

Movement reveals scale dependence in habitat selection of a large ungulate

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Abstract. Ecological processes operate across temporal and spatial scales. Anthropogenic disturbances impact these processes, but examinations of scale dependence in impacts are infrequent. Such examinations can provide important insight to wildlife–human interactions and guide management efforts to reduce impacts. We assessed spatiotemporal scale dependence in habitat selection of mule deer (*Odocoileus hemionus*) in the Piceance Basin of Colorado, USA, an area of ongoing natural gas development. We employed a newly developed animal movement method to assess habitat selection across scales defined using animal-centric spatiotemporal definitions ranging from the local (defined from five hour movements) to the broad (defined from weekly movements). We extended our analysis to examine variation in scale dependence between night and day and assess functional responses in habitat selection patterns relative to the density of anthropogenic features. Mule deer displayed scale invariance in the direction of their response to energy development features, avoiding well pads and the areas closest to roads at all scales, though with increasing strength of avoidance at coarser scales. Deer displayed scale-dependent responses to most other habitat features, including land cover type and habitat edges. Selection differed between night and day at the finest scales, but homogenized as scale increased. Deer displayed functional responses to development, with deer inhabiting the least developed ranges more strongly avoiding development relative to those with more development in their ranges. Energy development was a primary driver of habitat selection patterns in mule deer, structuring their behaviors across all scales examined. Stronger avoidance at coarser scales suggests that deer behaviorally mediated their interaction with development, but only to a degree. At higher development densities than seen in this area, such mediation may not be possible and thus maintenance of sufficient habitat with lower development densities will be a critical best management practice as development expands globally.

Key words: animal movement; hydrocarbon development; movement ecology; *Odocoileus hemionus*; oil and natural gas; resource selection function; wildlife.

INTRODUCTION

The scale (extent and grain) at which ecological processes operate and are measured is fundamental to our understanding of natural systems (Wiens 1989, Levin 1992). The topic of scale has received ample attention in the literature, providing insight into foraging theory (Senft et al. 1987), the impacts of habitat fragmentation and climate change (Opdam and Wascher 2004), and the drivers and characteristics of animal movement (Wittemyer et al. 2008, Fleming et al. 2014). Investigating ecological processes across multiple scales can reveal patterns that might otherwise be elusive (e.g., Borcard et al. 2004, Fleming et al. 2014). Thus,

assessments of scale dependence are important for providing insight into basic ecology and to improve predictions for species conservation and management (e.g., DeCesare et al. 2012).

The habitat selection patterns of animals are inherently scale dependent (Johnson 1980); numerous studies have shown that the selection process is influenced by spatial scale, with animals responding to their immediate environment while also making decisions that depend on the larger landscape context (e.g., Boyce et al. 2003, Johnson et al. 2004, Ciarniello et al. 2007). In addition, habitat selection is influenced by environmental and individual characteristics operating at multiple temporal scales including expected future reproductive output (McNamara and Houston 1986, Brown 1988), past experiences with an area (Wolf et al. 2009, Merkle et al. 2014), and the seasonal dynamics of food availability (Nielsen et al. 2003). Untangling the drivers of scale-dependent habitat selection is critical for understanding animal

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ecology because this behavior influences an array of ecological processes including predator-prey interactions (Brown 1999) and population dynamics (Pulliam and Danielson 1991), and often is used to address important conservation and management issues (Sawyer et al. 2006, Northrup et al. 2012).

The most common method for assessing the habitat selection process in animals is the resource selection function (RSF; Manly et al. 2002). Resource selection functions compare habitat covariates at locations used by an animal to those from an area deemed to be available for selection in a point process framework (Johnson et al. 2013). Resource selection functions provide a simple and natural means for examining variation in habitat selection across spatial scales by changing the size of the area deemed to be available for selection. This approach has been applied to a range of species and has advanced our understanding of spatially scale-dependent habitat selection patterns (Boyce et al. 2003, Ciarniello et al. 2007, DeCesare et al. 2012). The influence of spatiotemporal scale on habitat selection patterns is less often assessed, despite the fact that animal behavior is highly dependent on and is operating across these scales (Senft et al. 1987, Wittemeyer et al. 2008, Owen-Smith et al. 2010, Fleming et al. 2014). Advancements in time geography have served to focus conceptualization of the spatiotemporal nature of animal space use (e.g., Wall et al. 2014, Long et al. 2015), and methodological developments in the field of animal movement modeling provide new avenues to assess the spatiotemporal scale dependence of habitat selection patterns (Hooten et al. 2014).

While habitat selection patterns of animals are scale-dependent, they also vary substantially among individuals in a population because of differences in age, reproductive status, condition, or the individual environmental conditions experienced by an animal (Hebblewhite and Merrill 2008, Godvik et al. 2009, Dzialak et al. 2011a). Analysis of individual heterogeneity in behavior relative to local conditions and dynamics can provide insight to mechanistic drivers of selection and aid in understanding the habitat selection process (Hebblewhite and Merrill 2008, Godvik et al. 2009, Dzialak et al. 2011a). Such assessments typically are done through the examination of functional responses in habitat selection relative to local conditions of a certain habitat parameter. Extending this analytical framework to examine scale dependence in these functional responses can provide further insight into the process of habitat selection.

We assess the winter range habitat selection patterns of mule deer (*Odocoileus hemionus*) across scales in an area undergoing active natural gas development. Mule deer are an important recreational species in western North America that have experienced substantial declines across their range in recent decades (Unsworth et al. 1999). On their winter range, mule deer face a net negative energy balance (Torbit et al. 1985) and the potential for starvation due to malnutrition (Unsworth et al. 1999). Recent research has highlighted the potential

for anthropogenic development (specifically hydrocarbon exploration and production) to displace mule deer from preferred areas on their winter range, including in this study area (Sawyer et al. 2006, Northrup et al. 2015), raising concerns over potential population-level impacts. However, how scale influences these patterns is unknown and critically important for a robust understanding of development impacts. We fit resource selection functions (RSFs; Manly et al. 2002) across multiple scales in a hierarchical Bayesian framework, which provides both population and individual estimates of habitat selection, using methods recently developed in the animal movement literature. We then examine the potential for functional responses in deer habitat selection patterns and assess how these responses vary with scale. Our results offer insight into the scale dependence of deer behavior and the influence of anthropogenic development.

