

Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer

JOSEPH M. NORTHRUP¹, CHARLES R. ANDERSON JR.² and GEORGE WITTEMYER^{1,3}

¹Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO, USA, ²Mammals Research Section, Colorado Parks and Wildlife, Fort Collins, CO, USA, ³Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA

Abstract

Extraction of oil and natural gas (hydrocarbons) from shale is increasing rapidly in North America, with documented impacts to native species and ecosystems. With shale oil and gas resources on nearly every continent, this development is set to become a major driver of global land-use change. It is increasingly critical to quantify spatial habitat loss driven by this development to implement effective mitigation strategies and develop habitat offsets. Habitat selection is a fundamental ecological process, influencing both individual fitness and population-level distribution on the landscape. Examinations of habitat selection provide a natural means for understanding spatial impacts. We examined the impact of natural gas development on habitat selection patterns of mule deer on their winter range in Colorado. We fit resource selection functions in a Bayesian hierarchical framework, with habitat availability defined using a movement-based modeling approach. Energy development drove considerable alterations to deer habitat selection patterns, with the most substantial impacts manifested as avoidance of well pads with active drilling to a distance of at least 800 m. Deer displayed more nuanced responses to other infrastructure, avoiding pads with active production and roads to a greater degree during the day than night. In aggregate, these responses equate to alteration of behavior by human development in over 50% of the critical winter range in our study area during the day and over 25% at night. Compared to other regions, the topographic and vegetative diversity in the study area appear to provide refugia that allow deer to behaviorally mediate some of the impacts of development. This study, and the methods we employed, provides a template for quantifying spatial take by industrial activities in natural areas and the results offer guidance for policy makers, managers, and industry when attempting to mitigate habitat loss due to energy development.

Keywords: animal movement, Bayesian hierarchical model, energy development, habitat selection, movement ecology, mule deer, natural gas, resource selection function

Received 2 April 2015 and accepted 30 June 2015

Introduction

Since the early 2000s, the exploration and production (hereafter development) of hydrocarbons has increased rapidly in North America (United States Energy Information Administration [USEIA] 2012). The landscape-level disturbance resulting from this development has had a number of negative impacts on wildlife, including driving population declines and causing large-scale spatial displacement (Northrup & Wittemyer, 2013). This recent energy boom has been driven primarily by the development of shale resources (USEIA, 2012). Shale resources are proven to exist on every continent save Antarctica and their development is projected to continue to increase (USEIA, 2013). Thus, this sector is

poised to become a major driver of global land-use change and impacts to biodiversity.

Given its projected global footprint, there is a pressing need for robust quantification of habitat loss driven by hydrocarbon development. Such information can be used to aid in development planning, assess cumulative impacts, develop mitigation measures, and quantify the size of habitat offsets. However, understanding the impact of hydrocarbon development and subsequent mitigation measures is complex as the associated disturbances are spatially variable and temporally dynamic and their cumulative effects not well understood, which can obfuscate animal responses. In light of this complexity, there is a need for more complete information on the ways in which animals respond to development. Detailed understanding of the distance at which different types of development elicit responses from different species will be particularly important for

*Correspondence: Joseph M. Northrup, tel: +970 491 6598, fax: +970 491 5091, e-mail: joe.northrup@gmail.com

quantifying habitat impacts and identifying effective mitigation strategies as this industry becomes a major driver of global land-use change.

Examinations of the habitat selection patterns of wildlife provide a natural means for understanding the spatial impacts of development. Habitat selection is a fundamental ecological process by which animals distribute themselves across landscapes by selecting habitats that maximize their fitness (Fretwell & Lucas, 1969). Examinations of habitat selection provide insight into individual-based ecological processes (e.g., drivers of site fidelity: Creel *et al.*, 2005; and tradeoffs between foraging and predation risk: Switzer, 1997), but also to larger scale factors that influence population distribution and abundance (e.g., population dynamics: Pulliam & Danielson, 1991; speciation: Rice, 1987; and dispersal: Shafer *et al.*, 2012).

Human disturbance can alter habitat selection patterns of animals (e.g., Sawyer *et al.*, 2006), but the nature of this response and the subsequent ramifications for different species are complex. Humans directly convert habitat, but their activities also lead to functional habitat loss disproportionately greater than the area that is directly disturbed (e.g., Sawyer *et al.*, 2006). Responses also can be more nuanced, with humans being perceived as akin to predators, driving behavioral shifts reflecting tradeoffs between security and other demands such as foraging or reproduction (Frid & Dill, 2002; Hebblewhite & Merrill, 2008). Alternatively, animals can be attracted to human developments due to associated resources, or as protection against predation (Berger, 2007). This attraction can positively impact animals, but can also lead to greater potential for negative encounters with humans (Johnson *et al.*, 2004) and the formation of ecological traps (e.g., Northrup *et al.*, 2012b). In light of the array of complex responses of animals to human disturbance, research on the mechanisms driving changes in wildlife behavior are critical for developing appropriate mitigation measures.

