Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development

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Abstract. The disruption of traditional migratory routes by anthropogenic disturbances has shifted patterns of resource selection by many species, and in some instances has caused populations to decline. Moreover, in recent decades populations of mule deer (*Odocoileus hemionus*) have declined throughout much of their historic range in the western United States. We used resource-selection functions to determine if the presence of natural-gas development altered patterns of resource selection by migrating mule deer. We compared spring migration routes of adult female mule deer fitted with GPS collars ($n = 167$) among four study areas that had varying degrees of natural-gas development from 2008 to 2010 in the Piceance Basin of northwest Colorado, USA. Mule deer migrating through the most developed area had longer step lengths (straight-line distance between successive GPS locations) compared with deer in less-developed areas. Additionally, deer migrating through the most developed study areas tended to select for habitat types that provided greater amounts of concealment cover, whereas deer from the least developed areas tended to select habitats that increased access to forage and cover. Deer selected habitats closer to well pads and avoided roads in all instances except along the most highly developed migratory routes, where road densities may have been too high for deer to avoid roads without deviating substantially from established migration routes. These results indicate that behavioral tendencies toward avoidance of anthropogenic disturbance can be overridden during migration by the strong fidelity ungulates demonstrate towards migration routes. If avoidance is feasible, then deer may select areas further from development, whereas in highly developed areas, deer may simply increase their rate of travel along established migration routes.

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INTRODUCTION

Migration is a remarkable life-history strategy that represents an essential component of the ecological niche of a variety of taxa, including mammals (Dingle and Drake 2007). This seasonal movement between ranges allows animals to increase access to important forage resources (Baker 1978) and reduce risk of predation (Fryxell and Sinclair 1988), both of which affect survival and reproduction (Nicholson et al. 1997). For example, large herbivores living in temperate regions often move from low elevations in winter to higher elevations in spring and

summer, which provides release from a restricted food supply and access to newly available forage in spring (Garrott et al. 1987, Fryxell and Sinclair 1988, Mysterud 1999, Hebblewhite et al. 2008, Monteith et al. 2011). Such strategies ostensibly are favored by natural selection because the development of scale-dependent behaviors, which increase access to high-quality forage, improves both survival and reproductive success (Senft et al. 1987). Access to high-quality forage during spring migration is of particular importance for migratory ungulates living in temperate regions, because migration closely coincides with the timing of parturition (Singh and Milner-Gulland 2011).

Ungulate migrations generally occur along traditional routes (Baker 1978, McCullough 1985, Andersen 1991), many of which have been disrupted, especially over the past 4 decades, because of human activities (e.g., anthropogenic barriers and habitat loss; Sawyer et al. 2005, Harris et al. 2009, Beckmann et al. 2012). Bolger et al. (2008) observed that for many mammalian species (e.g., wildebeest, *Connochaetes taurinus*, Ottichilo et al. 2001; zebra, *Equis burchelli*, Williamson and Williamson 1985; and mule deer, *Odocoileus hemionus*, Bertram and Rempel 1977), the disruption of migratory routes has caused rapid population collapses. Indeed, populations of mule deer have declined throughout much of the Intermountain West, USA (Unsworth et al. 1999, Johnson et al. 2000, Stewart et al. 2002, Bishop et al. 2009, Hurley et al. 2011), and unprecedented levels of energy development throughout the region represent a critical threat to traditional migration routes for mule deer (Copeland et al. 2009). In particular, effects of natural-gas development can include the direct loss of habitat around well pads, access roads, and pipeline constructions, as well as indirect losses caused by increased human disturbance (e.g., traffic, noise) associated with infrastructure. These disturbances may displace mule deer or alter their patterns of habitat use along migration routes (Hayes and Krausman 1993, Sawyer et al. 2006). As a result, large-scale migration corridors that are protected or managed specifically to mitigate energy development may be critical for protecting the life-history strategy of long-distance migration by mule deer (Sawyer et al. 2005).

Effective conservation and planning must account for the inherent dynamics of ecological processes and effects of anthropogenic disturbance on habitat use and availability (Morrison 2001, Pressey et al. 2007). Land-use activities such as recreation, agriculture, and infrastructure development can influence spatial and temporal patterns of animal occurrence and demographics (Rost and Bailey 1979, Sawyer et al. 2009a, Dzialak et al. 2011). As landscape fragmentation increases because of human development and land-use practices, understanding effects of development and landscape characteristics on variation in range use, fidelity to migration paths, and demographics of animals will be of increasing importance for the conservation of these large, vagile mammals (Webb et al. 2011). For example, anthropogenic disturbances associated with energy development have been related to changes in resource selection by ungulates (Sawyer et al. 2006, Dzialak et al. 2011), as well as to reduced range fidelity (Webb et al. 2011).

Estimating resource-selection functions (RSFs) for mammals can be a valuable research tool for mitigating influences of human activities (Sawyer et al. 2006, Long et al. 2008, Harju et al. 2011). Conservation actions may be misguided, however, when resource selection is only evaluated for animals that already are influenced by high levels of human activity, because selection for some resources may be partially or largely a function of avoidance of human disturbance (Harju et al. 2011). We used resource-selection functions (Compton et al. 2002, Boyce 2006) to determine if varying levels of natural-gas development altered selection for landscape characteristics by migratory mule deer. We used a novel approach to define availability based on movement parameters collected from GPS collars, which included step length and turning angles between successive deer locations during spring migration.

We conducted our study in the Piceance Basin of northwestern Colorado, USA, from 2008 to 2010. The Piceance Basin supports one of the largest populations of migratory mule deer in North America, estimated at 21,000–27,000 animals over the past several decades (White and Lubow 2002). This region also includes one of the largest natural-gas reserves in North America, with projections of energy development through-

out northwestern Colorado over the next 20 years to increase from approximately 500 to 15,000 wells. Within the Piceance Basin, we monitored patterns of spring migration for mule deer that were exposed to differing levels of natural-gas development.

We hypothesized that, during spring migration, step lengths and turning angles of mule deer would vary with the level of natural-gas development and time of day because of disturbances associated with human activity. We predicted that mule deer in the most-developed areas would have longer step lengths with a more straight-forward direction of travel compared with deer in less-developed study areas. We further predicted that movement rates would be higher at night in highly developed areas compared with those of less development to compensate for deer avoiding human activities during the day. We also hypothesized that landscape characteristics and human disturbances associated with natural-gas development would influence resource selection by adult female mule deer along their migration routes in spring. We predicted that mule deer would select travel routes along south-facing aspects, with moderate slopes and low levels of ruggedness, at low elevations in all areas, regardless of levels of development. In contrast, we predicted that deer in the most highly developed areas would select for habitat types with greater concealment cover further from areas of human activity, such as roads and well pads, whereas in areas with low levels of development, selection by mule deer would be influenced more by habitat types that provide high forage availability and less by the presence of development.

STUDY AREA

We monitored four populations of mule deer that wintered in different areas of the Piceance Basin: North Ridge (53 km^2) in the northeastern portion of the Basin; Ryan Gulch (141 km^2) in the southwestern portion of the Basin; and North Magnilia (79 km^2) and South Magnolia (83 km^2) in the central portion of the Basin (Fig. 1). During spring migration, mule deer from North Ridge and North Magnolia moved in an easterly direction across US Highway 13 towards the Flat Top Mountain Range, where they resided at high

elevations during summer (Fig. 1). Mule deer from Ryan Gulch and South Magnolia migrated in a southerly direction to high elevations along the Roan Plateau (Fig. 1).

