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Winter Resource Selection by Mule Deer on the Wyoming–Colorado Border Prior to Wind Energy Development

Stephen L. Webb,[1] *Matthew R. Dzialak,*[2] *Karl L. Kosciuch,*[3] *and Jeffrey B. Winstead*[4]

Authors are [1]*Quantitative Ecologist,* [2]*Senior Wildlife Ecologist, and* [4]*Principal Biologist, Hayden-Wing Associates, LLC, Laramie, WY 82070, USA; and* [3]*Senior Wildlife Biologist, Tetra Tech EC, Inc, Portland, OR 97201, USA.*

Abstract

Areas identified as winter range are important seasonal habitats for mule deer (*Odocoileus hemionus*) because they can moderate overwinter mortality by providing thermal cover and forage. Therefore, identifying seasonally important resources is a conservation priority, especially when sensitive areas are proposed for development. We used data collected from global positioning system (GPS) collars fitted on female mule deer ($n=19$; one location every 3 h) to identify resources important during winter (23 February 2011–30 April 2011; 1 November 2011–15 January 2012) in a region spanning southern Wyoming and northern Colorado that has been proposed for wind energy development. The study period included portions of two consecutive winters but were pooled for analysis. We used methods to account for GPS biases, fractal analyses to determine perceived spatial scale, and discrete choice models and conditional logistic regression to assess resource selection prior to development (i.e., baseline data). Resource selection by female mule deer revealed similar patterns between active (0600–1800 hours) and nonactive (2100–0300 hours) periods. Deer selected most strongly for proximity to rock outcrops and shrubland and average values of slope. Deer tended to avoid roads and grasslands; all other landscape features had minimal influence on resource selection (hazard ratios near, or overlapping, 1). Using the fixed-effects coefficient estimates, we developed two spatially explicit maps that depicted probability of mule deer occurrence across the landscape. Based on an independent validation sample, each map (active and nonactive) validated well with a greater percentage of locations occurring in the two highest probability of use bins. These maps offer guidance to managing mule deer populations, conserving important seasonal habitats, and mitigating development (e.g., wind energy) in areas identified as important to mule deer.

Key Words: crucial range, discrete choice model, fractal analysis, global positioning systems, *Odocoileus hemionus*, resource selection function

INTRODUCTION

In many areas, mule deer (*Odocoileus hemionus*) herds annually migrate from higher elevation summer range to lower elevation winter range in response to weather and forage availability (Watkins et al. 2007; Cox et al. 2009; Monteith et al. 2011). Winter range typically provides food, cover, and protection from snow accumulation and adverse weather conditions (Mule Deer Working Group 2007). Important seasonal habitats, such as winter range, have the potential to influence population demographics such as survival and reproduction (Sawyer et al. 2006; Dzialak et al. 2011a). For example, winter range typically comprises a relatively small proportion of the total available range, which can result in deer congregating into smaller areas at greater densities (Mule Deer Working Group 2007). Therefore, loss or alteration of winter range may have greater population-level effects than loss or alteration of other seasonal habitats.

Winter range is considered a major limiting factor for mule deer throughout the western United States (Wallmo et al. 1977; Watkins et al. 2007). Fragmentation of winter range as a consequence of human activity is an ongoing concern among wildlife managers, and fragmentation (e.g., through development) can result in both direct and indirect effects on habitat and the animals that rely on the habitat. Identifying winter range, and the resources that form it, as part of a larger strategy that addresses other important habitats, is necessary for conservation planning. For example, Sawyer et al. (2006, 2009) documented changes in patterns of resource selection by mule deer during winter in response to energy development in Wyoming. In addition to direct loss of habitat from well pad construction, Sawyer et al. (2006) documented effective loss of habitat as a function of long-term avoidance of areas near development. This response, an immediate change in resource selection behavior as natural gas development occurred, would have been difficult to quantify had predevelopment, baseline telemetry data from wintering mule deer in the area been unavailable (Sawyer et al. 2006). Another way of understanding how behavior may change across pre- and postdevelopment periods involves sustainable landscape planning. Harju et al. (2011) showed that human activity altered resource selection behavior in elk (*Cervus elaphus*) and that spatial models (habitat suitability maps) reflecting altered behavior could be poor predictors of true habitat suitability and thus ineffective as planning tools. Gathering baseline, or predevelopment data ensures that conservation intervention is based on an understanding of innate patterns of resource selection and occurrence rather than patterns that may reflect avoidance behavior,

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Correspondence: Stephen L. Webb, Department of Computing Services, Samuel Roberts Noble Foundation, 2510 Sam Noble Pkwy, Ardmore, OK 73401, USA. Email: slwebb@noble.org

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habituation, or other processes by which animals may occur in suboptimal habitat.