In many areas of the western United States hydrocarbon development has taken place on mule deer (*Odocoileus hemionus* Rafinesque) winter range, where the species faces acute welfare issues related to decreased access to high quality forage (Parker *et al.*, 1984). Mule deer have experienced major population declines across their range (Unsworth *et al.*, 1999) and recent studies have shown deer to experience alterations of habitat selection patterns and large scale displacement in response to hydrocarbon development (Sawyer *et al.*, 2006, 2009). Obtaining information on the impact of development on deer habitat selection patterns is thus a major management priority, as extraction is projected

to continue to increase over the next several decades (USEIA, 2014).

We fit resource selection functions (RSFs) in a hierarchical Bayesian framework to understand responses of a mule deer population to hydrocarbon development on winter range. Resource selection functions are the most commonly used approach to examine the habitat selection process, but a major methodological and conceptual hurdle to their application is the sensitivity of results to definitions of habitat availability (Johnson, 1980; Hooten *et al.*, 2013; Lele *et al.*, 2013; Northrup *et al.*, 2013). With technological advances in global positioning system (GPS) radio collars, animal location data are being collected at increasingly fine scales revealing complex temporal autocorrelation structures (Wittmyer *et al.*, 2008; Boyce *et al.*, 2010) that can compound methodological issues related to defining availability in RSF analyses. Although methods exist for potentially managing this autocorrelation (see Fieberg *et al.*, 2010 for a review), approaches for addressing autocorrelation at the scale of the availability sample are limited. Using methods developed in the animal movement literature, Hooten *et al.* (2013) propose a dynamic movement-based method for determining availability on an individual animal and location-specific basis. We apply a similar methodology to address three questions: (1) how does hydrocarbon development (roads and well pads) influence deer habitat selection?; (2) do deer respond to energy development differently at night than during the day?; and (3) at what spatial scale do mule deer most strongly respond to different development features? Our results provide insights into the spatial and temporal factors influencing mule deer habitat selection and the influence of energy development on this behavior, while offering a template for assessing spatial habitat loss and guidance for the mitigation of development impacts on wildlife.

Materials and methods

Study area

We examined mule deer habitat selection on winter range in the Piceance Basin in Northwestern Colorado, USA, (39.954°N, 108.356°W; Fig. 1), during a time of ongoing development of natural gas. Deer in this area migrate from high elevations during the summer to low elevations during the winter, with winter range occupancy generally occurring between October and May (Lendrum *et al.*, 2013; Northrup *et al.*, 2014b). The area is topographically diverse and dominated by sagebrush (*Artemisia tridentata* Nutt.) and a pinyon pine (*Pinus edulis* Engelm.) and Utah Juniper (*Juniperus osteosperma* Torr.) shrubland complex. The vegetation of the area is described in detail by Bartmann & Steinert (1981) and Bartmann *et al.* (1992). The dominant human activity in the area is

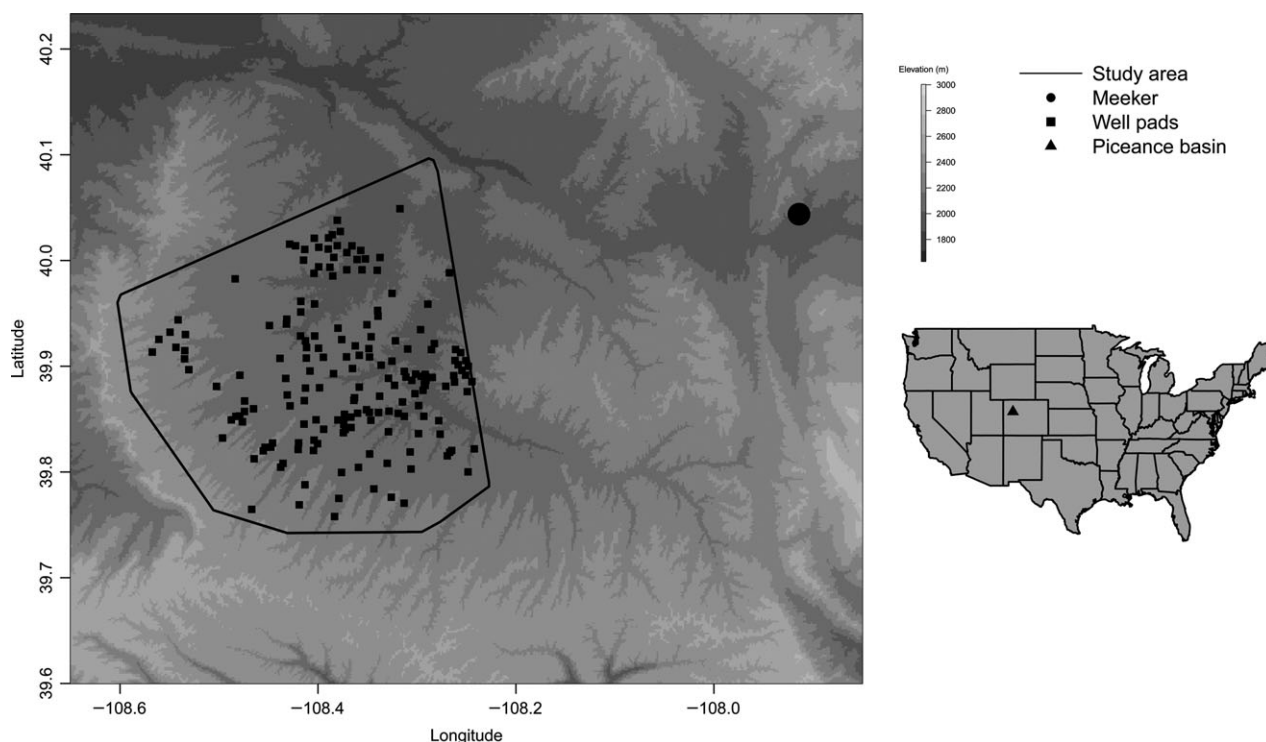


Fig. 1 Study area location in the United States, closet human settlement (Meeker, CO), and outline of winter range study area used by adult female mule deer in the Piceance Basin of Northwest Colorado.