The climate of the region was typified by warm dry summers (28°C average high) and cold winters (−12°C average low); most annual moisture was from snow (144.0 cm; Western Regional Climate Center, 2008–2010). The primary winter habitat for mule deer ranged from 1,675 to 2,285 m in elevation, and summer habitat ranged from 2,000 to 2,800 m. The Piceance Basin varied topographically with numerous ridges and draws. The area contained other large herbivores including North American elk (*Cervus elaphus*), wild horses (*Equus caballus*), and moose (*Alces alces*), the latter of which occurred infrequently on summer range. Common species of large carnivores included coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americana*).

Pinion pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) were the dominant overstory species on winter range; common shrubs included big sagebrush (*Artemisia tridentata*), Utah serviceberry (*Amelanchier utahensis*), mountain mahogany (*Cercocarpus montanus*), bitterbrush (*Purshia tridentate*), Gamble's oak (*Quercus gambelii*), mountain snowberry (*Symphoricarpos oreophilus*), and rabbitbrush (*Crysothamnus* spp.; Bartmann et al. 1992). Primary vegetation communities on summer range included a Gambel's oak-mountain shrub complex at lower elevations. This community was mixed with quaking aspen (*Populus tremuloides*)-Douglas-fir (*Pseudotsuga menziesii*) forest, and Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forest at higher elevations (Garrott et al. 1987). The study area was dissected by numerous drainages vegetated by stands of big sagebrush, saltbrush (*Atriplex* spp.), and black greasewood (*Sarcobatus vermiculatus*), with most of the primary drainages converted to mixed-grass hay fields. Botanical nomenclature follows Weber and Wittmann (2001).

Within the Piceance Basin, levels of natural-gas development varied markedly (Fig. 1). North Ridge (low development) contained no development on either winter or summer range; however, the transition between those ranges included increased levels of human activity from vehicle
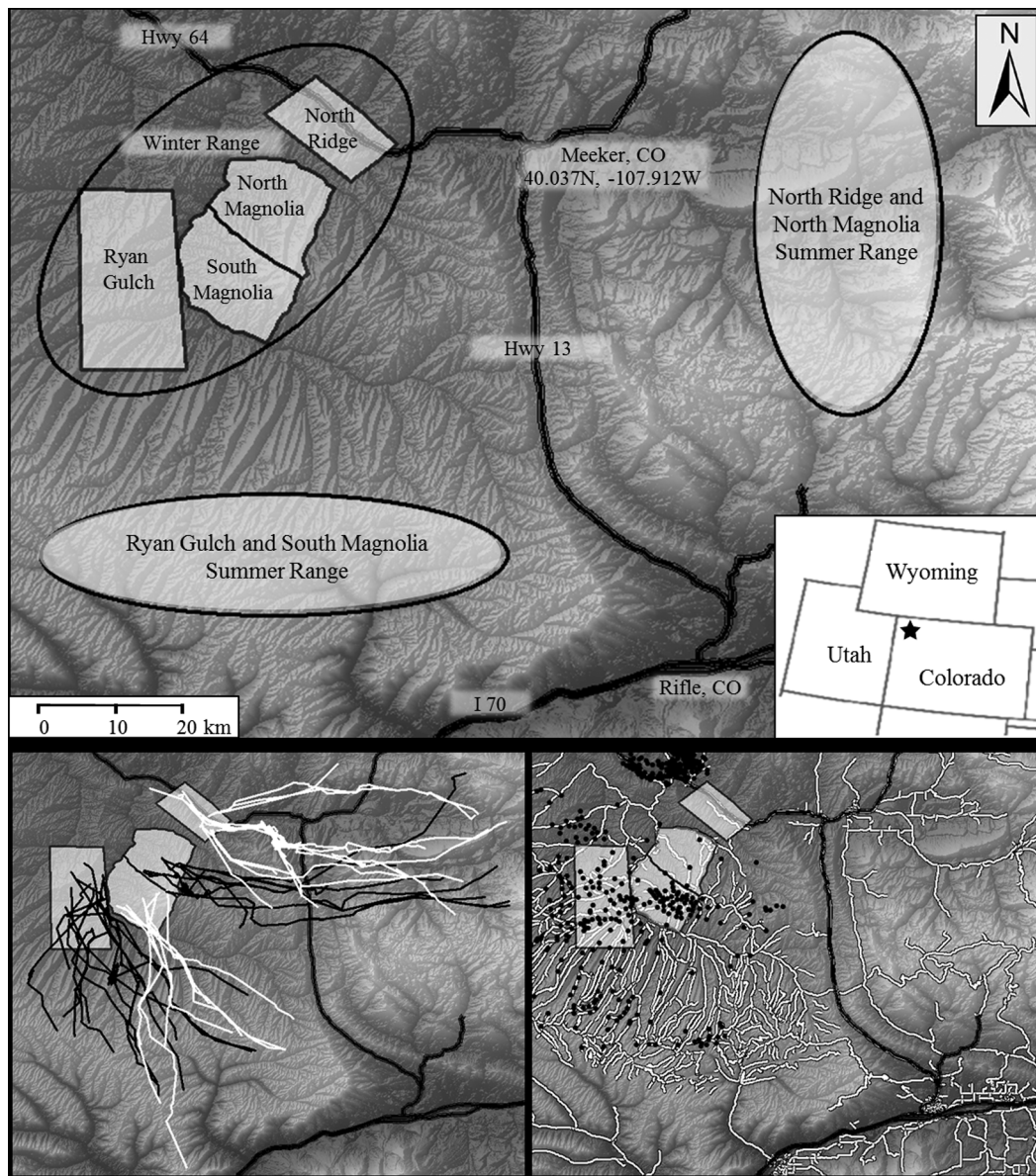
Fig. 1. (Top) Study areas in the Piceance Basin of northwestern Colorado, USA, (lower left) spring 2009 migration routes of adult female mule deer ($n = 52$), and (lower right) active natural-gas well pads (black dots) and roads (state, county, and natural-gas; white lines) from May 2009.

traffic and housing infrastructure because of proximity to the town of Meeker, Colorado. North Magnolia (medium-low development) exhibited a low density of active well pads on winter range (≤ 0.05 pads/km^2) and along migration paths (0.17 pads/km^2), and no active well pads on summer range, although deer crossed one major highway with scattered ranch hold-

ings along their migration path. Ryan Gulch (medium-high development) exhibited moderate development on winter range (0.37 pads/km^2), and throughout the transition range (1.54 pads/km^2), with a decreased density of development on summer range as deer spread across the landscape (0.06 pads/km^2). South Magnolia (high development) had the highest level of develop-

ment activity on winter range (0.70 pads/km^2), and along migration corridors (1.99 pads/km^2), with low levels of development on summer range (0.04 pads/km^2).