The Mule Deer Initiative of Wyoming (Mule Deer Working Group 2007) addressed the need for a continued effort to increase knowledge of deer distribution, migration, and habitat use because of their importance in managing deer more effectively. With increasing development for energy resources across the western United States, we set forth to collect baseline data on resource needs of mule deer during winter because an area of crucial winter range for mule deer is located within the perimeter of our study area, which has been proposed for development of wind energy. The proposed development would include wind turbines and associated access roads and electrical collection lines. Recent work has addressed effects of natural gas and oil development on mule deer (Sawyer et al. 2006, 2009) and elk (Dzialak et al. 2011a, 2011b; Harju et al. 2011), but a paucity of data exists on the effects of wind energy development on large vertebrates. Much research has focused on avian species, but only one study to date has examined the potential influence of wind energy development on a large ungulate (i.e., elk in Oklahoma; Walter et al. 2006).

The larger goal of this work was to provide baseline (i.e., predevelopment) data on winter resource selection of mule deer that can be used during the planning phases of development (e.g., infrastructure siting locations and timing) and to infer any future changes in behavior. The objectives of this study were to 1) estimate and predict resource selection of female mule deer during winter and 2) provide spatially explicit maps of deer occurrence that can be used in the decision-making process related to development, management, and conservation. The general approach we employed to meet the aforementioned objectives included the use of 1) methods to account for bias associated with habitat-related inconsistency in GPS fix success rate and accuracy, which increases the predictive ability of spatially explicit maps (Webb et al. 2013b), 2) fractal analyses to determine perceived spatial scale for mule deer, and 3) discrete choice models and conditional logistic regression to assess resource selection (i.e., resource selection functions [RSFs]; Manly et al. 2002). These data then can be used for designating winter range based on available resources within an area, for planning and mitigation purposes in response to proposed development, and to balance wind energy development with the conservation of resources necessary for the long-term persistence of mule deer populations.

METHODS

Study Area

The project area (~9 248 ha) was located in southeastern Wyoming, USA, situated along the Wyoming-Colorado border. Most land (81%) was under private ownership (7 504 ha), and to a lesser extent under state (907 ha) or federal management (Bureau of Land Management; 837 ha). An area of crucial winter range for mule deer is located within the project area (2 590 ha), and was delineated by the Wyoming Game and Fish Department from visual observations of mule deer during the 1980s and 1990s. No paved road occurred within the study area; only improved (use of heavy equipment to maintain natural or exotic material on road surface) and unimproved roads (heavy equipment was not used to maintain roads). The study area was used primarily as second home getaways that were occupied minimally during winter with the exception of one large private landholding that used the rangeland for grazing cattle. However, a portion of the study area has been proposed for development of wind energy.

Topography was variable ranging from flat to gently sloping grasslands, deep riparian gullies, and steep rock outcrops. Elevation ranged from 2 100 m to 3 100 m and slope from 0° to 52°. Five broad classes of vegetation/landscape features occurred throughout the study area: grassland, shrubland, riparian, forest, and rock outcrop. Predominant plant species included mountain big sagebrush (*Artemisia tridentata vaseyana*), antelope bitterbrush (*Purshia tridentata*), alderleaf mountain mahogany (*Cercocarpus montanus*), skunkbush sumac (*Rhus trilobata*), Saskatoon serviceberry (*Amelanchier alnifolia*), quaking aspen (*Populus tremuloides*), willow (*Salix* spp.), rabbitbrush (*Chrysothamnus* spp.), alder (*Alnus* spp.), narrowleaf cottonwood (*Populus angustifolia*), and lodgepole pine (*Pinus contorta*). Average (1948–2010) minimum January temperature was −12.7°C, average maximum July temperature was 26.8°C, and average annual snowfall was 123.2 cm (Western Regional Climate Center 2011).

Capture and Handling

We captured adult ($\geq$2.5 yr-old), female mule deer ($n=19$) from 21 to 22 February 2011 using helicopter and net-gun capture techniques, which have been found safe for a wide range of ungulate species with low direct and postcapture mortality (Webb et al. 2008). We aged deer to ensure that sampled deer were $\geq$2.5 yr old, measured morphometric traits and body condition, affixed uniquely numbered tags in each ear, and collected blood for tests of pregnancy-specific protein B (BioTracking, LLC, Moscow, ID, USA). Deer were fitted with global positioning system (GPS) collars (TGW-4583, Telonics, Inc, Mesa, AZ, USA) that were equipped with Argos satellite uplink capabilities (www.argos-system.org). Collars were programmed to collect one GPS location every 3 h (i.e., eight locations/day) with data being transmitted via the Argos system every 7 d. The Wyoming Game and Fish Department approved animal capture and handling protocols (Chapter 33 Permit no. 33-796).