natural gas development, with winter cattle grazing occurring primarily in the valley bottoms. Density of natural gas well pads across the study area were approximately 0.18 well pads km^{-2} in 2008, 0.20 well pads km^{-2} in 2009 and 0.20 well pads km^{-2} in 2010, although local densities ranged from 0–6 pads km^{-2} . The area is popular for hunting during the fall, and experiences warm, dry summers with monsoonal precipitation and cold winters, with the majority of moisture resulting from snow melt in the spring.

Mule deer data

We monitored adult (>1 year old) female mule deer on their winter range between January 2008 and December 2010. Adult females were studied as they are the age and sex class known to be the dominant driver of population dynamics. Deer were captured using helicopter net gunning during December and March of each year and were fit with store-on-board global positioning system (GPS) radio collars (G2110D, Advance Telemetry Systems, Istanti, MN, USA and model 4400, Lotek Wireless, Newmarket, ON, Canada) programmed to attempt a relocation once every 5 hours. All procedures were approved by the Colorado State University (protocol ID: 10-2350A) and Colorado Parks and Wildlife (protocol ID: 15-2008) Animal Care and Use Committees. Collars were equipped with timed release mechanisms set to release after 16 months. At this time collars were recovered, and data were downloaded. Due to the potential behavioral impacts of capture on mule deer (Northrup *et al.*, 2014a), we censored all data for one week fol-

lowing capture. Deer in this area are migratory, so we only included data occurring between the termination of fall migration and the initiation of spring migration. Migration termination and initiation were estimated visually in ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, USA). We removed all locations for which the positional dilution of precision (PDOP) was >10 (<1% of locations: D'eon & Delparte, 2005; Lewis *et al.*, 2007). We calculated the percent of successful GPS fixes for each individual by dividing the number of successful GPS fixes for each individual by the number of total locations by the number of attempted fixes. Overall fix success rate was 93%, which exceeds the threshold commonly used to indicate the need for habitat-bias corrections in habitat modeling (Frair *et al.*, 2004; Hebblewhite *et al.*, 2007). Lastly, we divided locations into night and day, with night classified as the time between sunset and sunrise (http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

Predictor variables

We chose an approach for RSF modeling that maximized our understanding of the impacts of development. We first chose a set of environmental covariates for RSF modeling that we hypothesized to be important predictors of deer resource selection based on previous studies (Pierce *et al.*, 2004; Sawyer *et al.*, 2006, 2009; Stewart *et al.*, 2010). These covariates represented our best understanding of how mule deer selected habitat. We then added to these covariates different representations of natural gas development to understand deer

response to development while also accounting for environmental characteristics that they are known to respond to. The environmental covariates included the terrain variables slope (*slope*), and elevation (*elev*), calculated from a digital elevation model. In addition, we obtained land cover data from the Colorado Vegetation Classification Project (<http://ndis.nrel.colostate.edu/coveg/>). This land cover database has 69 classes, however our study area is dominated by two classes (44% sagebrush and 39% pinyon-juniper). While numerous land cover classes existed in our study area, all classes other than pinyon-juniper and sagebrush were relatively rare, and not all deer interacted with all of the other categories. Thus, we combined all categories into two classes that all deer interacted with. These classes consisted of treed or open (*tree*). Lastly we calculated the distance to treed edges (*d_edge*). We also digitized all roads in the study area from aerial imagery from the National Agricultural Imagery Program (NAIP) and calculated the distance to the nearest road from each location (*d_rds*), and also included a quadratic term for the distance to roads.

To obtain information on development, we downloaded the location of all oil and natural gas wells in the study area from the Colorado Oil and Gas Conservation Commission website (cogcc.state.co.us), which maintains a daily updated database of the locations, drilling onset date and drilling completion date of oil and natural gas wells throughout the state. We classified each well in our study area into one of three classes: (1) wells actively being drilled (wells in this stage generally see continuous 24/7 human activity); (2) wells that were actively producing natural gas with no drilling activity; and (3) wells that were abandoned (see Appendix S1 for further details). We created a series of time-specific spatial layers representing the status of each well accurate to the day. These layers were generated for the entire time period during which collared deer were active on winter range in the study area (Oct–May of each year). We grouped individual wells by pad visually using a layer for well pads digitized from the NAIP imagery. We then classified each pad as a drilling, producing, or abandoned pad for every day of the study period. If a pad had any wells that were being actively drilled, the entire pad was classified as drilling. Likewise, if the pad had both abandoned and producing wells, it was classified as producing. Our ultimate unit of replication was the well pad, as pads can contain multiple wells that can be in different stages.