METHODS

Animal capture

We net-gunned mule deer from a helicopter (Krausman et al. 1985) to obtain a sample of adult ($\geq$1.5 years old) females ($n = 205$; North Ridge = 60, North Magnolia = 43, South Magnolia = 42, and Ryan Gulch = 60) during 2008–2010. Total number of deer captured was 45 during January 2008, 60 during March 2009, and 100 during March 2010. All deer were fitted with GPS collars programmed to attempt a fix once every 5 h during spring migration. We only retained 3D fixes or fixes with a positional dilution of precision <10 m (D'eon and Delparte 2005); 90% of fixes had <20 m accuracy. Fourteen females received remotely downloadable GPS collars during the first year of study (GPS-4400S; Lotek Wireless, Newmarket, Ontario, Canada), and remaining females received store-on-board GPS collars (G2110B; Advanced Telemetry Systems, Isanti, Minnesota, USA). All collars were equipped with timed drop-off mechanisms, scheduled to release during April of the year following deployment, and mortality sensors that increased pulse rate following 4–8 h of inactivity. All aspects of animal handling and research complied with methods adopted by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011), and were approved by an Animal Care and Use Committee at Idaho State University (protocol # 670 0410).

Patterns of resource selection

We retrieved GPS collars from the field each spring or following mortality events. Deer locations were plotted in ArcGIS 9.3 (ESRI, Redlands, California, USA) and spring migration routes identified. Only deer that completed spring migration were included in analyses ($n = 167$). We used Hawth's Analysis Tools to derive 95% kernel-density estimates of seasonal ranges for each individual. We determined the initiation of spring migration based on the day a particular deer left the winter range on a trajectory path

(i.e., three successive locations leading away from winter range), and arrival on summer range was determined as the first location inside the summer range for that same deer (Garrott et al. 1987).

We estimated resource-selection functions based on a matched-case design (Manly et al. 2002, Boyce 2006) to model resource selection by mule deer along migration paths. Locations from individual deer represented used points. Random locations were generated based on step lengths and turning angles derived from deer locations to define available habitat for each sub-population (i.e., study area) along migratory paths. Hence, we used a critical life-history characteristic of mule deer to determine the scale at which to measure availability of habitat characteristics during migration (sensu Bowyer and Kie 2006). Constructed on principles of a correlated random walk (Turchin 1998), "steps" were characterized by the straight-line distance between animal locations and turning angles determined as the angle from a previous step length to the next. Steps that had >5 h between locations were not included in analyses. We used Hawth's Analysis Tools (Beyer 2004) to determine a distribution of average step lengths and turning angles from known locations of mule deer ($n = 6{,}433$). We then grouped turning angles into 20° bins to create an average frequency distribution for each study area (Fortin et al. 2005). Step-length distributions were separated into 1-km bins, with a maximum step-length of 8 km. We chose 8 km as the maximum distance because <1% of the steps for each area were greater than that distance. An 8-km buffer was then placed around the outermost set of used locations as a boundary for the distribution of random locations. Each observed step was then paired with 10 random steps derived from the distribution of known steps and turning angles with a correlated random-walk simulation (Geo-spatial Modelling Environment, Beyer et al. 2010). We chose 10 random locations because those points provided a relatively uniform distribution across the area of interest. We did not allow used and random locations to overlap to avoid a loss of statistical power (Bowyer and Kie 2006). We analyzed steps separately for day ($n = 3{,}651$) and nighttime ($n = 2{,}782$) use, because of fluctuation in human activities associated with

time of day. We used sunrise (5:59 h) and sunset (20:17 h) of the median departure date (5 May) of deer from winter range to divide diel patterns into day and night.

Landscape variables

Sawyer et al. (2006) identified five landscape variables as potentially important predictors of winter distributions of mule deer in areas with oil and gas development: elevation; slope; aspect; road density; and distance to wells. We expanded that list by including additional variables for modeling resource selection by female mule deer along migration routes in spring. We examined five characteristics of landscape structure including elevation (m), slope (%), aspect (transformed into categories of North, East, South, West), terrain ruggedness (vector ruggedness measure; VRM), and vegetation type. In addition, we included two anthropogenic disturbances associated with natural-gas development: distance to nearest well pad; and distance to nearest road. Within the least-developed areas, well pads were present at low density (<0.05 pads/km^2) only on winter range, and not throughout the migration corridor. Consequently, we did not include distance to well pad as a predictor variable for those two study sites. Prior to analyses, we transformed elevation, distance to nearest well pad, and distance to nearest road so that a 1-unit change in elevation represented 50 m, and a 1-unit change in distance to well pads and roads represented 100 m. Accordingly, odds ratios for those variables indicate the predicted change in odds of selection by mule deer for every 50-m change in elevation, and 100-m change in distance to roads. Mean, SD, and range of all continuous variables, prior to transformation, for used and random locations by study area are provided in Appendix A.

We estimated elevation using a digital-elevation model (DEM) at a resolution of 30 m (http://datagateway.nrcs.usda.gov/). We then used Arc-GIS 9.3 Spatial Analyst Tools to derive values of slope and aspect from the DEM. A vector ruggedness measure also was derived from the DEM following the method of Sappington et al. (2007). Ruggedness values ranged between 0 (flat) and 1 (most rugged). A map of vegetation types was obtained from the Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/), which provided a land-scape-level vegetation dataset for the state of Colorado at a resolution of 25 m. The vegetation map included 87 habitat classes, which we reclassified into six categorical habitats based on similarity of vegetation types: (1) forbs and grasslands (herbaceous); (2) sagebrush-steppe; (3) pinion-juniper dominated (PJ); (4) aspen and conifer stands (forest); (5) riparian; and (6) bare rocky ground (barren).

Locations of well pads were obtained from the Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/). We selected well-pad records from June during 2008–2010 and designated each well as either producing or in development. Datasets for roads were obtained from the TIGER/Line shape files of the U.S. Census Bureau (http://www.census.gov/geo/www/tiger/shp.html) and the Colorado Department of Transportation (http://apps.coloradodot.info/dataaccess/). We included county roads, highways, and roads used for purposes of natural-gas extraction in our models. We did not differentiate levels of vehicle use among roads because there was insufficient information to do so.

Independence of locations

We used association matrices to investigate the spatiotemporal association among individual radio-collared deer (ASSOC1; Weber et al. 2001, Long et al. 2008). We considered deer to be associated (i.e., part of the same herd) if a pair of individuals were within 500 m of each other during $>50\%$ of the total number of days during migration. No patterns of association were detected; therefore, all deer remained in the analyses as separate sample units.

Data analyses

To estimate resource-selection functions, we compared used and random locations along spring migration routes with conditional logistic regression (PROC LOGISTIC; SAS Institute Inc. 1990, Compton et al. 2002, Boyce 2006). Each individual mule deer was considered as a stratified variable to control for variation among individuals (i.e., individuals were sampling units), and the logistic model for each study area was conditioned upon that variable (Long et al. 2009a). Prior to modeling, we used a correlation matrix to evaluate collinearity ($|r| > 0.7$) among predictor variables (PROC CORR; SAS Institute,

Cary, North Carolina). Distance to developing well pads was highly correlated with distance to producing well pads ($|r| > 0.9$), so we combined categories to create a single variable for distance to well pads. No other predictor variables were correlated (all $|r| < 0.50$) and therefore, they remained in the modeling process. To initially evaluate potential differences in patterns of resource selection between two broad categories of development (least developed = North Ridge and North Magnolia, most developed = South Magnolia and Ryan Gulch), we fit a global model that included all main effects along with possible main effect × development-level interactions for both night and daytime locations (Long et al. 2008). Statistical significance ($P \leq 0.05$) of interaction terms indicated a difference in selection for that variable between development levels. After evaluation of the global model, we then modeled each study area separately for night and day, with all possible combinations of the seven predictor variables (Long et al. 2008). Whenever distance to well pads entered the model, we also included distance to roads, and vice versa, because we considered these two variables as indicative of levels of development. For categorical variables, we used southerly aspect, which we predicted to receive high use, and sagebrush-steppe, because of its importance to mule deer (Stewart et al. 2010, Anderson et al. 2012), as reference categories.