Covariate Development

Vegetation Mapping. We used a geographic information system (GIS) to develop a study area specific vegetation cover-type map using high-resolution (1.0-m) imagery obtained from the National Agriculture Imagery Program (NAIP; USDA Farm Service Agency, Salt Lake City, UT) and Feature Analyst 5.0 (Visual Learning Systems, Inc, 2010) for ArcGIS 10.0 (ESRI, Redlands, CA). We combined the true-color and near-infrared bands of the imagery using Feature Analyst (FA), which resulted in four spectral bands (i.e., red, green, blue, and near-infrared). We also specified the green spectral band be used to develop a texture band. We used a 10-m digital elevation model (DEM) to develop an elevation band, which finally resulted in six bands (i.e., four spectral bands, one texture band, and one elevation band). We conducted a supervised classification using delineated polygons of known vegetation type that were heads-up digitized by a researcher familiar with the study area; these polygons of known type were used as training polygons in FA. We resampled vegetation cover types that occurred over extensive areas (i.e., forest, grassland, and shrubland) to 2-m resolution and vegetation cover types that were more restricted, linear, or irregularly shaped (i.e., riparian and rock outcrops) to 1-m resolution. We used the Manhattan classifier pattern and a width of 3 pixels to classify extensive vegetation types. For more restricted vegetation types, we used the Bull's Eye 2 classifier and a width of 5 pixels for rock outcrops and 31 pixels for riparian areas. For more information on using FA and its applications in resource selection studies, refer to Visual Learning Systems (2010), Dzialak et al. (2011b), and Webb et al. (2013b).

Topography and Landscape Features. We used GIS to map landscape, topographic, and vegetation features known or suspected to influence behavior of mule deer (Kufeld et al. 1988; Thomas and Irby 1991; Pierce et al. 2004; D'Eon and Serrouya 2005; Sawyer et al. 2006; 2009; Anderson et al. 2012). The DEM was reclassified to 30-m resolution and used to calculate slope (degrees) and terrain roughness (standard deviation of elevation). Terrain roughness was calculated at 3 spatial scales: 90 m (3×3; number of pixel rows and columns), 540 m (18×18), and 1 080 m (36×36).

We heads-up-digitized (1:500 to 1:2 000 scale) roads (improved and unimproved), anthropogenic ground development (buildings, houses and structures; hereafter development), and agriculture fields using NAIP aerial imagery. We applied a buffer to roads based on average width of roads as determined by Webb et al. (2011). We set buffer distances to 4.02 and 2.07 m for improved and unimproved roads, respectively. However, we only considered improved roads because most unimproved roads received little use except for a few days per year. Before analysis, we converted vector layers for vegetation (i.e., forest, grassland, riparian, rock outcrop, and shrubland) and landscape features (i.e., roads, development, and agriculture) to raster grids. Using Spatial Analyst for ArcGIS and the Distance Toolbox, we calculated the Euclidean distance from each grid cell to the nearest cell containing the respective vegetation (i.e., forest, grassland, riparian, rock outcrop, and shrubland) and landscape (i.e., agriculture, development, and roads) feature.

Weighting Landscape Layers. When using GPS technology, habitat type or terrain can impose analytical limitations on the data because the probability of acquiring a GPS location (i.e., fix rate) may be lower in certain habitats resulting in loss of data (Frair et al. 2004; Nielson et al. 2009). Similarly, locational error (distance between estimated GPS location and true GPS location) can be affected by habitat type or terrain. Therefore, bias may be introduced into analyses that can lead to incorrect interpretation of results (i.e., over- or underestimation of resource use). To overcome these limitations, we used previously developed techniques and maps to account for these forms of bias (Webb et al. 2013b). Inverse weighting was used to account for location error and fix rate and was applied to vegetation (i.e., forest, grassland, riparian, rock outcrop, and shrubland) and topographic (i.e., slope and roughness) layers. We extracted the weighted values from all raster layers to locations of GPS points of deer and randomly generated points using Spatial Analyst. See Webb et al. (2013b) for a complete description of methods and weighting techniques.