Using the resulting data, we created different covariates to represent active natural gas development. Our approach consisted of fitting a single model structure with nested concentric buffers around well pads. Including concentric buffers in the models allows us to identify the distance at which deer ceased to respond to well pads. We created eight covariates for this model: the number of well pads within 400 m (measured to the edge of the well pad; *drill_400* and *prod_400*), the number of pads between 400–600 m (*drill_600* and *prod_600*), the number of pads between 600–800 m (*drill_800* and *prod_800*) and the number of pads between 800–1000 m (*drill_1000* and *prod_1000*). The smallest buffer distance assessed (i.e., 400 m) corresponded to the approximate mean distance moved between successful deer relocations spaced

5 h apart. We initially attempted to assess responses to the number of pads within 200 m but convergence failed for both night and day models that included these covariates after more than 2 million iterations (traceplots showed poor mixing). On closer examination, this appeared to result from few deer locations within 200 m of well pads classified as being drilled [23 locations during the night (0.17% of night time locations) and 17 locations during the day (0.11% of daytime locations)]. We excluded abandoned pads from analysis as there was no extraction activity associated with these features.

Model formulation

We estimated RSFs separately for night and day locations using hierarchical conditional logistic regression (*sensu* Duchesne *et al.*, 2010), in a Bayesian framework where all coefficients varied by individual. In this framework, each used location is paired with a set of random locations drawn from an area deemed to be immediately available to the animal at that time (Boyce, 2006). Following Revelt & Train (1998), and Duchesne *et al.* (2010), the probability that an animal (*n*) chooses a resource unit (*y*) represented by a suite of habitat covariates (x_y) from a set of available alternative resource units (*J*), represented by suite of habitat covariates (x_j) at time *t* can be written as follows:

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

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:

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

$$\mu_\beta \sim \text{normal}(\mathbf{0}, 1000000I)$$

$$\log(\sigma_\beta^2) \sim \text{normal}(0, 1000000)$$

Characterizing availability

In a RSF model using conditional logistic regression, each used location is paired with random locations sampled within a distance of the used location presumed to be immediately available to the animal (Boyce, 2006). There is no standard approach for determining this distance for drawing availability, although methods in the literature include using the average distance moved between successive GPS locations (Boyce *et al.*, 2003), or drawing from empirical step length and turn angle distributions (Fortin *et al.*, 2005). Although such methods clearly have biological underpinnings, few definitions of availability have accounted for the dynamic movement behavior of animals.

With the proliferation of studies using GPS radio collar data, there currently exists an array of methods, developed in the animal movement literature, that model the dynamic movement behavior of animals (e.g., Hooten *et al.*, 2013). We

used the continuous-time correlated random walk (CTCRW) model described by Johnson *et al.* (2008) to categorize availability (*sensu* Hooten *et al.*, 2013). The CTCRW model describes movement as an Ornstein-Uhlenbeck process, where the velocity of an animal at the current time step is dependent on its previous velocity, an autocorrelation parameter, and an error term scaled by the time between known locations (Johnson *et al.*, 2008). Hooten *et al.* (2013) use the results of the CTCRW model to characterize resource availability as the predictor distribution for the location and velocity of an animal at any time, which is a description of the uncertainty in the location at the current time given all preceding data. The location of this predictor distribution varies with the location and speed of the animal and thus its position relative to the used location is dynamic and dependent on the current behavior of the animal.

We fit the a CTCRW model for each individual animal using the 'crawl' package (Johnson *et al.*, 2008) in the R statistical software (R Core Team, 2013). The coordinates of a set of random locations were drawn from the predictor distribution specific to each used location. To ensure a sufficiently large availability sample (Northrup *et al.*, 2013), we explored the stability of coefficient estimates from models fit to varying availability sample sizes (5, 25, 50, 100, 250, 500 and 1000 random locations per used location). Drawing from a set of 10 000 random locations per observed location, we ran 25 models at each availability sample size to examine variation in coefficient estimates as a function of the availability sample. Once the sample size that provided stable covariate estimates had been determined, we drew that number of random locations for each used location for each individual for the hierarchical model described above.

Model fitting

Using the model formulation and data described above, we fit models to deer locations across all years. We first standardized all continuous predictor covariates $(x - \bar{x})/\sigma$. We tested for correlations among covariates that appeared in the same model (Appendix S2) to ensure that no covariates were highly correlated ($|r| > 0.7$). Using the Bayesian hierarchical framework described above, we fit RSFs using a Markov-Chain Monte Carlo (MCMC) procedure written in the R programming language. We ran two parallel chains for each model for 1 000 000 iterations, discarding the first 100 000 as burn-in. We selected starting values for each parameter chain that were expected to be overdispersed relative to the posterior distributions and monitored convergence to the posterior distribution by examining traceplots of MCMC samples against iterations to determine if there was proper mixing, and by calculating the Gelman-Rubin diagnostic (mean values <1.1 indicate convergence; Gelman & Rubin, 1992). In addition to fitting the single model structure discussed above, we also fit a set of models each with a single covariate representing the number of well pads within overlapping buffer distances (see Appendix S2 for more details). This approach was taken to aid our inference in relation to the concentric buffers analysis discussed above. One of the most basic assumptions of model fit-

ting is that the model is a faithful representation of the data generating process. To test this assumption we performed posterior predictive checks (Appendix S2; see examples in Gelman & Hill, 2007).