MATERIALS AND METHODS

Study area

This study took place on mule deer winter range in the Piceance Basin of Northwest Colorado (39.954° N, 108.356° W). The Piceance Basin is a semi-arid system with warm dry summers and cold winters where most of the annual moisture is received in the form of snowfall. The area is diverse vegetatively and topographically, with dominant plant species including sagebrush (*Artemesia tridentata* Nutt.), pinyon pine (*Pinus edulis* Engelm.), and Utah Juniper (*Juniperus osteosperma* Torr.). The vegetation of the area is described in detail by Bartmann and Steinert (1981) and Bartmann et al. (1992). Natural gas extraction was ongoing throughout the study, but other human disturbances were limited, aside from an increase in activity associated with elk (*Cervus elaphus*) and deer hunting in the fall. Development density increased across years from 0.18 well pads/km² in 2008 to 0.20 well pads/km² in 2009 and 2010 across the entire study area. Development density also varied spatially at a local scale between 0 and 6 pads/km².

Mule deer data

Between 2008 and 2010 we captured and collared 54 adult female mule deer (>1 year old) in a single winter range capture area. We captured deer each year starting in January 2008 and continuing through March 2010 using helicopter net gunning. We flew capture areas and captured deer opportunistically and then transferred them to a central processing site. At this site, deer were fit with global positioning system (GPS) radio collars (G2110D, Advance Telemetry Systems, Isanti, Minnesota, USA; and model 4400, Lotek Wireless, Newmarket, Ontario, Canada) set to attempt a relocation once every 5 h (see Northrup et al. 2014 for details of capture procedure). Collars were programmed to

automatically release after 16 months (April of the year following capture). Deer were released on site following processing.

We omitted the first week of data from analysis to guard against the potential effects of capture on deer behavior (Northrup et al. 2014). We also removed all locations for which the positional dilution of precision (PDOP) was >10 (D'eon and Delparte 2005, Lewis et al. 2007). All telemetry fix rates were $>90\%$, with the overall average fix rate being 93%. Deer in this area are migratory, and we were only interested in assessing winter range habitat selection. We classified winter range data during the first year that each individual deer was collared as all data between capture and when the deer began directed movement away from their winter range minimum convex polygon home range (MCP) without return. During the second winter, we classified the start of the winter range data as the time when deer ceased directed movement away from summer range. This classification scheme resulted in the dates of winter range occupancy varying across individuals and years. For winter 2008, the first year of captures, the average spring migration departure date was 11 May. For winter 2009 (fall 2008–spring 2009) the average fall migration arrival date was 4 November and the average spring migration departure date was 6 April. For winter 2010 (fall 2009–spring 2010) the average fall migration arrival date was 2 November, and the average spring migration departure date was 29 April. For this study, night was classified as the time between sunset and sunrise (*data available online*).⁶ A previous assessment of habitat selection patterns of mule deer in this area found that there were strong differences in habitat selection patterns between night and day (Northrup et al. 2015), and we wanted to examine how these differences varied with scale. Data during summer or migration were excluded from the analyses that follow.

Definition of scales

Resource selection functions compare environmental covariates at the locations where animals occurred (the used sample) to covariates at locations deemed to have been available for the animal to select (the availability sample). To assess how mule deer selected habitat at different scales, we kept the used sample constant and assessed availability at different spatiotemporal scales following the general approach of Hooten et al. (2014). A continuous time correlated random walk (CTCRW; Johnson et al. 2008) model that describes movement as a continuous Ornstein–Uhlenbeck process was used to assess availability. In this model, the velocity of the animal along each coordinate axis (i.e., latitude and longitude) is assumed to be normally distributed and dependent on the previous known velocity along each

coordinate axis, an autocorrelation parameter, and an error term that is scaled by the time between GPS locations (Johnson et al. 2008). With a known starting location, the CTCRW model can be used to obtain a predictor distribution at any point, which is an estimate of the animal's location, with associated error, based on all preceding data (Hooten et al. 2014). Hooten et al. (2014) used the predictor distributions as a representation of what is available to the animal at a given time. Using this method of classifying availability is similar to step-selection functions (Fortin et al. 2005) and offers several benefits including that the availability sample is probabilistically based on the movements of the animal. Improving on the step-selection function, the CTCRW method allows the animal's behavior at the current location to be taken into account in drawing the availability sample. For example, when the animal has been immobile for several locations, the predictor distribution will be close to its current location, whereas if the animal is highly mobile at a point in time, the predictor distribution will incorporate the speed and direction that the animal is moving.

Following the above methodology (described in greater detail by Hooten et al. 2014), we obtained predictor distributions for each deer location at each of four spatiotemporal scales: 5, 10, 25, and 170 h. The movements of large ungulates have strong temporal patterns, with the strongest patterns typically seen at 6-, 12-, and 24-h periods (Wittemyer et al. 2008, Boyce et al. 2010). We fit autocorrelation functions to the movements of deer in our study to assess patterns in our system (Appendix S1: Fig. S1). The scales that we chose to analyze match the prevalent time scales as closely as possible and thus provide inference at temporal scales that most closely match the deer's behavioral patterning. In addition, we assessed movements at the 170-h scale (approximately weekly) as we were interested in testing how behavior at the finer scales compared to those at coarser scales. The 170-h scale was the coarsest scale that still provided sufficient data to fit the CTCRW models. For the 5-h scale, we fit the CTCRW models to all data for each individual using the crawl package in the R statistical software (Johnson et al. 2008, R Core Team 2012). This model directly accounts for missing data by estimating missing locations, though in all habitat selection analyses that follow, we only included non-missing data. For the larger scales, the data must be rarefied, which can lead to unequal sample sizes for models fit with availability samples from different scales. To address this sampling issue, we created multiple rarefied datasets such that all data were included in at least one sample (i.e., for the 10-h scale we removed the 1st, 3rd, 5th, 7th, etc., locations from the 5-h dataset to create one rarefied dataset and then went back and removed the 2nd, 4th, 6th, 8th, etc., locations from the 5-h dataset to create a second dataset). This resulted in two datasets for each individual at the 10-h scale (the first starting at hour 0 and the second starting