Winter Resource Selection

Fractal Analysis. We estimated a biologically derived spatial scale perceived by mule deer using fractal analysis (Nams 2005; Webb et al. 2009; Dzialak et al. 2011b; Webb et al. 2011) to set the radius around each deer location for use within a discrete-choice model. This analysis involved using relocations to develop a movement path for each mule deer during portions of two consecutive winters (23 February–30 April 2011, and 1 November 2011–15 January 2012). We used the VFractal estimator in the program Fractal 5.0 (Nams 1996) to calculate fractal dimension (*D*) as a function of spatial scale. All mule deer were combined into a single analysis where each movement path (i.e., one path/mule deer/winter) was treated as a replicate (Nams 1996). We plotted correlation versus path length to detect changes in movement relative to spatial scale (spatial scale is equivalent to path length). We used correlation plots to detect patch size perceived by animals, which occurs when correlation is negative (Nams 2005).

Discrete-Choice Framework. Discrete-choice models (McCracken et al. 1998; Cooper and Millspaugh 1999; Manly et al. 2002; Kuhfeld 2010) estimate the probability of deer selecting a particular resource by matching each used deer location with a set of three nonchosen locations. Nonchosen locations were drawn from within a circular buffer centered on the GPS location. The radius of the buffer was defined uniquely for each deer and location and was based on the movement distance of the deer and perceived spatial scale determined by fractal analysis.

Before implementing a hierarchical variable reduction and selection approach, we created quadratic terms ($quadratic = original^2$) for the slope and roughness to account for nonlinear relationships (Dzialak et al. 2011b); elevation was not considered because of correlation with slope and roughness. We also natural log-transformed all distance variables (i.e., distance to agriculture, development, roads, grassland, rock outcrops, shrubland, riparian, and forest) to allow for a decreasing magnitude of influence with increasing distance (Dzialak et al. 2012; Webb et al. 2012). To assure that a natural log transformation (ln) was not attempted on a cell with a value=0, we added 0.1 to all original values. In summary, we developed covariates depicting 11 landscape features, but did not include elevation into analysis, which resulted in 10 landscape features whereby each was assessed for a linear relationship (all variables), quadratic relationship (slope and roughness), or a log-linear relationship (all eight distance variables).

After creating new variables, we conducted a two-step variable selection approach to reduce the number of variables in the final model. First, we used an information-theoretic approach (Burnham and Anderson 2002) to evaluate what type of relationship (i.e., linear, quadratic, or natural log transformed) was most appropriate for each landscape variable. We retained the relationship for each variable with the lowest Akaike's Information Criterion (AIC) adjusted for small sample size (AICc; Burnham and Anderson 2002). When models for

Figure 1. Correlation of tortuosity among adjacent path segments based on fractal analysis, which was used to estimate perceived patch size by female mule deer (*Odocoileus hemionus*) in southern Wyoming and northern Colorado during winter. The shaded boxes (gray) identify when correlation became negative (i.e., 284–413 m and 663–949 m), providing an estimate of the perceived patch sizes within which deer were likely to respond to landscape features.

the same landscape variable were within five units of another model then the model with the simplest relationship was chosen. Second, we assessed correlation among remaining landscape variables using PROC CORR (SAS 9.2, SAS Institute, Inc, Cary, NC) and eliminated covariates for $r \geq 0.5$. Distance to forest was removed and distance to agriculture was retained because few deer used forested areas (Webb et al. 2011).

After variable reduction, we used conditional logistic regression implemented in the PHREG procedure in SAS 9.2 (Kuhfeld 2010). Due to repeated measures on the same deer, we defined the strata as the location set (i.e., used location matched with three nonused locations) nested within deer identification. Discrete-choice models were run for data extracted from weighted maps with the highest validation (Webb et al. 2013b); weighted maps were developed using test collars to avoid over- or underestimating resource use (Webb et al. 2013b). Last, data were analyzed for two periods: an active (0600–1800 hours) and nonactive (2100–0300 hours) period, which was based on seasonal and temporal movement patterns of mule deer in this region (Webb et al. 2013a).

Mapping Animal Occurrence and Validation. Based on the population-level coefficient estimates from the discrete choice analysis, we mapped the relative probability of resource use as defined by Manly et al. (2002) for both the active and nonactive periods. After mapping relative probability of use, we calculated quantiles that placed data into five equal-sized bins (highest, high, moderate, low, and lowest); each bin made up 20% of the landscape. These five bins were used to validate maps using an independent validation sample of deer. Next, we refined the RSF maps to exclude rock outcrops from the spatial pattern of predicted occurrence because deer were unable to physically use steep rock outcrops (Webb et al. 2013b). In GIS, we used the rock outcrop layer as a mask to render all areas with rock outcrops unavailable to the deer. Last, we validated the deer occurrence maps (active and nonactive periods) by plotting locations from an independent validation sample of deer on each map. We used the percentage of locations occurring in each bin as a means of assessing the validity of how well each model mapped spatially. The validation sample consisted of 4 317 (active = 2 702; nonactive = 1 615) locations from four female mule deer (~20% of sample).