Results

Model specifications

We monitored 53 adult female mule deer across 3 years (18 per year, with one individual collared for consecutive years), for a total of 29 083 winter range (Oct–May) locations ($\bar{x} = 548.7$ locations per deer). Both 250 and 500 available locations per used location provided sufficiently accurate estimation of coefficients. Upon initiation of model fitting, 500 locations proved to be computationally infeasible on a high-performance supercomputer. Thus we included 300 available locations per used location. All parameters converged to their posterior distribution (i.e., all mean Gelman-Rubin values were <1.1). There were strong similarities to the models fit with concentric buffers and additional models fit with single covariates representing the number of pads within overlapping buffers (Appendix S2), thus we only present results of the concentric buffers analysis.

Ecological and anthropogenic drivers of selection

Deer selected open areas over treed areas and areas further from edges during the night, while during the day, deer selected treed areas over open areas and areas closer to edges (Fig. 2). In addition, deer selected areas closer to roads during the night than during the day (Fig. 3). Throughout the day and night, deer selected areas with steeper slopes and at higher elevations, although the strength of this selection was greater during the night (Table 1, Fig. 2). Deer responses to drilling and producing well pads varied by buffer distance (Fig. 4). During both night and day deer avoided drilling well pads at the 0–400 m buffer and the 400–600 m buffer. During the night this avoidance persisted to the 600–800 m and 800–1000 m buffers, but was relatively weak at the furthest buffer distance. Contrarily, deer showed no avoidance of the areas 600–800 m and 800–1000 m from drilling well pads during the day (Fig. 4). During the day, deer also avoided well pads actively producing natural gas at the 0–400 m buffer and 400–600 m buffer, while showing no avoidance of the areas between 600–1000 m from these pads (Fig. 4). During the night deer displayed weaker avoidance of producing well pads within the smallest buffer (0–400 m) than during the day, while displaying selection for areas at all other buffer distances (Fig. 4).

Table 1 Covariate names, median posterior coefficient (coeff.) values, and proportion (prop.) of posteriors above and below 0 for resource selection function models fit to GPS data from adult female mule deer in the Piceance Basin, Colorado, USA during the night and day separately.

| Covariate | Night coeff. | Night prop. < 0 | Night prop. > 0 | Day coeff. | Day prop. < 0 | Day prop. > 0 |
|---------------------------|--------------|-----------------|-----------------|------------|---------------|---------------|
| <i>d_edge</i> | 0.11 | 0.00 | 1.00 | -0.17 | 1.00 | 0.00 |
| <i>slope</i> | 0.17 | 0.00 | 1.00 | 0.05 | 0.01 | 0.99 |
| <i>elev</i> | 0.91 | 0.00 | 1.00 | 0.69 | 0.00 | 1.00 |
| <i>d_rds</i> | -0.35 | 1.00 | 0.00 | 0.17 | 0.00 | 1.00 |
| <i>d_rds</i> ² | -0.43 | 1.00 | 0.00 | -0.30 | 1.00 | 0.00 |
| <i>tree</i> | -0.27 | 1.00 | 0.00 | 0.08 | 0.01 | 0.99 |
| <i>prod_400</i> | -0.06 | 0.71 | 0.29 | -0.41 | 1.00 | 0.00 |
| <i>drill_400</i> | -0.73 | 0.99 | 0.01 | -0.82 | 1.00 | 0.00 |
| <i>prod_600</i> | 0.08 | 0.19 | 0.81 | -0.14 | 0.98 | 0.02 |
| <i>drill_600</i> | -0.40 | 0.96 | 0.04 | -0.28 | 0.99 | 0.01 |
| <i>prod_800</i> | 0.12 | 0.03 | 0.97 | -0.04 | 0.77 | 0.23 |
| <i>drill_800</i> | -0.27 | 0.95 | 0.05 | 0.00 | 0.49 | 0.51 |
| <i>prod_1000</i> | 0.07 | 0.05 | 0.95 | 0.02 | 0.29 | 0.71 |
| <i>drill_1000</i> | -0.09 | 0.78 | 0.22 | 0.04 | 0.29 | 0.71 |