We calculated Akaike's Information Criterion adjusted for small sample size (AICc), ΔAICc, and Akaike weights (w_i) for each model (Burnham and Anderson 2002). We intended to use model-averaged parameter estimates and unconditional standard errors (SE) to assess the influence of each predictor variable on resource selection (Burnham and Anderson 2002). Our global models, however, contained >95% of the Akaike weights, with the next-best models having a ΔAICc of >30 for all study areas. Consequently, we used the global model for interpreting patterns of resource selection for each study area and time of day. We converted parameter estimates to odds ratios by exponentiation for simplicity of interpretation. If the 95% confidence interval around an odds ratio contained 1, then that variable was considered not significant. We considered odds ratios for each predictor variable to differ significantly among

study areas if their 95% confidence intervals did not overlap (Long et al. 2008, Anderson et al. 2012). We tested descriptive statistics among study areas and years using analysis of variance (ANOVA) with Bonferroni pairwise comparisons in Minitab 16.1.0 (State College, Pennsylvania, USA, 2010). Additionally, we calculated a Pearson correlation coefficient to determine if step lengths were correlated with the distance traveled along migratory routes among study areas.

We used k-fold cross validation (Boyce et al. 2003, Anderson et al. 2005, Long et al. 2009b) to evaluate predictive strength of the resource-selection functions for adult female mule deer within study areas, for both day and nighttime models. We withheld 1 year at a time as test data and used the remaining 2 years as training data, which resulted in three total iterations for each model. During each iteration of the procedure, we used the model derived from the training data to obtain predicted RSF values for the random locations for each deer. Next, we sorted random locations from lowest to highest based on their predicted values and binned them into 10 groups of equal size (Boyce et al. 2003, Anderson et al. 2005, Long et al. 2009b). We then obtained predicted RSF values for test data using the same model, and placed locations from the test dataset into the bins we created with the random data based on their associated RSF values (Anderson et al. 2005, Long et al. 2009b). Finally, we regressed the number of locations from the test dataset in each bin against the median RSF value of the random locations, and recorded the coefficient of determination (r^2) and its slope. We averaged these statistics across the three iterations for each model, and considered the combination of a high coefficient of determination and a positive slope to be indicative of a model that predicted well (Long et al. 2009b). In addition, we calculated a Spearman's rank correlation (r_s), which makes no assumptions concerning line shape, for each iteration of the procedure and used the mean value as an additional metric of predictive strength.

RESULTS

Step lengths and turning angles

Step lengths were significantly longer ($P < 0.05$) at night than during the day for all study

areas (Fig. 2). Step lengths also were significantly greater in South Magnolia (high development) compared with all other study areas (Fig. 2). Furthermore, within broad development categories (least developed, most developed), deer from the study areas with higher development had longer step lengths than their counterparts experiencing lower development. Deer from North Magnolia had longer step lengths than deer from North Ridge, and deer from South Magnolia had longer step lengths than deer from Ryan Gulch (Fig. 2). Step lengths were not correlated with distance traveled ($r = -0.002$, $P = 0.93$). In addition, deer from all study areas exhibited a strong tendency to travel in a generally forward direction during both day and night ($\bar{x} = -0.08°$, SD $\pm$ 90.05°, $n = 5,610$).

Resource selection

Global models of resource selection for mule deer that contained interactions between each main effect (i.e., slope, elevation, habitat type) and level of development (least developed vs. most developed) indicated notable differences in patterns of selection between levels of development during both day and night. The daytime model indicated significant differences in selection for distance to roads ($P = 0.0002$), elevation ($P < 0.0001$), slope ($P = 0.0005$), and aspect ($P = 0.0057$) between the least developed and most developed sites. Similarly, the nighttime model indicated significant differences in selection for distance to roads ($P = 0.0021$), elevation ($P < 0.0001$), and slope ($P = 0.0004$) between the least developed and most developed study areas; therefore, we produced separate model sets for each study area.

Percentage of vegetation types occurring along the migratory paths of mule deer was similar among study areas (Appendix B; Friedman's 2-way ANOVA for goodness of fit, $\chi^2_5 = 96.4$, $P < 0.001$), which allowed for meaningful comparisons. Models of resource selection indicated that female deer generally selected sagebrush-dominated communities significantly more than other vegetation types across study areas (odds ratios for most habitat types <1.0; Fig. 3). No significant difference occurred in selection of sagebrush versus pinyon juniper habitat by deer from South Magnolia (high development) during the day, or in selection of sagebrush habitat versus barren
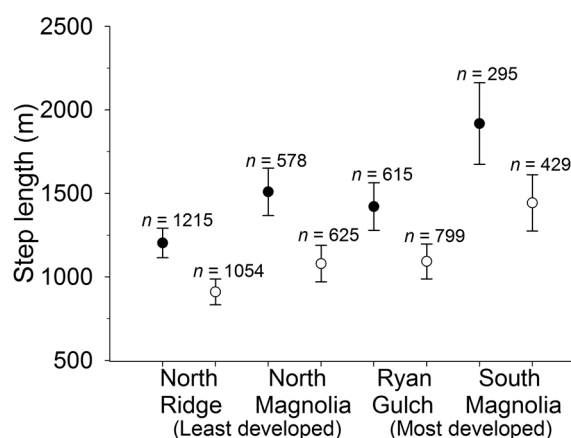

Fig. 2. Step lengths (m) for adult female mule deer ($n = 167$) during spring 2008–2010 migration in four study areas of the Piceance Basin, northwestern Colorado, USA for night (solid circle) and day (open circle) locations. Error bars = 95% CI and n = number of step lengths for each category.

ground in that study area regardless of time of day (CI's overlapping 1.0; Fig. 3). Similarly, no difference was observed in selection of sagebrush habitat versus barren ground in Ryan Gulch (medium-high development) during the day, and in selection of sagebrush versus riparian habitats in North Magnolia (medium-low development) during the night.

Deer from South Magnolia (high development) selected habitat types that provided a greater degree of concealment cover (e.g., pinyon-juniper) more strongly than deer from either of the least developed study areas (North Ridge, low development, during the day, and North Magnolia, medium-low development, during both day and night; Fig. 3). In contrast, deer from North Ridge and North Magnolia (least developed) selected habitat types that increased access to both forage and cover (e.g., aspen-conifer forests) more strongly than did deer from South Magnolia (high development) regardless of time of day (Fig. 3). Additionally, deer from North Ridge (low development) selected aspen-conifer habitats more strongly at night than deer from Ryan Gulch (medium-high development; Fig. 3).