RESULTS

We analyzed data for 19 female mule deer. On average, we collected 1 062 GPS locations/individual (± 227 SD) during winter, which ranged from 170 (minimum) to 1 137 (maximum) locations/individual. One female was struck by a vehicle < 30 days after collaring, which resulted in only 170 locations being collected; all other deer survived the entire study period (apparent annual survival = 94.7%). Average age of females was 4.8 yr (± 1.5 SD) and ranged from 2.5 yr to 8.5 yr.

We used correlation plots to detect patch size perceived by animals, which occurs when correlation is negative (Nams 2005), to define biologically derived buffer radii around used locations. Correlation in tortuosity between adjacent path segments first became negative between 284 m and 413 m (Fig. 1) and then again from 663 m to 949 m, indicating multiple spatial scales perceived by female mule deer. Therefore, we set the buffer distance around used deer locations to 413 m for instances when movement distance was ≤ 413 m between successive locations. Otherwise we used 949 m buffer distances for records where movement was between 413 m and 949 m, and the actual movement distance as the buffer distance when movement was > 949 m.

During the active period (0600–1800 hours), slope and proximity to rock outcrops and shrubland, followed by avoidance of areas near grasslands and roads, were important resources driving behavior (i.e., hazard ratios did not overlap 1; Table 1). Slope was best described by a quadratic relationship (Table 1); deer tended to avoid intermediate values of slope and select more for lower and greater values of slope. Distance to rock outcrops and shrubland were best described by negative log-linear relationships (Table 1) indicating selection for proximity to these features. Distances to roads and grassland were best described by positive, log-linear relationships (Table 1), indicating that deer preferred remote areas relative to these features. Although less influential, the relationships for distance to agriculture and development were best described by negative, linear relationships (Table 1), indicating that deer were found closer to developments and agriculture.

Relationships most important to mule deer during the nonactive period (2100–0300 hours) mirrored those that were important during the active period (Table 1). Slope followed by proximity to shrubland and rock outcrop, and avoidance of grassland and roads were the most influential variables (i.e., hazard ratios did not overlap 1). Selection for rugged terrain (i.e., roughness) was statistically significant, but had hazard ratios near one (Table 1). All remaining landscape variables during nonactive times had similar relationships (i.e., positive [selection] or negative [avoidance]) when compared to active periods (Table 1).

Using the fixed-effects coefficient estimates, we mapped the spatial pattern of predicted occurrence for active (Fig. 2A) and

Table 1. Coefficient estimates (± SE) and hazard ratios modeled using a discrete-choice model for probability of female mule deer (*Odocoileus hemionus*) resource use during active (0600–1800 hours) and nonactive (2100–0300 hours) periods in southern Wyoming and northern Colorado during winter (November–April). Landscape values were weighted prior to analysis (Webb et al. 2013b) to avoid over- or underestimating resource use because of biases associated with fix success and locational error of GPS collars. Coefficient estimates in bold were significant at $P \leq 0.05$.

	Active period			Nonactive period		
Variable	Estimate	SE	Hazard ratio	Estimate	SE	Hazard ratio
Agriculture (linear)	**−0.0001**	0.0001	1.000	**−0.0001**	0.0001	1.000
Development (linear)	**−0.0004**	0.0001	1.000	**−0.0002**	0.0001	1.000
Road (natural log)	**0.1310**	0.0295	1.140	**0.1414**	0.0284	1.152
Slope (linear)	**−14.2035**	1.2203	0.000	**−14.4410**	1.0517	0.000
Slope (quadratic)	**4.6208**	0.4273	101.58	**4.6653**	0.3993	106.20
Roughness (linear)	-4.34^{-9}	1.32^{-8}	1.000	$\mathbf{1.10^{-8}}$	3.47^{-9}	1.000
Grass (natural log)	**0.0681**	0.0320	1.071	**0.0732**	0.0265	1.076
Rock (natural log)	**−0.3637**	0.0826	0.695	**−0.5691**	0.1295	0.566
Shrub (linear)	**−1.3128**	0.1473	0.269	**−1.5263**	0.1742	0.217
Riparian (linear)	0.0120	0.0074	1.012	0.0018	0.0067	1.002

nonactive (Fig. 2B) periods. The two maps consisted of the same seven covariates with the exception of roughness; roughness was included into the spatial pattern of predicted occurrence during the nonactive period. Because coefficient estimates were similar in sign and magnitude (Table 1), there were only subtle differences in the predicted pattern of occurrence between active (Fig. 2A) and nonactive (Fig. 2B) periods. During the active period, 70.8% of the validation sample (n=2 702 locations) occurred within the two highest probability of use bins (Table 2) whereas 56.1% of the validation locations (n=1 615) occurred within the two highest probability of use bins during the nonactive period (Table 2).