⁶http://aa.usno.navy.mil/data/docs/RS_OneYear.php

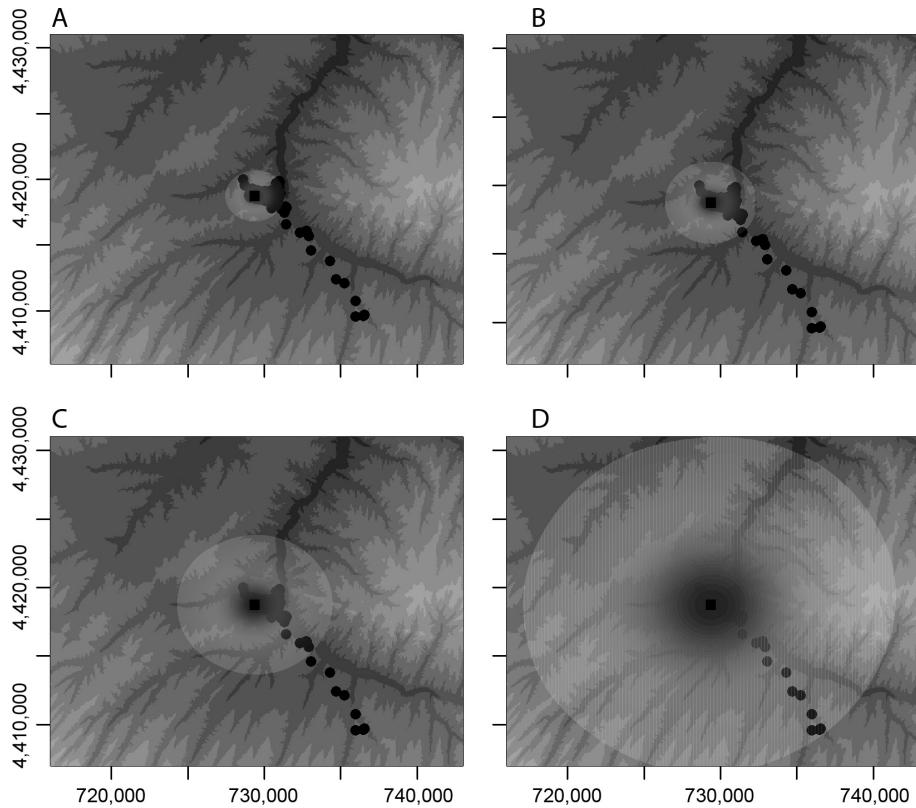


FIG. 1. Availability distribution for a single GPS location (black square) from a female mule deer assessed at scales of (A) 5 h, (B) 10 h, (C) 25 h, and (D) 170 h. All GPS locations for this individual are displayed in the black points.

at hour 5), five datasets at the 25-h scale and 34 datasets at the 170-h scale. We then fit the CTCRW model to each rarefied dataset and obtained predictor distributions for every used location again using the crawl package in R (see Fig. 1 for illustration). The CTCRW model fit using the crawl package outputs a mean and variance associated with each predictor distribution. To obtain an availability sample from these distributions, we drew the coordinates of available locations from normal distributions with the above means and variances (Fig. 1). After availability datasets were obtained, the multiple rarefied datasets within a scale were recombined to produce a single dataset at each scale. We note that though data were separated and rarefied to obtain predictor distributions, identical used datasets were included across all analyses. The predictor distributions in essence represent estimates of where the animal would be at the next time step based on all previous movements, with the time scale of these movements varying from 5 to 170 h (Fig. 1).

Fitting resource selection functions

Following the definition of availability using these CTCRW models, we fit RSFs at each of the four scales

using hierarchical conditional logistic regression in a Bayesian hierarchical framework (sensu Duchesne et al. 2010). We first determined a suite of habitat covariates that were of interest to mule deer ecology and management (Pierce et al. 2004, Sawyer et al. 2006, Stewart et al. 2010). These covariates fell into two classes, environmental and anthropogenic. For environmental covariates, we downloaded a land-cover layer from the Colorado Vegetation Classification Project (*data available online*), and reclassified the 69 classes into two categorical classes, treed and open.⁷ Our study area was composed of 44% sagebrush and 39% pinyon-juniper woodland, thus we included a single land cover covariate, tree, indicating if the habitat was treed or not. In addition, we calculated the distance to any treed edges to create the covariate *d_edge*. Using a digital elevation model, we calculated the covariates slope and elev representing the slope in degrees and elevation in meters. For anthropogenic disturbance features, we created three covariates representing the distance to roads (*d_rds*) and the number of well pads that had active drilling (*drill*) or were in the production phase (*prod*) within a 400 m buffer. Previous assessments in this area have shown 400 m to be the distance at which deer

⁷ <http://ndis.nrel.colostate.edu/coveg/>

TABLE 1. Scale at which availability was drawn, time (day or night), and median coefficient estimates (proportion of posterior <0, proportion of posterior >0) for each covariate included in resource selection functions fit to GPS data from adult female mule deer in the Piceance Basin, Colorado, USA.

Scale	Time	d_edge	slope	elev	d_rds	d_rds. ²	prod	drill	tree
5 h	day	-0.18 (1, 0)	0.05 (0.01, 0.99)	0.61 (0, 1)	0.16 (0, 1)	-0.3 (1, 0)	-0.36 (1, 0)	-0.84 (1, 0)	0.09 (0, 1)
	night	0.11 (0, 1)	0.17 (0, 1)	0.81 (0, 1)	-0.4 (1, 0)	-0.47 (1, 0)	-0.21 (0.99, 0.01)	-0.78 (1, 0)	-0.28 (1, 0)
10 h	day	-0.22 (1, 0)	0.05 (0.02, 0.98)	0.6 (0, 1)	0.17 (0.01, 0.99)	-0.39 (1, 0)	-0.46 (1, 0)	-1.18 (1, 0)	0.09 (0.01, 0.99)
	night	0.11 (0, 1)	0.14 (0, 1)	0.4 (0.06, 0.94)	-0.43 (1, 0)	-0.57 (1, 0)	-0.28 (0.99, 0.01)	-1.31 (1, 0)	-0.34 (1, 0)
25 h	day	-0.23 (1, 0)	0.02 (0.2, 0.8)	0.31 (0.05, 0.95)	0.09 (0.16, 0.84)	-0.52 (1, 0)	-0.53 (1, 0)	-1.64 (1, 0)	0.04 (0.19, 0.81)
	night	0.05 (0.1, 0.9)	0.11 (0.02, 0.98)	0.35 (0.04, 0.96)	-0.44 (1, 0)	-0.67 (1, 0)	-0.36 (1, 0)	-1.49 (1, 0)	-0.36 (1, 0)
170 h	day	-0.31 (1, 0)	-0.12 (0.98, 0.02)	-0.13 (0.82, 0.18)	0.02 (0.43, 0.57)	-0.67 (1, 0)	-0.62 (1, 0)	-2.23 (1, 0)	-0.05 (0.78, 0.22)
	night	-0.06 (0.93, 0.07)	-0.05 (0.73, 0.27)	-0.13 (0.82, 0.18)	-0.63 (1, 0)	-0.85 (1, 0)	-0.6 (1, 0)	-2.36 (1, 0)	-0.47 (1, 0)