South-facing slopes were selected significantly less than other aspects in all study areas during both day and night (all odds ratios >1.0, Fig. 4). Models also indicated that deer selected gentle
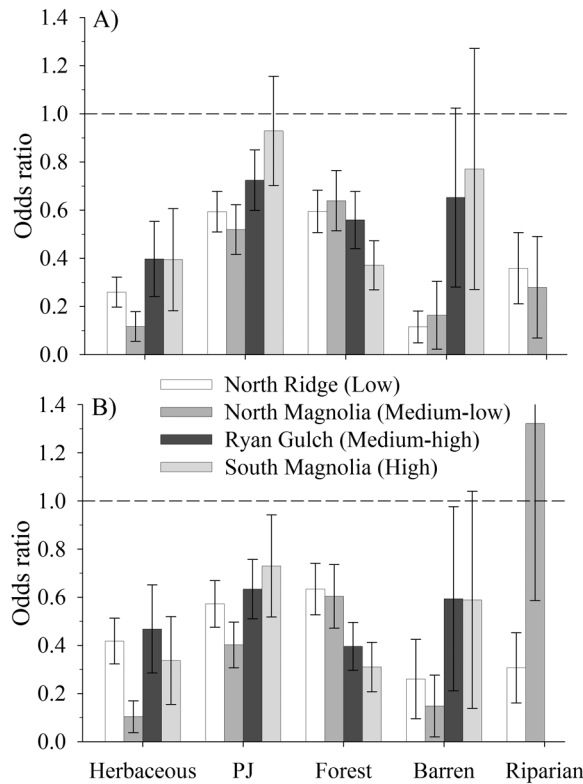
Fig. 3. Odds ratios for grasses (herbaceous), pinyon-juniper (PJ), aspen and conifer (Forest), bare-rocky ground (Barren), and riparian habitat (Riparian) obtained from resource-selection functions for adult female mule deer ($n = 167$) during spring 2008–2010 migration from 4 study areas in the Piceance Basin, northwestern Colorado, USA for day (A) and night (B). Odds ratios indicate the percent change (1 = no change) in odds of use by mule deer for each habitat type relative to sagebrush steppe. Error bars = 95% CI.

slopes and gentle terrain (low VRM) across study areas (all odds ratios <1.0). Selection for elevation, however, varied with respect to study area (Figs. 5, 6). Deer from South Magnolia (high development) showed the greatest response to elevation, with a 13.4% increase in the odds of selection for every 50-m increase in elevation during the day, and a 13.3% increase in odds of selection for every 50-m increase in elevation at night (Figs. 5, 6). Conversely, deer from North Ridge (low development) showed selection for low elevations, with a 7.8% increase in odds of selection for every 50-m decrease in elevation during the day, and a 7.7% increase in odds of

selection for every 50-m decrease in elevation at night.

In the most developed study areas (Ryan Gulch, South Magnolia), female deer selected areas closer to well pads, regardless of time of day (Figs. 5, 6). Deer from Ryan Gulch (medium-high development) selected areas farther from roads (~4.5% increase in odds of selection for every 100-m increase in distance to roads during both day and night), whereas deer from South Magnolia (high development) showed the opposite pattern (≤3.7% decrease in odds of selection for every 100-m increase in distance to roads; Figs. 5, 6). In the least developed study areas (North Ridge, North Magnolia), the only significant effect of roads was for deer from North Ridge (low development), which selected areas further from roads during the day (0.5% decrease in odds of selection for every 100-m increase in distance to roads; Fig. 5).

Cross-validation analyses indicated that resource-selection functions were highly predictive for all study areas except Ryan Gulch (Table 1). Mean slopes of the regression lines were positive for all models, and mean coefficients of determination and Spearman rank correlations were high for all models other than those for Ryan Gulch (Table 1). Lower predictive strength indicated that there was more variability in patterns of selection during spring migration among individual deer, among years, or both, in Ryan Gulch than in the other study areas.

DISCUSSION

We obtained several critical tests of our hypotheses related to patterns of spring migration of adult female mule deer in an area strongly influenced by anthropogenic disturbances. Patterns of resource selection and movement differed between deer that migrated through areas of highest well-pad density and those that migrated through the least-developed areas. Patterns of behavior exhibited by deer that migrated through the sites of intermediate development did not differ from those of deer that migrated through either the highly developed or the least-developed study areas. Consequently, we hypothesize that mule deer may exhibit a threshold response to natural-gas development in which behavior is altered only
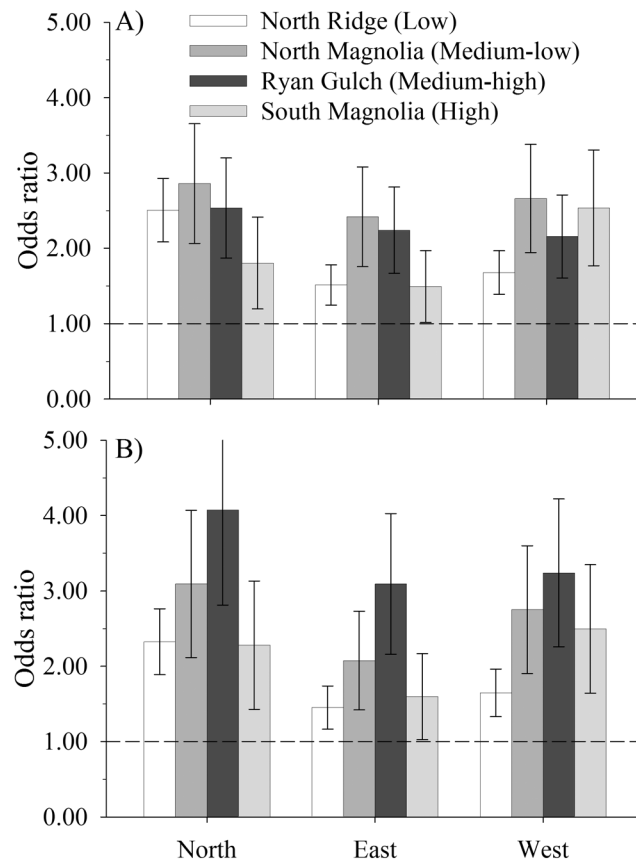
Fig. 4. Odds ratios for north-, east-, and west-facing aspects obtained from resource-selection functions for adult female mule deer ($n = 167$) during spring 2008–2010 migrating from four study areas in the Piceance Basin, northwestern Colorado, USA, for daytime (A) and nighttime (B). Odds ratios indicate the percent change ($1 =$ no change) in odds of use by mule deer for each habitat type relative to south-facing aspects. Error bars $=$ 95% CI.

after a relatively high degree of development occurs on the landscape. Additionally, we hypothesize that the low predictive strength of the resource-selection functions for deer occurring in Ryan Gulch, compared with high predictive strength of models for other areas, likely occurred because some deer captured from Ryan Gulch during the first 2 years of the study ultimately migrated outside of the boundary of the study area.