DISCUSSION

Development for wind energy is expanding rapidly because it is an alternative energy source (e.g., alternative to oil, gas, and coal) that can reduce carbon emissions and foreign dependence on other fuels (Lutz et al. 2011). Much research has been focused on the potential effects of wind energy development and infrastructure on birds and bats (Kunz et al. 2007; Kuvlesky et al. 2007; Pearce-Higgins et al. 2012). However, only one known study to date has examined the potential influence of wind energy development on a large mammal species (Walter et al. 2006). Although our data came from portions of two consecutive winters, the necessity of predevelopment, or baseline, data is of utmost importance in conservation science (Magurran et al. 2010) and is needed to assess change, whether natural or anthropogenic. Therefore, these data serve multiple purposes. First, these data can be used during the siting phases of development, meaning that high-priority areas can be avoided to minimize potential impacts to mule deer. Second, crucial ranges can be defined or refined based on the functional needs that resources provide during winter. Much of what was previously identified as crucial winter range for mule deer does in fact contain the landscape components that comprise preferred areas during winter as indicated by a high probability of occurrence. Last, and most importantly, these results can be used as baseline data for which future studies of this population of mule deer can be assessed in response to development and long-term persistence of infrastructure. When development occurs, wildlife may lose habitat directly when native vegetation is converted to sites for infrastructure, or indirectly through avoidance behaviors (Sawyer et al. 2006, 2009; Wilson et al. 2012). At this time, if development occurs in preferred areas, it is unknown how deer will respond to direct loss of habitat and indirect changes in behavior (Wilson et al. 2012), and whether this will have any long-term implications on population demographics (Dzialak et al. 2011b).

Providing applied maps (i.e., spatially explicit maps of occurrence) and information underlying the final products (e.g., occurrence patterns relative to vegetation and topographic features) are important for a number of reasons. For instance, winter range conditions and landscape features have the potential to influence population demographics (Sawyer et al. 2006; Harju et al. 2011). Linking demographic performance with animal occurrence is a powerful tool (Dzialak et al. 2011b); however, we could not link occurrence with demographic variables, such as survival, during this study because most deer (18 of 19; 94.7%) survived the study period with the exception of the one individual that was struck by a vehicle. Therefore, it can be assumed that the resources available to mule deer in this study region were of relatively high quality to allow for survival during harsh, winter conditions. Thus, these patterns of occurrence, along with underlying selection patterns of landscape features, can be used to identify and protect similar habitat across the region. In fact, recent studies reported that fitness measures are dictated by the selective use of habitat resources (McLoughlin et al. 2005, 2006; Dzialak et al. 2011b) with selective use being controlled by physiological needs (e.g., favorable thermal environments and energy acquisition) and avoidance of risk (whether actual or perceived).

The resources that comprised winter range give support that thermal environments, energy acquisition, and risk of predation or disturbance are working to shape behavior of mule deer in this population. Proximity to rock outcrops and shrubland, and for intermediate slopes, characterized resource selection by female mule deer. Avoidance of roads and grassland vegetation types also were important. Other landscape features such as roughness and distance to agriculture and development were