most strongly responded to well pads (Northrup et al. 2015), and thus we wanted to examine the influence of scale on this response, though we note that results might differ depending on the scale of the covariates selected. We also incorporated a quadratic term for the distance to roads. The roads covariate was created by digitizing all roads in the area from National Agricultural Imagery Program (NAIP) aerial imagery. The statuses of well pads in the study area were highly dynamic with new wells being drilled and then transitioning from being drilled to producing over the study period. To capture these dynamics, we downloaded freely available development data from the Colorado Oil and Gas Conservation Commission (*available online*).⁸ The Commission maintains a daily updated database of every well drilled in the state of Colorado along with its status. We classified every well in our study area on every day for which we had data as either a producing well (actively producing natural gas) or a drilling well (actively being drilled), based on the status and dates in the Commission database. Next, we grouped wells onto well pads by examining the NAIP imagery and assigning wells to the pads on which they fell (well pads in this area often have numerous wells on the same pad due to the use of directional drilling). We classified each well pad as either producing (at least one well was actively producing natural gas with no drilling activity) or drilling (at least one well was being actively drilled). These layers represented activity conditions accurate to the day throughout the study. All layers were calculated at a pixel size of 25 × 25 m.

We next assessed the number of available locations needed to obtain accurate coefficient estimates (Warton and Shepherd 2010, Aarts et al. 2012, Northrup et al. 2013). We fit individual conditional logistic regression models to each deer using the survival package in R (Therneau 1999), using differing numbers of available

locations (5, 25, 50, 100, 250, 500, 750, and 1,000) per used location. Following Northrup et al. (2013), we repeated this process 25 times for each individual and constructed plots of the resulting coefficient estimates to determine the sample size that provided stable estimates. At the 5-h scale, between 250 and 500 random locations were needed per used location (we used 500 locations), while at the 10- and 25-h scale 750 locations were needed. At the 170-h scale 1,000 random locations were needed.

Following determination of the availability sample size, we fit a hierarchical conditional logistic regression model with slopes varying for each individual for each covariate (Revelt and Train 1998, Duchesne et al. 2010). This model takes the following form:

$$[y_{tn}|\beta_n] = \frac{\exp(x'_{y_{tn}} \beta_n)}{\sum_{j=1}^J \exp(x'_{j_{tn}} \beta_n)},$$

where y_{tn} is the used resource unit at time t for animal n , which is represented by habitat covariates (x_y) and was chosen from a set of available alternative resource units (J), represented by habitat covariates (x_j). Using this probability mass function, we can estimate coefficients for each individual and the population as a whole by placing the model in a Bayesian hierarchical framework as follows:

$$\beta_n \sim \text{normal}(\mu_\beta, \sigma_\beta^2 I)$$

$$\mu_\beta \sim \text{normal}(0, 1,000,000 I)$$

$$\log(\sigma_\beta^2) \sim \text{normal}(0, 1,000,000).$$

We fit the above model using a Markov chain Monte Carlo (MCMC) procedure written in R. We fit a single model structure (Table 1) to data at each scale so that

⁸cogcc.state.co.us

we could examine variation in coefficient estimates across scales. Prior to fitting models, we examined pairwise correlations among covariates and only included covariates that were not highly correlated ($|r| < 0.7$). We then standardized all continuous covariates ($x - \bar{x}/\sigma$). We fit one model for night and one for day to assess differences between these time periods. To assess convergence of the MCMC procedure, we ran the algorithm twice for each model with initial values chosen so that they were likely to be overdispersed relative to the posterior distributions. We assessed convergence using the Gelman–Rubin diagnostic (Gelman and Rubin 1992) and by examining traceplots of the posterior distributions. We ran models for varying iterations due to the fact that some converged earlier than others. All models converged (i.e., mean Gelman–Rubin diagnostic values were all <1.1) though a varying number of iterations and burn-in were needed for each model (Table 2).

Functional responses

Following convergence, we examined the relationship between the individual deer parameters (β_n) and the anthropogenic development features that the deer interacted with throughout the winter. Specifically, we examined the coefficients for drilling and producing pads as a function of the density of each type of pad in the deer's range. We also examined the response of deer to roads relative to the density of roads in their range. We estimated winter ranges using the adaptive local convex hull method (a-LoCoH; Getz et al. 2007) with the adaptive distance value taken as the maximum distance between any two GPS locations for each deer. Because we fit a quadratic relationship for the response to roads, we examined the relationship between the density of roads in each deer's range and the distance at which selection was predicted to be the highest using the median posterior coefficient values. As stated above, the density of development within a deer's range

is indicative of the features they interacted with throughout the winter on their range, and thus we were interested in understanding how these features influenced deer behavior across scales.

RESULTS

Resource selection functions at multiple scales

Deer habitat selection patterns differed across scales (Appendix S1). Deer either displayed scale invariance in regards to the direction of selection (i.e., consistent avoidance or selection of a feature) but a change in the magnitude of this response, or scale dependence in the direction of the response, with the sign of selection changing across scales.

During the day, deer displayed scale invariance in the magnitude of their response to edges (selection), well pads of both types and roads (avoidance; Appendix S1) with the magnitude of coefficients increasing as scale increased (Table 1). All other covariates were highly scale dependent in their direction (Table 1). Deer displayed selection for steeper slopes and higher elevations during the day at the 5- and 10-h scale, but the strength of this selection declined for both covariates at the 25-h scale and switched to selection for less steep slopes and lower elevations at the 170-h scale (Table 1). A similar pattern was seen with treed land cover, with deer selecting treed areas at the 5- and 10-h scale, with weaker selection at the 25-h scale and moderate avoidance at the 170-h scale (Table 1).