We hypothesized that step lengths and turning angles would vary with respect to levels of natural-gas development and time of day during which mule deer migrated. As predicted, mule deer migrating thorough the study area of greatest well-pad density had longer step lengths compared with deer migrating through the least-developed areas. Again, however, deer did not

exhibit a difference in behavior when migrating through areas of moderate development (i.e., medium-low and medium-high). Avoidance of disturbed areas, such as those associated with natural-gas development, may affect patterns of migration by causing mule deer to alter rates of movement, potentially increasing energetic costs (sensu Parker et al. 1984). Increased energetic costs at a time when deer are physically stressed (i.e., after sever winters, increased development levels) could potentially lead to decreased survivorship (Parker and Robbins 1984). In addition, Hayes and Krausman (1993) observed that in areas with high levels of human disturbance, patterns of habitat use by female mule deer varied with respect to time of day. We observed longer step lengths for mule deer at night compared with daytime, although contrary to
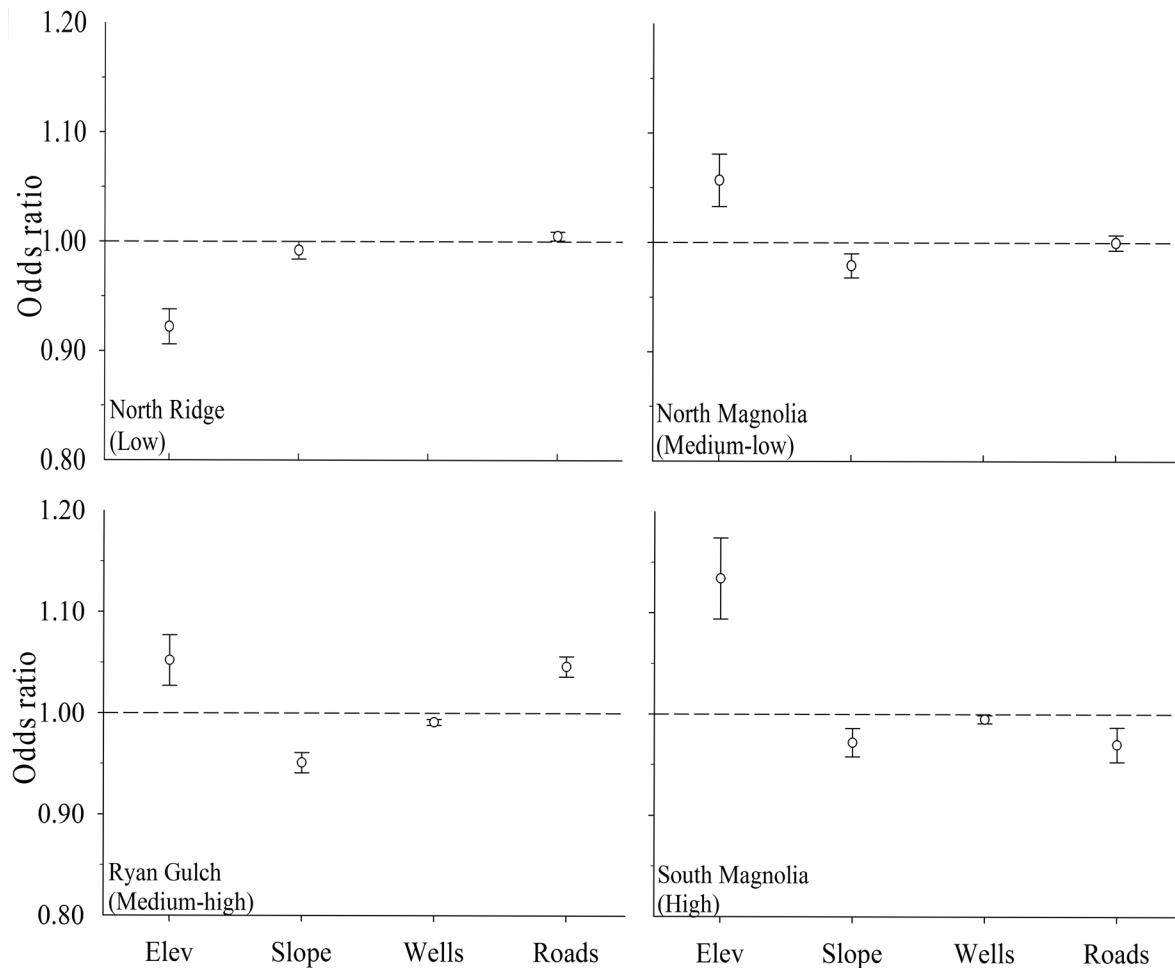
Fig. 5. Daytime odds ratios for elevation (m; Elev), slope (%), terrain ruggedness (VRM), distance to well pads (m; Wells), and distance to roads (m; Roads) obtained from resource-selection functions for adult female mule deer ($n = 167$) during spring 2008–2010 migrating from four study areas in the Piceance Basin, northwestern Colorado, USA. Odds ratios indicate the percent change (1 = no change) in odds of use by mule deer for every 50-m increase in elevation, 1 % increase in slope, change in terrain ruggedness (VRM), and 100-m increase in distance to wells and roads. Error bars = 95% CI.

our prediction, this pattern was observed regardless of development level. Movement rates of cervids often are highest during crepuscular hours and greatly diminished during midday (Bowyer 1981, Beier and McCullough 1990, Ager et al. 2003), which may explain the generality of our results across development levels. Similarly, turning angles did not vary among levels of development or with time of day in our study, resulting in rejection of our third prediction that mule deer in developed areas would travel in a more straight-forward direction compared with

deer in the least-developed study areas.