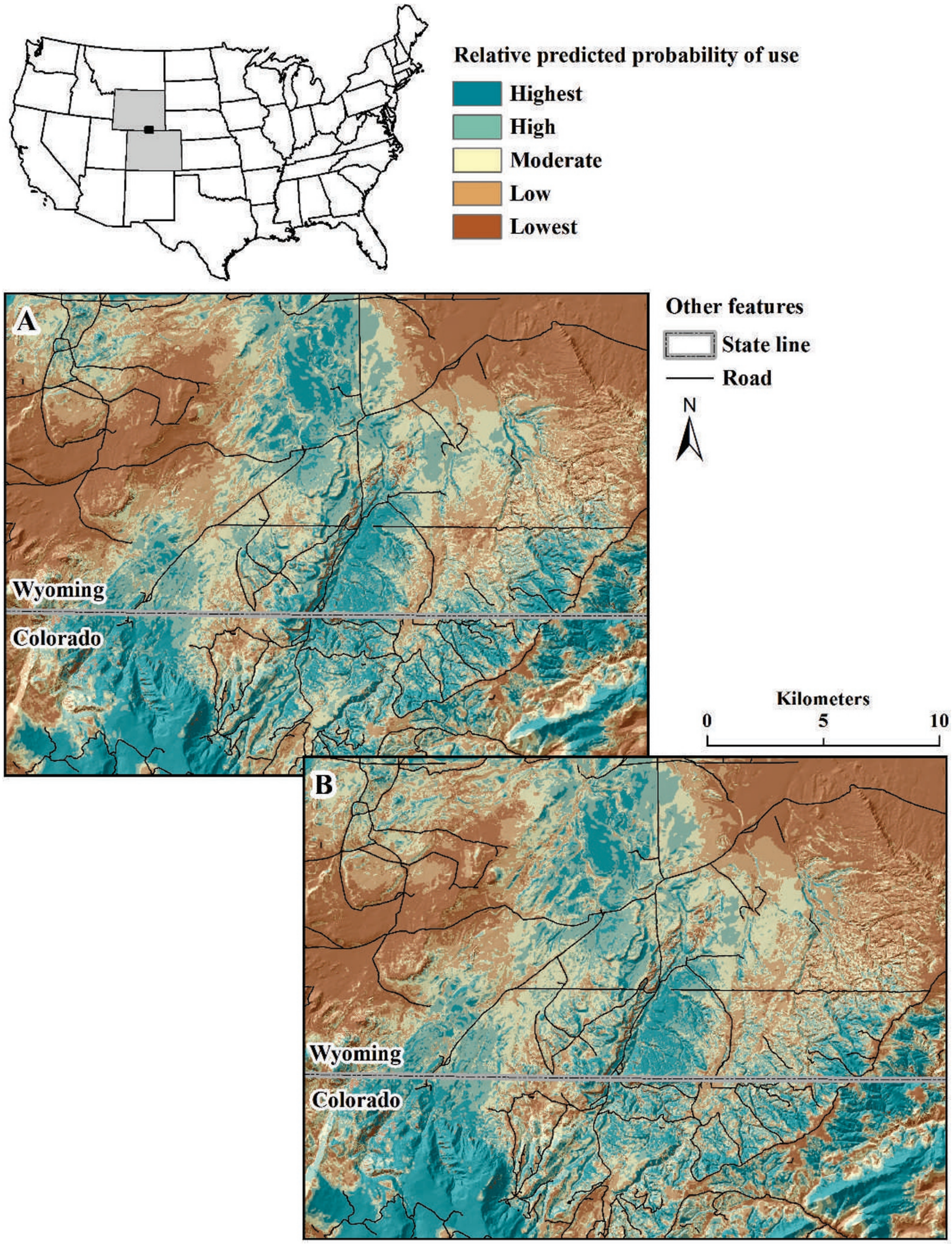

Figure 2. Spatially explicit depiction of occurrence during the active (0600–1800 hours; **A,** and nonactive (2100–0300 hours; **B,** periods by female mule deer (*Odocoileus hemionus*) in southern Wyoming and northern Colorado during winter (November–April).

statistically significant; statistical significance aside, their magnitude of influence is questionable because hazard ratios were near one. Several of the aforementioned landscape variables mitigate the unfavorable thermal conditions that deer face. Landscape features such as rugged terrain (e.g., rock outcrops) and vegetation cover types (e.g., shrubland) can provide more favorable thermal environments by blocking wind and having greater microclimate characteristics (e.g., temperature) than surrounding areas. Finding favorable thermal environments is of paramount importance during winter because deer are constantly in a position of negative energy balance because of unfavorable thermal conditions, especially in southeastern Wyoming (e.g., cold temperatures and high winds), and limited forage availability (Moen 1976). Rugged terrain and shrubland habitats also may restrict snow accumulation, which can reduce energy expenditure during locomotion (Gilbert et al. 1970; Moen 1976; Parker et al. 1984; Kufeld et al. 1988).

Native shrub-steppe communities are preferred by mule deer during winter (Anderson et al. 2013) because they provide thermal and security cover, and important winter forage, especially when snow makes other low-lying herbaceous vegetation unavailable. As mentioned previously, shrublands are important thermal environments, but also serve as foraging sites and in reducing risk (i.e., security cover). It is well known that shrubs are important to mule deer during winter (e.g., Carpenter et al. 1979; Pierce et al. 2004), composing the greatest percentage of the diet on a seasonal and annual basis (Kasworm et al. 1984; Kucera 1997; Nicholson et al. 2006; Torstenson et al. 2006). Shrublands also provide security cover from predation or disturbance from anthropogenic activities. For example, mule deer tended to use areas where cover provided concealment from predation by mountain lions (*Puma concolor*) and forage was plentiful (Pierce et al. 2004), a characteristic of most shrub-steppe communities. The multiple-use of shrub-steppe communities by mule deer during winter underscores the importance of conserving these communities (Anderson et al. 2013) for the long-term well-being of mule deer, especially when these communities are at risk of development across much of the Intermountain West (Cox et al. 2009).