During the night, deer displayed scale invariance in their selection of treed land cover and avoidance of well pads of both types, with the degree of avoidance increasing with scale (Table 1). Deer also displayed relatively consistent responses to roads, however, as scale increased, there was some evidence of increasing avoidance of the areas closest to roads (Fig. 2). During the night, deer displayed similar scale dependent responses to slope and elevation as during the day; deer selected steeper slopes and higher elevations at the 5- and 10-h scales, with declining selection at 25 h and selection of less steep slopes and lower elevations at the 170-h scale (both of these coefficients were rather weak, with the posteriors overlapping 0; Table 1). In regards to edges, deer displayed scale dependence in their selection patterns during the night, avoiding edges at the 5- and 10-h scale, displaying weaker selection at the 25-h scale and selecting areas close to edges at the 170-h scale (Table 1).

At all scales, we documented some differences in selection between night and day, though the specific differences varied across scales and the contrast between night and day weakened as scale increased (Table 1; Appendix S1). At the 5- and 10-h scales, deer selected open areas, far from edges, on steeper slopes and closer to roads during the night, while they selected treed areas, close to edges, on more moderate slopes and further from

TABLE 2. Scale at which availability was drawn, time (day or night), total MCMC iterations run, and number of iterations removed as burn-in for hierarchical resource selection functions fit to GPS data from adult female mule deer in the Piceance Basin, Colorado, USA.

Scale	Time	Total iterations	Burn-in
5 h	day	400,000	50,000
5 h	night	400,000	100,000
10 h	day	600,000	50,000
10 h	night	200,000	20,000
25 h	day	1,700,000	400,000
25 h	night	800,000	30,000
170 h	day	3,400,000	1,000,000
170 h	night	200,000	50,000

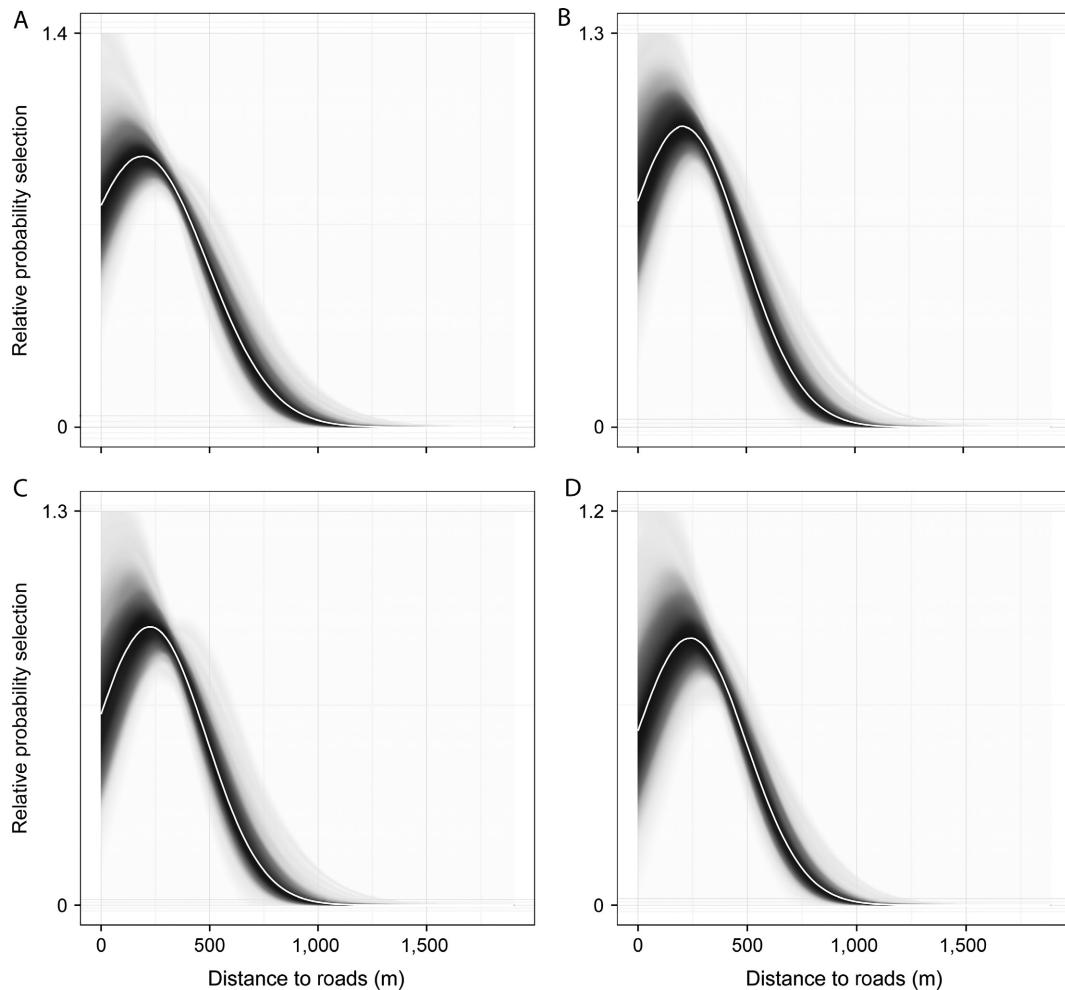


FIG. 2. Posterior predicted habitat selection as a function of distance from roads from resource selection functions fit to night time GPS locations of adult female mule deer in the Piceance Basin, Colorado, USA, with availability drawn at the (A) 5-h scale, (B) 10-h scale, (C) 25-h scale, and (D) 170-h scale. Gray scale represents posterior density of predictions.

roads during the day. In addition, at the 5-h scale the avoidance of well pads (both producing and drilling) was stronger during the day than the night. As the scale increased, the differences between night and day became obscured, until they were relatively similar at the 170-h scale (Appendix S1).