We also hypothesized that landscape characteristics and human disturbances associated with natural-gas development would influence resource selection by female mule deer along migration routes during spring. Although sage-brush-steppe was the primary habitat selected, we observed that during the day, deer migrating through the highly developed landscapes selected pinyon-juniper habitats more often than deer migrating through the least-developed landscapes. In a shrub-steppe community, scattered
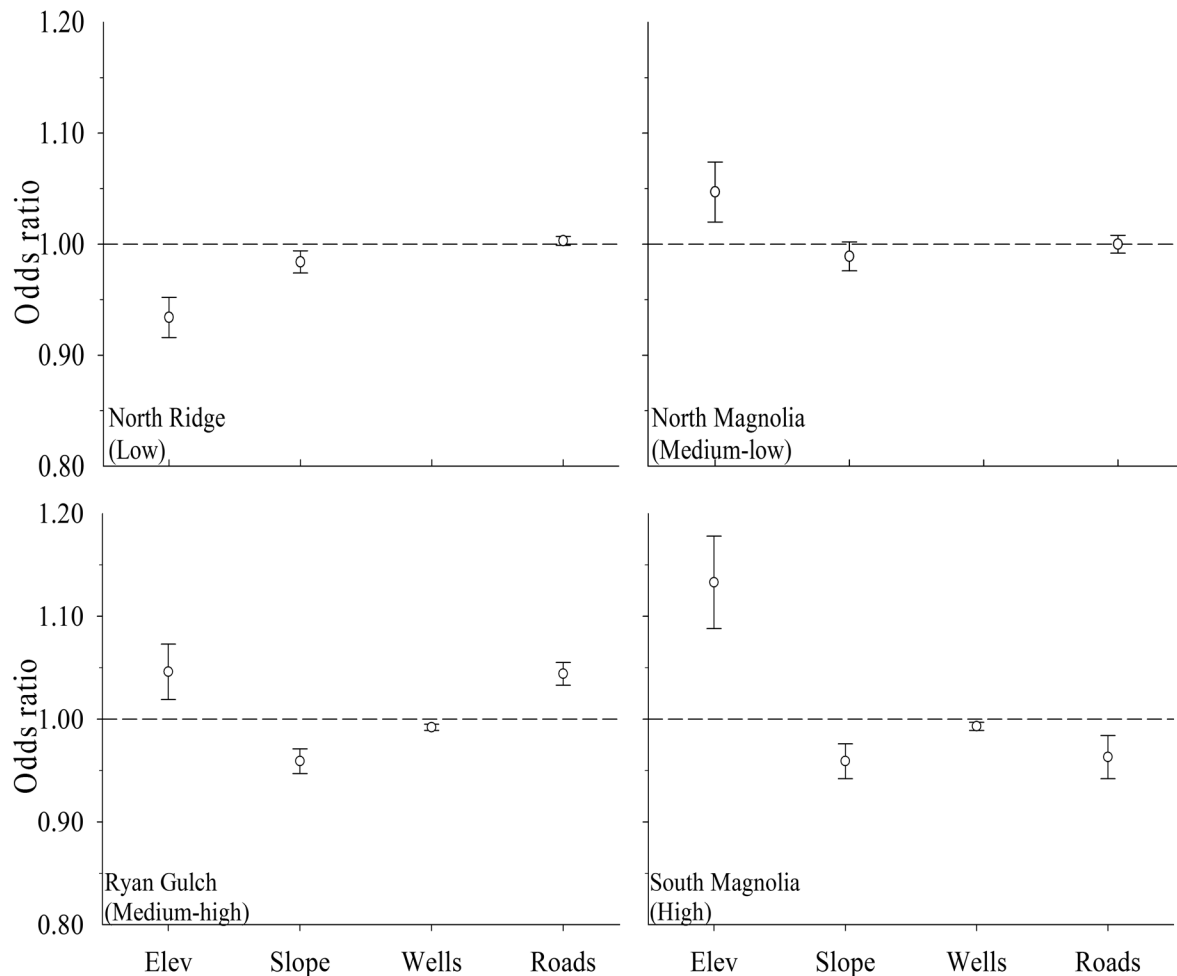
Fig. 6. Nighttime odds ratios for elevation (m; Elev), slope (%), terrain ruggedness (VRM), distance to well pads (m; Wells), and distance to roads (m; Roads) obtained from resource-selection functions for adult female mule deer ($n = 167$) during spring 2008–2010 migration from four study areas in the Piceance Basin, northwestern Colorado, USA. Odds ratios indicate the percent change (1 = no change) in odds of use by mule deer for every 50-m increase in elevation, 1 % increase in slope, change in terrain ruggedness (VRM), and 100-m increase in distance to wells and roads. Error bars = 95% CI.

trees may provide improved microclimates for deer (Parker and Gillingham 1990), or serve as concealment cover from perceived risks (Bowyer 1986). Similarly, McClure et al. (2005) demonstrated that risk, or risk avoidance, was more pronounced with deer living in urban environments, compare with their counterparts living in rural environments. Deer inhabiting urban areas attempted to minimize risks associated with harassment by concentrating in areas with greater concealment cover. Deer were more likely to select for aspen and conifer stands along the

least-developed migration corridors compared with the area of greatest development. Thomas and Irby (1990) observed that deer selected aspen patches that provided cover and nutritious forage during migration. The difference in habitat selection we observed between development levels also could have resulted from the long, continuous forest stands along migration corridors in the least-developed areas, which contrasted with the most-developed areas, where a patch-work mosaic of forest stands resulted in pinyon-juniper being the more accessible cover

Table 1. Cross-validation results for resource-selection functions for spring migration of adult female mule deer ($n = 167$), indicating slope, coefficient of determination (r^2), and Spearman rank correlation (r_s), Piceance Basin, northwestern Colorado, USA, 2008–2010.

Model	Mean		
	Slope	r^2	r_s
North Ridge day	99.71	0.91	0.94
North Ridge night	76.53	0.90	0.92
North Magnolia day	6.36	0.77	0.81
North Magnolia night	3.52	0.79	0.87
Ryan Gulch day	5.11	0.38	0.44
Ryan Gulch night	4.09	0.31	0.52
South Magnolia day	1.49	0.70	0.80
South Magnolia night	3.71	0.75	0.81

type.

Mule deer selected for moderate slopes with less-rugged terrain, but avoided south-facing slopes, across development levels. This result was contrary to our prediction that deer would select south-facing slopes. The use of south and west aspects by mule deer is thought to be associated with higher solar radiation and higher primary production (Bowyer et al. 1998, D'Eon and Serrouya 2005). Nicholson et al. (1997), however, observed that migratory deer selected for north-facing slopes, which had a greater proportion of available water and were further from human disturbance than south-facing slopes. Similarly, Garrott et al. (1987) observed a shift in use from southerly to northerly aspects in April, prior to migration. These observations are comparable to our results, which may be an effect of the relatively dry climate of the Piceance Basin. Ager et al. (2003) observed a change in habitats selected by mule deer towards flatter slopes during the onset of spring, which also was consistent with our observations. Mule deer also selected for higher elevations along migratory routes in all study areas except North Ridge. We suspect this outcome may be a result of increased availability of agriculture fields at lower elevations and the use of a natural travel corridor created by the White River and associated tributaries, which are not present in the migration paths of deer on the other study areas. Agricultural lands consisting of forbs and grain crops can be beneficial to mule deer as newly available vegetation emerges in spring (Garrott et

al. 1987, Stewart et al. 2010, Anderson et al. 2012). Although agricultural fields are present in South Magnolia, the rapid movements observed through that area may preclude deer from using those fields in a similar manner as deer from North Ridge.

Deer selected areas closer to well pads in the most developed areas, which was contrary to our prediction. Our results differ from previous studies in which ungulates have been observed to avoid anthropogenic disturbances (Nicholson et al. 1997, Dyer et al. 2001, Cameron et al. 2005, Sawyer et al. 2006, Singh et al. 2010). For example, Sawyer et al. (2006) observed that, during winter months, mule deer were less likely to occupy areas in close proximity to well pads than those farther away. Additionally, Singh et al. (2010) noted that the location and density of calving aggregations of Saiga antelope (*Saiga tatarica*) also have been affected by human disturbance on spring and summer ranges. During migration, however, ungulates demonstrate a strong fidelity to particular routes (Garrott et al. 1987, Thomas and Irby 1990, Andersen 1991, Sawyer et al. 2009*b*, Sawyer and Kauffman 2011). In addition, although migration routes often include stopover sites (Sawyer et al. 2009*b*, Sawyer and Kauffman 2011), in the Piceance Basin migration was rapid and traditional stopovers did not occur. Perhaps such fidelity and the rapid rate at which migrations occurred in the Piceance Basin (median spring migration periods = 3-8 days), overrode the behavioral response to avoid anthropogenic disturbances. The unprecedented rates of natural-gas development in the Piceance Basin and other areas throughout the Intermountain West may not allow deer sufficient time to adapt and alter their behaviors.

Deer often are observed thriving in areas of human development, such as residential environments. Natural-gas development may disturb deer more than residential development, because once residential neighborhoods are established they are relatively permanent, which may allow deer sufficient time to acclimate. Natural-gas developments, however, are constantly changing in nature and intensity. In the Piceance Basin, development first began in what is now the highly developed study area, and while acclimation is a possible explanation for the lack of

avoidance, without pre-development data this possibility cannot be addressed directly. Sawyer et al. (2006) noted that changes in habitat selection appeared to be immediate, with no evidence of well-pad acclimation occurring over the 3 years during which their study took place. Furthermore, mule deer selected areas further from well pads as development progressed (Sawyer et al. 2006). The Pinedale Anticline, Wyoming, USA, however, is a very different landscape than the Piceance Basin. Deer do not have concealment cover on the Anticline because of wide open, flat, sagebrush winter range versus the topographic and vegetative diverse conditions present in the Piceance Basin, and these conditions may have minimized deer behavioral responses as development progressed.