Two vegetation types (i.e., agriculture and grassland) were similar in structure and function, but grassland was selected against, and agriculture selected for, albeit minimally. It is well known that most deer, including mule deer, are concentrate selectors, which select for highly nutritious and digestible plants (Hofmann 1989). Although grasses, and grassland vegetation types, can receive increased use during certain times of the year (e.g., autumn and winter; Kufeld et al. 1988) or following prescribed fire (Hobbs and Spowart 1984). In these instances, grasses can make up a greater percentage of the diet, but still do not meet the nutritional needs of most small to medium-sized ungulates (Hofmann 1989). Deer however did show weak selection for areas in proximity to agricultural plantings. In this study area, agriculture plantings were limited in distribution and area and were planted exclusively in alfalfa (*Medicago sativa*). Therefore, deer may have received greater benefit in terms of forage needs by using available alfalfa fields on occasion relative to grasslands because alfalfa has more desirable plant characteristics, which is similar to other plants in the family Fabaceae, than graminoid species (Martinka 1968; Austin and Urness 1993). Last, agricultural fields were smaller in size and in close proximity to security cover (e.g., riparian areas and shrublands), whereas grasslands were much larger in size and were void or security or thermal cover. This may explain the subtle differences in selection for agricultural fields and avoidance of grasslands during winter.

The last factor contributing to resource selection, and thus fitness, is the probability of risk associated with the choice of resource units. In this population, deer may respond to anthropogenic risk features or predation by natural predators such as mountain lions (*Puma concolor*) or black bears (*Ursus americanus*; S. L. Webb and M. R. Dzialak, personal observation, 2011). Once more, the use of shrubland, rock outcrops, and rugged terrain can serve as security cover where risk is minimized. It is well documented that most deer species avoid roads (Cole et al. 1997; Sawyer et al. 2009; Dzialak et al. 2011b); this study was no different in that deer avoided areas around roads. In most cases, roads are the anthropogenic features that receive the greatest amount of human activity, which can be perceived as a risk. This perceived risk is in addition to direct mortality associated with roads (i.e., deer-vehicle collisions). However, not all forms of anthropogenic features will be perceived as a risk, which depends on the type and level of human activity (Dzialak et al. 2011a; Harju et al. 2011). For example, some anthropogenic features such as homes can be an artificial refugium from hunting or natural predators. Large, natural predators also tend to avoid areas of human activity (van Dyke et al. 1986; Hebblewhite et al. 2005), which further creates a refugium from predation when deer use areas around anthropogenic structures. In this population, female mule deer exhibited only weak selection for areas closer to anthropogenic features. The interaction between animal occurrence and human activity is complex (Dzialak et al. 2011a; Harju et al. 2011), as in the case of strong avoidance of roads and weak selection for anthropogenic features, which requires special attention when designating winter range.

Table 2. Percentage (%) of female mule deer (*Odocoileus hemionus*; $n=4$) locations ($n=4\,314$) withheld as a validation data set correctly classified during the active (0600–1800 hours; $n=2\,702$ locations) and nonactive (2100–0300 hours; $n=1\,615$ locations) periods. Percentages may not sum to 100 due to rounding.

	Period	
Probability of use bin	Active	Nonactive
Highest	45.9	27.6
High	24.9	28.5
Moderate	12.2	17.5
Low	6.8	12.1
Lowest	10.1	14.3

IMPLICATIONS

Throughout southern Wyoming and northern Colorado, private lands occupy a large percentage of the landscape. These private landholdings typically occur in valley bottoms that offer high-quality wintering areas to mule deer (Watkins et al. 2007; Cox et al. 2009). Joint efforts between federal, state, and private entities will be important to manage mule deer populations and protect seasonally important ranges, particularly lower elevation ranges that are used by wildlife during winter (Cox et al. 2009). Not only is it important to consider spatial aspects of occurrence, but also the temporal aspects; that is why we focus on active and nonactive periods of mule deer during winter because winter is a limiting season to many animal populations in extreme environments (Wallmo et al. 1977; Watkins et al. 2007, but see Julander et al. 1961; Cook et al. 2004). The types of products developed herein (i.e., spatially explicit maps of animal occurrence) will be important for managing populations and conserving habitat, and during preplanning and scoping phases of development. For instance, these maps identify areas of high probability of deer occurrence; thus, if and when wind energy development occurs, siting plans may seek to minimize infrastructure and disturbance in these areas and focus development in areas less used by wildlife. These empirically derived spatial maps of mule deer occurrence also can be used to define, or refine, boundaries of crucial winter range.

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