Functional responses

Deer functional responses to anthropogenic features varied across scales and by feature (Fig. 3; Appendix S1). Deer generally displayed greater avoidance of both well pad types in lower well pad density areas (Appendix S1). In addition, the distance from roads at which deer displayed the highest selection was less when the density of roads was higher (Fig. 3; Appendix S1). In general, functional responses were weaker at the 170-h scale though there was variation in this pattern (Fig. 3; Appendix S1).

DISCUSSION

In contrast to previous, area-based studies on scale dependence in habitat selection, we were able to investigate changes in behavior across spatiotemporal scales by applying novel methodology, developed in the field of animal movement modeling (Hooten et al. 2014). This methodology varies from traditional assessments of scale dependence in RSF analyses by using movements at different temporal scales to define available habitat. The CTCRW models that we used allows for more biologically driven definitions of scale to be used. Typical multi-scale habitat selection analyses use outlines of study areas or regions as their definitions of availability. In our analysis, we used the underlying patterning of mule deer movement behavior (i.e., autocorrelation) to define scales. Behavioral patterning across similar time scales has been seen in other ungulates (e.g. Wittemyer et al. 2008, Boyce et al. 2010) and our modeling framework

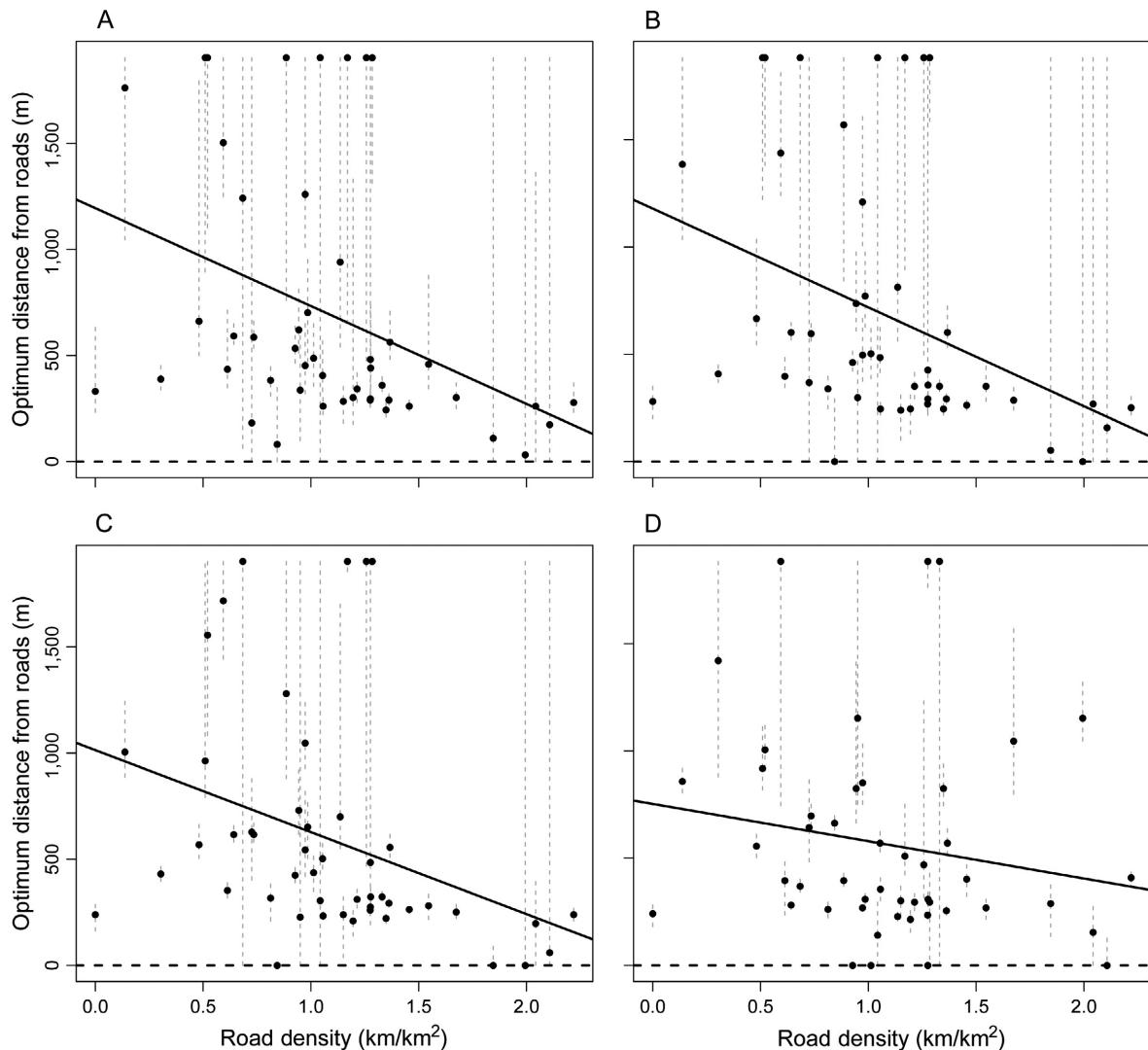


FIG. 3. Daytime functional responses in the distance at which relative probability of selection was predicted to be highest relative to road density within deer home ranges in the Piceance Basin, Colorado, USA, with availability drawn at the (A) 5-h scale, (B) 10-h scale, (C) 25-h scale, and (D) 170-h scale. Black lines represent best fit linear regressions. Optimal selection distances were obtained from individual coefficient estimates with points representing medians and gray bars representing 95% credible intervals.

allows the availability distribution to be defined by movements at these scales. Given that animal space use and movement are inherently time based, these methods are more appropriate for animal tracking data, and more effectively capture the dynamics reflected in this behavioral process. This methodology revealed highly nuanced behaviors, with deer displaying scale-dependent responses to certain habitat features and scale-invariant responses to others. Deer also varied their responses dependent on the conditions in their individual ranges and between night and day. These results clarify the manner in which this species structures its behavioral decisions at various scales relative to the environment and offer insight into what habitat factors are most influential to their space-use patterns.