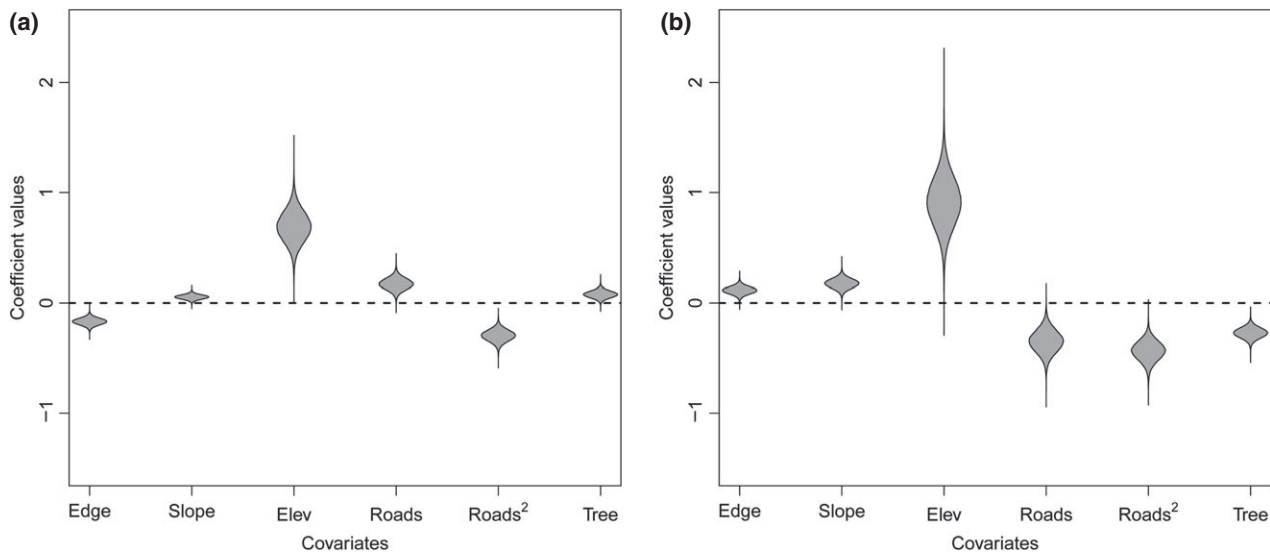


Fig. 2 Posterior distributions of population-level coefficients for RSF models during the (a) day and (b) night for 53 adult female mule deer in the Piceance Basin, Northwest Colorado. Dashed line indicates 0 selection or avoidance of the habitat features. Displayed coefficients are for non-well pad covariates only, but are taken from models including well pad covariates. ‘Edge’ refers to the distance to treed edges in meters, ‘Slope’ was measured in degrees, ‘Elev’ refers to elevation in meters, ‘Roads’ refers to the distance to roads in meters, and ‘Tree’ refers to treed land cover.

Discussion

Hydrocarbon development is projected to continue to increase in the United States and elsewhere (USEIA, 2013, 2014) and thus is set to become a major driver of global land-use change. As such, there is a pressing need for assessments of the nature of impacts to wildlife and the spatial extent to which these impacts extend. The habitat selection patterns of deer in our system were strongly influenced by hydrocarbon develop-

ment, with deer displaying both spatial displacement and alterations in temporal behavioral patterns relative to these features. The nature of these responses differed depending on disturbance type, time of day, and the distance from development. Our methodology, which accounted for the dynamic nature of deer behavior by allowing for the resource availability sample to change relative to current speed of the deer, and ensured the sample was conditioned by time and location, allowed us to identify the dynamic nature of the responses to

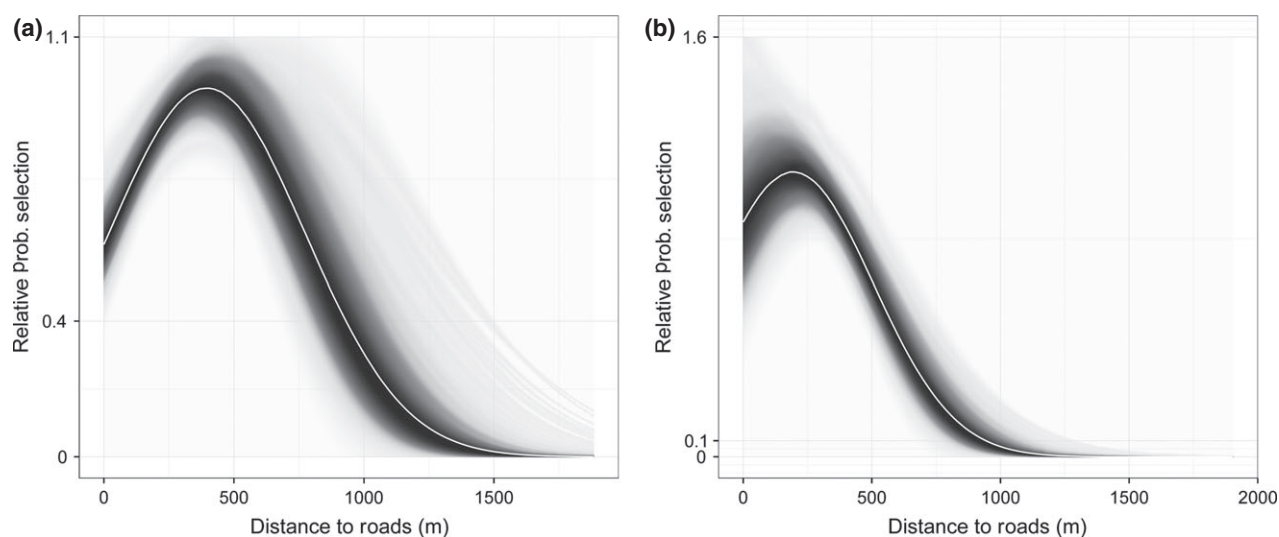


Fig. 3 Posterior distribution of predicted selection as a function of distance to roads from resource selection function models fit to data during the (a) day and (b) night for 53 female mule deer in the Piceance Basin, Northwest Colorado.