Within the most developed study areas, mule deer avoided roads along migration routes in the moderately developed sectors, while selecting areas closer to roads in sectors of higher development. We hypothesize that deer may avoid high-traffic areas if they can do so without greatly altering their migration routes. If development levels are too great, however, deer may not have the option of avoiding roads (Wagner et al. 2011). Storm et al. (2007) suggested that in areas with high levels of human development, such as suburban environments, the ability for deer to exhibit an avoidance of anthropogenic disturbances may be diminished because of such uniform and wide-spread disturbance. Our hypothesis is further supported by deer also avoiding roads along migration routes that passed nearest the town of Meeker, where vehicle traffic was moderate, and slight alterations in patterns of movement allowed for avoidance of traffic without greatly altering migration routes. Disturbance caused by humans may be analogous to predation risk (Berger et al. 1983, Frid and Dill 2002). The risk-disturbance hypothesis postulates that animal responses should track disturbance stimuli, with responses being stronger when perceived risk is greater (Frid and Dill 2002). Our results support that hypothesis, including deer selecting concealment cover in the most developed area.

Interspecific competition with North American elk also might explain behavioral responses of mule deer during migration. Mule deer demonstrate strong avoidance of elk (Johnson et al. 2000, Stewart et al. 2002, Long et al. 2008, Stewart et al. 2010), and elk occur in large herds throughout the Piceance Basin (White et al. 2001). In addition, elk tend to avoid roads and other human activities (Johnson et al. 2000, Stewart et al. 2002, Ager et al. 2003, Long et al. 2008). If mule deer are displaced because of interference or exploitive competition, mule deer would be expected to distribute themselves into lower-quality habitats, which might result in deer using areas closer to roads to avoid elk.

As the intensity of human land use increases, so does the potential for disruption of important migration routes (Thomas and Irby 1990). Anthropogenic disturbances may affect wildlife via direct and indirect mortality, habitat loss, or by altering behavior (Trombulak and Frissell 2000, Sawyer et al. 2006). The need for effective conservation of migration routes of mammals necessitates a more complete understanding of the biology of this complex behavior (Bolger et al. 2008, Wilcove 2008, Monteith et al. 2011). Results of this study have broad implications for the conservation of mammals that make long-distance migratory movements. For example, the ability of long-distance migrators to avoid anthropogenic disturbance may depend, in part, on the degree to which they would be required to alter their traditional migratory paths to do so. Furthermore, faster rates of movement through more highly developed areas may impose additional energetic costs if, for example, the ability of females to take advantage of ideal forage conditions along migratory routes is reduced (Sawyer et al. 2009b, Sawyer and Kauffman 2011). The ability of herbivores to track phenological progression of newly emergent vegetation across the landscape is of particular importance to pregnant females attempting to supporting the increased demands of late gestation (Parker et al. 2009). Understanding factors affecting movements between seasonal ranges can be critical for biologists to sustain viable populations of these large migratory ungulates (Berger 2004, Sawyer et al. 2005). As anthropogenic development increases, biologists must balance the need for human expansion with maintenance of healthy populations of mammals. Improved understanding of responses of mammals to development activities could allow landscape alterations to be manipulated to maintain neces-

sary behaviors (i.e., migration, foraging, parturition), while still allowing infrastructure development for human benefits.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Descriptive statistics of the continuous variables included in the conditional logistic-regression models of resource-selection functions by female mule deer (167 deer, 6,433 used locations; 64,330 random locations) by study area, during spring migration in the Piceance Basin, northwestern Colorado, USA, 2008–2010.

Variable and Study area	Used locations				Random locations			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Elevation (m)								
North Ridge	2,158.94	184.20	1,764.38	2,795.23	2,261.61	266.30	1,721.67	3,344.86
North Magnolia	2,297.23	148.20	1,912.75	2,838.41	2,300.51	253.50	1,757.44	3,428.61
Ryan Gulch	2,269.04	172.40	1,871.76	2,799.31	2,255.67	207.70	1,511.37	3,075.65
South Magnolia	2,314.25	169.90	1,915.48	2,745.73	2,269.74	214.00	1,520.88	2,812.14
Slope (%)								
North Ridge	11.21	6.80	0.09	39.38	12.66	8.10	0.00	50.50
North Magnolia	11.86	7.30	0.13	40.22	13.18	8.30	0.00	62.58
Ryan Gulch	10.91	6.90	0.03	36.63	14.04	8.90	0.00	63.26
South Magnolia	11.96	6.80	0.01	34.67	15.45	9.50	0.00	69.88
Terrain ruggedness								
North Ridge	0.07	0.13	0.00	0.88	0.07	0.13	0.00	0.97
North Magnolia	0.08	0.14	0.00	0.96	0.08	0.14	0.00	0.96
Ryan Gulch	0.09	0.10	0.00	0.87	0.10	0.15	0.00	0.93
South Magnolia	0.09	0.10	0.00	0.84	0.10	0.15	0.00	0.97
Distance to well pads (m)								
North Ridge	17,329.86	13,864.40	604.31	89,412.57	23,413.54	19,730.00	0.00	95,251.58
North Magnolia	9,122.54	10,165.20	195.85	73,566.37	16,294.64	15,908.00	0.00	80,021.54
Ryan Gulch	3,104.30	3,581.60	45.32	33,431.44	3,712.87	4,899.90	0.00	39,264.85
South Magnolia	3,362.08	2,866.80	64.71	22,523.16	5,379.02	5,806.00	0.00	30,231.00
Distance to roads (m)								
North Ridge	1,592.32	1,136.00	2.11	8,116.62	1,718.93	1,449.00	0.00	7,966.56
North Magnolia	1,181.47	1,121.60	0.36	5,606.49	1,298.99	1,217.30	0.00	7,150.39
Ryan Gulch	752.15	840.10	1.42	6,801.27	609.19	866.00	0.00	6,730.35
South Magnolia	440.82	639.60	0.67	6,467.18	829.16	1,145.40	0.00	6,667.89

Appendix B

Table B1. Percentage of available habitat (64,330 random locations), by study area, occurring in each of the 7 habitat types and 4 aspect categories included in the conditional logistic regression models of resource-selection functions by female mule deer during spring migration in the Piceance Basin, northwestern Colorado, USA, 2008–2010.

Variables	Study area			
	North Ridge	North Magnolia	Ryan Gulch	South Magnolia
Habitat				
Herbaceous	8.32	3.24	2.42	1.43
Sage-steppe	39.40	40.10	41.16	41.03
PJ	17.31	21.57	31.51	26.37
Forest	32.33	29.68	20.21	24.97
Barren	1.05	1.11	2.14	2.67
Riparian	1.60	0.98	0.13	0.22
Aspect				
North	27.52	24.63	21.17	19.38
East	24.42	26.28	31.48	28.95
South	18.21	16.74	15.41	17.10
West	29.85	32.35	31.94	34.56