Scale dependence in habitat selection patterns

Animals display variation in habitat selection across scales because different behavioral processes influence their decisions at different scales (Johnson 1980, Senft et al. 1987). At coarser scales, processes such as physiological tolerances, physical barriers, and access to broad categories of habitat (e.g., cover and forage habitat) influence their decisions. At finer scales, foraging and nutrient intake optimization become more important and they likely respond to microsite features (Senft et al. 1987). In our study, the primary driver of deer habitat selection at the coarsest scale (weekly) was anthropogenic development, with all other factors being selected for or avoided to a lesser degree. Thus, at

this scale deer were distributing their movements primarily to avoid interaction with human disturbance, avoiding areas closest to roads, and those with a larger number of (producing and drilling) well pads. At finer spatiotemporal scales, deer responded less strongly to development than at coarser scales and more strongly to habitat features, though development was still important in determining selection patterns. This result likely reflects that finer spatiotemporal scales capture a different dominant behavioral process than coarser scales. In this study, finer scale analyses appear to be related primarily to selection for cover and forage characteristics, reflecting the framework of Senft et al. (1987). This notion is further supported by stronger differences in habitat selection patterns between night and day at finer scales, a dynamic thought to reflect differential use of cover and foraging habitat by ungulates during the night and day (e.g., Ager et al. 2003, Dzialak et al. 2011b). However, we note that while it is very likely that different behavioral processes are driving the multi-scale selection behavior that we documented, we did not directly assess different behaviors and thus these conclusions in regards to foraging are speculative.

Although mule deer in our study displayed weaker avoidance of development at finer scales, they still were avoiding these areas. These dynamics paint a complex picture of mule deer behavior in response to this disturbance. Examinations of scale-dependence in habitat selection can indicate what factors are most important to, or might be limiting for, a species (Rettie and Messier 2000). The scale-invariant (in terms of direction) response to development, along with the large magnitude coefficients for development covariates, indicates that this feature was the primary driver of deer habitat selection in the study area. However, it is notable that the strength of avoidance declined with finer scales, indicating that the coarser scale decisions of deer in regards to development allowed individuals to partially behaviorally mediate some of the impact at finer scales. That is, deer were selecting areas from the broader landscape that had less development, allowing finer scale selection to occur in relation to forage and cover properties (though still structured at finer scales by anthropogenic features). We note that the covariate that we used to represent development (the number of pads within 400 m) does not capture all of the dynamics occurring at a pad, and thus is a general response to development that likely misses some of the more nuanced responses to specific activities on which we lacked data. Likewise, the spatial environmental data might not accurately capture the factors most critical for determining mule deer behavior, and analysis results can be sensitive to the scale of covariates used, and thus our results are only directly applicable to this scale. However, we note that this scale has been seen previously to be the one at which deer most strongly responded to development in this area.

Functional responses to anthropogenic development

Although deer responded to anthropogenic development in a largely scale-invariant manner, they also displayed functional responses in selection relative to development density. These functional responses showed that individuals in more developed areas more weakly avoided development at all scales other than the weekly scale. Although most deer avoided roads and well pads, individuals with the highest densities of these features actually selected areas closer to roads and with more well pads, similar to responses that have been seen for other species in human-dominated areas (Hebblewhite and Merrill 2008). These functional responses held for both night and day, indicating that the density of development in a deer's range explained more of the variation in deer selection than the spatio-temporal scale dependent responses documented. Analogous results have been seen in elk, where development was a much stronger driver of individual behavior than reproductive state and behavior varied across individuals in developed areas to a greater degree than in undeveloped areas (Dzialak et al. 2011a). That the majority of individuals avoided these developments indicates that they serve to displace deer, consistent with previous studies in other areas (Sawyer et al. 2006). The presence of significant functional responses indicates that deer with the highest development densities either have little space in their range to which they can be displaced or are habituated to the development. Considering the strong range fidelity by mule deer in this area (Northrup et al. 2016), it is most likely that deer had little area to which they could be displaced. In contrast, individuals in areas with low densities have access to habitat away from development and tend to select those areas. These results have potentially strong management implications relating to the development densities at which deer are impacted. The high range fidelity and behavioral plasticity of deer can mask potentially impending demographic consequences. At some development density, deer are likely to face impacts to individual fitness, though we note that development densities in our area have not reached sufficient levels to entirely displace deer, and demographic responses are not apparent (Anderson 2015). Assessing behavioral changes in deer as development increases or decreases across their range would provide greater mechanistic understanding of these behavioral interactions. Furthermore, assessing how reproductive performance, condition, or survival is impacted by development could provide insight into whether individuals experiencing the highest disturbance densities might be beginning to display demographic responses. We also urge caution in the interpretation of these results, as the specific mechanism of selection (i.e., how animal preference for habitat does or does not change with varying availability) can alter the expected direction of functional responses (Van Moorter et al. 2013).

CONCLUSIONS

Responses to habitat features that transcend scale are indicative of primary drivers of ecological systems. Mule deer in our system structured their habitat selection patterns relative to anthropogenic disturbance at all scales, though with stronger responses at coarser scales. Furthermore, individual variation in responses to development was driven by the amount of undeveloped habitat to which deer had access. In conjunction, these results indicate that deer were able to behaviorally mediate the effect of development to some degree, though certain individuals were exposed to densities of development that precluded their ability to do so at finer scales. These results highlight the importance of maintaining refuge habitat for deer in energy development fields. However, doing so will be difficult during active development given that sound and light disturbances extend beyond the development footprint. Identification of habitats that are most critical for deer during important times of the year (e.g., during severe winters and during fawning) will be critical to implementing minimum area protection. In the absence of such information, maintaining a mosaic of development densities across the larger landscape could help to provide habitat that is sufficiently undisturbed for enough individual deer that any demographic effects are minimized at the population level. Furthermore, avoiding areas of greatest deer density during winter will be critical.

While the observational nature of this study does not allow us to identify specific thresholds of development above which deer might not have areas to be displaced, we can infer that densities on the upper end of our study area clearly elicited behavioral impacts. Deer in our study also patterned their behavior temporally around development infrastructure, indicating that they are responding to human activity and presence. Thus, mitigation measures and industry best management practices should focus on not only reducing the footprint of development but also managing the timing and intensity of human activity (i.e., light, noise, and traffic) to reduce disturbance. It is important to recognize that these impacts have yet to manifest demographically in our study area, though these behavioral changes could be precursors to demographic effects that may not emerge until development density precludes deer ability to spatially avoid these features on the landscape.