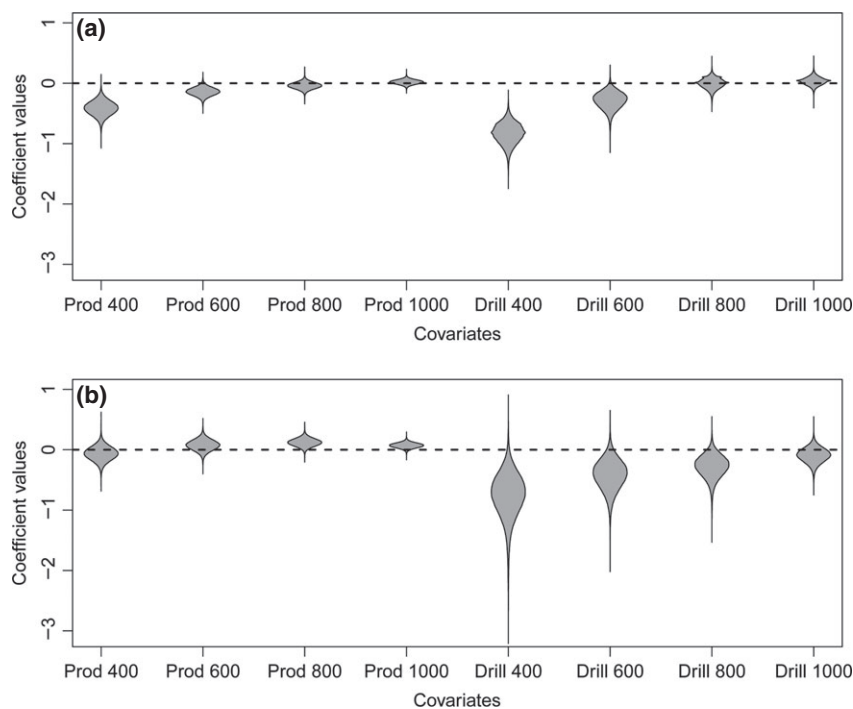


Fig. 4 Posterior distributions of population-level coefficients related to natural gas development for RSF models during the (a) day and (b) night for 53 female mule deer in the Piceance Basin, Northwest Colorado. Dashed line indicates 0 selection or avoidance of the habitat features. 'Drill' and 'Prod' refer to well pads where there was active drilling or not, respectively. The numbers following 'Drill' or 'Prod' represent the concentric buffer over which the number of well pads was calculated (e.g., 'Drill 600' is the number of well pads with active drilling between 400–600 m from the deer location).

development. Our results advance understanding of how animals perceive and adjust their behavior to minimize exposure to human disturbances, offering important insight for measures to mitigate the impacts of

human land-use change associated with development. The approach we took can serve as a template for future work quantifying habitat take by land-use conversion.

The drilling stage of natural gas development elicited the strongest response by deer in our system. Deer strongly avoided areas within 600 m of well pads with active drilling at all times, and this avoidance persisted out to 1000 m at night (with the strongest responses within 800 m). During both day and night, the strength of avoidance of drilling well pads increased as distance decreased, with essentially no locations falling within 200 m of these pads. Sawyer *et al.* (2009) also documented a greater avoidance of active drilling than other energy development activities by mule deer, indicating that this activity is the predominate stressor during hydrocarbon development. Thus, measures aimed at mitigating impacts from drilling, such as seasonal drilling restrictions, sound and light barriers, and reductions in vehicle traffic, are likely to have the greatest benefit to deer.

The other development infrastructure (i.e., roads and producing pads) altered deer behavior, but to a lesser extent. Deer avoided the areas closest to both of these development types to some degree, but the strength and scale of the responses varied between night and day, with stronger avoidance during the day when deer also selected areas with greater vegetative cover. It appears deer temporally modulate their behaviors so as to avoid these features during the most disturbing times of day (e.g., in relation to circadian traffic pulses). Dzialak *et al.* (2011) documented a similar pattern for elk in a natural gas field, with animals subject to disturbance selecting 'security cover' more strongly during the day. This behavior might be a common response by mobile wildlife to disturbance that has any type of temporal signature (e.g., roads; Northrup *et al.*, 2012a).

Understanding the spatial scale at which wildlife behavior is impacted by human disturbance is critical for developing effective mitigation strategies and quantifying the full footprint of development. As hydrocarbon development expands globally, developing frameworks for consistently assessing the spatial habitat take from this land-use change is a critical need. Our analysis design, examining selection or avoidance of concentric buffers around development, allowed us to identify the threshold distance where avoidance ceased and can serve as a template for future assessments. Deer displayed complete avoidance of areas within 200 m of well pad edges (approximately 2% of the critical winter range used by deer in our study). This distance should be considered the minimum at which indirect habitat loss occurs. However, avoidance was demonstrated to a distance of at least 800 m around drilling pads at night, and 600 m around producing pads during the day. These distances equate to greater than 20% of the critical winter range being impacted by

