling habitat included limited shrub coverage, a higher proportion of herbaceous litter, and slightly diminished proximity to mesic areas. Note the shallow mesic area (albeit dry), established by snowmelt, situated within an extensive area of limited shrub coverage in panel **(b)**. Photos by C.V. Olson.

Models that included anthropogenic features, terrain, and topographic features performed poorly, capturing far less information in the data than the top model. Aldridge and Boyce (2007) found that broods avoided areas with a high density of human development, including oil and natural gas wells. In a nearby Wyoming study area, we found consistent avoidance of rough terrain at the patch scale (90 m^2) among brooded females (Dzialak et al. 2011b). Companion studies in this and nearby study areas found that the specific response of sage-grouse to anthropogenic and other landscape features was mediated by behavioral mode. Certain behavior such as nest site (and possibly winter range) selection showed relative generality across regions, whereas other behavior such as nesting off-bout occurrence showed a higher degree of region-specificity (Dzialak et al. 2013a; 2013b). A meaningful relationship between brooded sage-grouse and anthropogenic or terrain features likely exists in this area, with different analytical approaches among studies (i.e., information theoretic versus variable reduction) contributing to differing inference. But it is also plausible that resource acquisition during brood-rearing is highly adaptable to spatial and temporal patterns in floristic and predatory composition of the local area such that inference on the relationship between brood occurrence and particular landscape features should be investigated regionally.

Conclusions

Most overlap in the selection for resources occurred between encamped and non-behaviorally adjusted models, although selection patterns for some features, primarily mesic areas, were similar across all behaviors and models. These results draw attention to the key brood-rearing process of between-patch movement and to the range of landscape features that play a role in this process. The combined raster surface (Figure 3) makes the analytically derived characteristics of habitat spatial. This surface validated well and offers a reliable habitat management tool that is readily amenable to application in efforts to focus sustainable landscape planning. As a GIS product, the raster surface can be included in infrastructure siting, habitat avoidance, and reclamation processes by GIS users with the managing agencies and industry. In lower-elevation Intermountain landscapes, mesic conditions that establish important brood-rearing patches often arise through deposition of water for agriculture or are produced as a byproduct of energy development. While the use of produced water may create brood-rearing habitat, there is evidence that such habitat, when in proximity to infrastructure, results in an ecological trap by establishing resource subsidies that modify predator abundance or effectiveness in ways that are detrimental to brooded females (see Dzialak et al. 2011b; Webb et al. 2012). Potential encampment sites may only be used when connected by suitable travel corridors composed of unique resources. If suitable travel corridors were not available, then potential encampment sites may no longer function in the persistence of populations because animals may not be able to reach encamped sites or may face greater risk when traveling to these sites. Therefore, a relevant aim of future research would be to further characterize habitat in terms of connectivity (Harju et al. 2013b), stopover sites (Sawyer et al. 2009), and to more specifically quantify risk associated with behavioral modes or activities (e.g., during encampment or traveling).

Abbreviations

AIC: Akaike's information criterion; AICc: Akaike's information criterion corrected for small sample size; *D*: distance between successive GPS locations; DEM: digital elevation model; GIS: geographic information system; GPS: global positioning system; HLI: heat load index; NED: National Elevation Dataset; PTT: platform terminal transmitters; UHF: ultra-high frequency; UTM: Universal Transverse Mercator; w_i: Akaike weights.

Competing interests

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Authors' contributions

MRD designed the study, provided statistical assistance, analyzed portions of the data set, and helped to draft the manuscript. CVO designed the study, managed data, and helped to draft the manuscript. SLW analyzed data and helped to draft the manuscript. SMH provided statistical analysis and helped to draft the manuscript. JBW designed the study and reviewed manuscript drafts. All authors have read and approved the manuscript.

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