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REFERENCES

- Aarts, G., J. Fieberg, and J. Matthiopoulos. 2012. Comparative interpretation of count, presence-absence and point methods for species distribution models. *Methods in Ecology and Evolution* 3:177–187.
- Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer. *Journal of Mammalogy* 84:1076–1088.
- Anderson Jr., C. R. 2015. Population performance of the Piceance basin mule deer in response to natural gas resource extraction and mitigation efforts to address human activity and habitat degradation. *Colorado Parks and Wildlife*, Fort Collins, Colorado, USA.
- Bartmann, R. M., and S. F. Steinert. 1981. Distribution and movements of mule deer in the White River Drainage, Colorado. *Colorado Division of Wildlife*, Fort Collins, Colorado, USA.
- Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs* 121:1–39.
- Borcard, D., P. Legendre, C. Avois-Jacquet, and H. Tuomisto. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832.
- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421–431.
- Boyce, M. S., J. Pitt, J. M. Northrup, A. T. Morehouse, K. H. Knopff, B. Cristescu, and G. B. Stenhouse. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philosophical Transactions of the Royal Society B* 365:2213–2219.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37–47.
- Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* 1:49–71.
- Ciarniello, L. M., M. S. Boyce, D. R. Seip, and D. C. Heard. 2007. Grizzly bear habitat selection is scale dependent. *Ecological Applications* 17:1424–1440.
- DeCesare, N. J., et al. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications* 22:1068–1083.
- D'eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology* 42:383–388.
- Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* 79:548–555.
- Dzialak, M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing, J. B. Winstead, and S. L. Webb. 2011a. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. *PLoS ONE* 6:e14597.

- Dzialak, M. R., S. L. Webb, S. M. Harju, J. B. Winstead, J. J. Wondzell, J. P. Mudd, and L. D. Hayden-Wing. 2011b. The spatial pattern of demographic performance as a component of sustainable landscape management and planning. *Landscape Ecology* 26:775–790.
- Fleming, C. H., J. M. Calabrese, T. Mueller, K. A. Olson, P. Leimgruber, and W. F. Fagan. 2014. From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. *American Naturalist* 183:E154–E167.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–511.
- Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE* 2:e207.
- Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699–710.
- Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45: 834–844.
- Hooten, M. B., E. M. Hanks, D. S. Johnson, and M. W. Alldredge. 2014. Temporal variation and scale in movement-based resource selection functions. *Statistical Methodology* 17:82–98.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* 41:238–251.
- Johnson, D. S., J. M. London, M. A. Lea, and J. W. Durban. 2008. Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89:1208–1215.
- Johnson, D. S., M. B. Hooten, and C. E. Kuhn. 2013. Estimating animal resource selection from telemetry data using point process models. *Journal of Animal Ecology* 82:1155–1164.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology* 73: 1943–1967.
- Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. *Journal of Applied Ecology* 44:663–671.
- Long, J. A., S. L. Webb, T. A. Nelson, and K. L. Gee. 2015. Mapping areas of spatial-temporal overlap from wildlife tracking data. *Movement Ecology* 3:1–14.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, the Netherlands.
- McNamara, J. M., and A. I. Houston. 1986. The common currency for behavioral decisions. *American Naturalist* 127:358–378.
- Merkle, J. A., D. Fortin, and J. M. Morales. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters* 17:924–931.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. *Ecoscience* 10:1–10.
- Northrup, J. M., G. B. Stenhouse, and M. S. Boyce. 2012. Agricultural lands as ecological traps for grizzly bears. *Animal Conservation* 15:369–377.
- Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology* 94:1456–1463.
- Northrup, J. M., C. R. Anderson Jr., and G. Wittemyer. 2014. Effects of helicopter capture and handling on movement behavior of mule deer. *Journal of Wildlife Management* 78: 731–738.
- Northrup, J. M., C. R. Anderson Jr., and G. Wittemyer. 2015. Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. *Global Change Biology* 3961–3970.
- Northrup, J. M., C. R. Anderson, and G. Wittemyer. 2016. Environmental dynamics and anthropogenic development alter philopatry and space-use in a North American cervid. *Diversity and Distributions* 22:547–557.
- Opdam, P., and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 117:285–297.
- Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B* 365:2267–2278.
- Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat selection by mule deer: Forage benefits or risk of predation? *Journal of Wildlife Management* 68:533–541.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137:S50–S66.
- R Core Team. 2012. R: a language and environment for statistical computing. R Development Core Team, Vienna, Austria. <https://www.r-project.org/>
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478.
- Revelt, D., and K. Train. 1998. Mixed logit with repeated choices: households' choices of appliance efficiency level. *Review of Economics and Statistics* 80:647–657.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396–403.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, and M. A. Hurley. 2010. Spatial distributions of mule deer and North American elk: resource partitioning in a sage-steppe environment. *American Midland Naturalist* 163:400–412.
- Therneau, T. M. 1999. A package for survival analysis in S. Technical Report, Mayo Foundation, New York. <http://www.mayo.edu/hsr/people/therneau/survival.ps>
- Torbit, S. C., L. H. Carpenter, D. M. Swift, and A. W. Alldredge. 1985. Differential loss of fat and protein by mule deer during winter. *Journal of Wildlife Management* 49:80–85.
- Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. *Journal of Wildlife Management* 63:315–326.
- Van Moorter, B., D. Visscher, I. Herfindal, M. Basille, and A. Mysterud. 2013. Inferring behavioural mechanisms in habitat selection studies getting the null-hypothesis right for functional and familiarity responses. *Ecography* 36: 323–330.

- Wall, J., G. Wittemyer, V. LeMay, I. Douglas-Hamilton, and B. Klinkenberg. 2014. Elliptical time-density model to estimate wildlife utilization distributions. *Methods in Ecology and Evolution* 5:780–790.
- Warton, D. I., and L. C. Shepherd. 2010. Poisson point process models solve the “pseudo-absence problem” for presence-only data in ecology. *Annals of Applied Statistics* 4:2203–2204.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Wittemyer, G., L. Polansky, I. Douglas-Hamilton, and W. M. Getz. 2008. Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. *Proceedings of the National Academy of Sciences USA* 105:19108–19113.
- Wolf, M., J. Frair, E. Merrill, and P. Turchin. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* 32: 401–410.

SUPPORTING INFORMATION

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DATA AVAILABILITY

Data associated with this manuscript are available at the Colorado State University Digital Repository: <http://hdl.handle.net/10217/173564>