producing pads (area within 600 m) and 2% by drilling pads (area within 600 m; the density of drilling pads is much lower in the study area), during the day, with 6% impacted by producing pads (area within 200 m) and 6% by drilling pads (area within 800 m) during the night. In addition, 28% of the critical winter range fell within 100 m of roads (the distance at which the relative probability of selection fell to half of the peak value during the day) and 15% fell within 50 m of roads (the distance at which the relative probability of selection fell to half of the peak value during the night). Although these values do not equate to complete habitat loss, they do indicate that more than half of the critical winter range was impacted by development during the day, and more than one quarter of the range was impacted during the night. The costs of this reduction (avoidance by deer) likely include the time lost during travel or from foraging in suboptimal areas during times of high human activity (Lima & Dill, 1990; Creel & Christianson, 2008), both of which can have impacts on nutritional condition and ultimately reproductive success (Houston *et al.*, 2012). It is important to recognize that fitness costs of range avoidance likely are compounded during the winter when deer face a negative energy balance. We note that to date the deer population in this study area has been increasing (Anderson Jr., 2014), so this avoidance at the observed development intensity has not resulted in a population decline, although it is impossible to tell if the population would be increasing at a greater rate in the absence of development. The spatial scales of reduced use relative to specific types of infrastructure as defined in this study should be considered by managers when attempting to develop mitigation strategies.

In a recent published assessment of mule deer response to natural gas development, Sawyer *et al.* (2006) found larger-scale displacement of deer from the area around development than those reported here. Although our results show similar general behavioral responses (i.e., alteration of habitat selection patterns), the scale of displacement was less. This likely relates to differences in the landscapes between the study areas, where the Piceance system has substantially greater topographic and vegetative diversity than the open, flat areas in the Pinedale area of Wyoming where Sawyer *et al.* (2006) conducted their work. We hypothesize that the structural diversity of the habitat and topography provide refuge areas for deer in our system at relatively close proximity to infrastructure that allows them to behaviorally mediate impacts. Such complexity in habitat structure can provide refuge for wildlife and should be considered and maintained by managers and developers when planning projects, through spacing of roads and pads to ensure sufficient areas outside the 800 m

buffers around drilling pads and 50–100 m buffers around roads.

Oil and gas development is projected to continue to increase in the United States (USEIA, 2014), with major shale development likely to occur globally within the next decade. Quantifying the spatial extent of development related impacts to wildlife is critical for appropriately gauging the repercussions of this activity and identifying potential mitigation measures, which are critical for sustainable development practices (Northrup & Wittemyer, 2013). Importantly, drilling is temporary, as human activity declines once drilling is complete and wells begin producing (Sawyer *et al.*, 2009). The temporary nature of this activity provides an opportunity to either avoid drilling during the winter months, or structure development in a manner that allows refuge habitat during the most acute periods of stress. Many drilling pads in an area, as might occur with rapid development, leads to large functional losses in habitat, apparently driving abandonment of areas by deer (e.g., Sawyer *et al.*, 2006). Where development is conducted at lower densities, or in a manner that ensures that sufficient area is left undeveloped (i.e., refuge habitat is maintained), impacts are likely to be reduced. Even where drilling occurs in a manner that provides refuge, consideration of the spatial structure of the final footprint of roads, producing wells and facilities is critical to ensure adequate space for deer to structure their behaviors in a manner that mitigates negative impacts during the late stage production phase. Coupling spatial patterning of the permanent development footprint with approaches that reduce human activity at these areas, such as remote liquid gathering systems, will reduce the amount of disturbance (e.g., Sawyer *et al.*, 2009) and subsequently any negative impacts. Contrasting results from the Piceance Basin and Pinedale provides insight to features that may allow deer to behaviorally mediate disturbance (although this should not be construed as eliminating all negative impacts; Lima & Dill, 1990), although the exact nature of these components in different systems requires more rigorous examination. Therefore, it is critical for future studies to identify thresholds to gain better understanding of the disturbance-habitat relationship and ensure sustainable development practices in areas with sensitive wildlife.

Acknowledgements

Mule deer capture and monitoring was funded and/or supported by Colorado Parks and Wildlife (CPW), White River Field Office of Bureau of Land Management, ExxonMobil Production/XTO Energy, WPX Energy, Shell Exploration and Production, EnCana Corp., Marathon Oil Corp., Federal Aid in Wildlife Restoration (W-185-R), the Colorado Mule Deer Foun-

ation, the Colorado Mule Deer Association, Safari Club International, Colorado Oil and Gas Conservation Commission, and the Colorado State Severance Tax. We thank L. Wolfe, C. Bishop, D. Finley, and D. Freddy (CPW) and numerous field technicians for project coordination and field assistance. We thank Quicksilver Air, Inc. for deer captures, and L. Gepfert (CPW) and Coulter Aviation, Inc. for fixed-wing aircraft support. We thank J. Tigner, and S. Downing for assistance with interpretation of development data. We thank M. Hooten, B. Gerber and P. Williams for analysis advice. N.T. Hobbs, M. Hooten, H. Johnson (CPW), K. Logan (CPW), A. Maki and 2 anonymous reviewers provided comments on an earlier draft that greatly improved the manuscript. This research utilized the CSU ISTeC Cray HPC system supported by NSF Grant CNS-0923386.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Appendix S1.** Detailed description of well classifications.
- Appendix S2.** Overlapping buffers analysis, model structures, results of all fitted models and posterior predictive checks.