

Winter Habitat Selection of Mule Deer Before and During Development of a Natural Gas Field

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Abstract

Increased levels of natural gas exploration, development, and production across the Intermountain West have created a variety of concerns for mule deer (*Odocoileus hemionus*) populations, including direct habitat loss to road and well-pad construction and indirect habitat losses that may occur if deer use declines near roads or well pads. We examined winter habitat selection patterns of adult female mule deer before and during the first 3 years of development in a natural gas field in western Wyoming. We used global positioning system (GPS) locations collected from a sample of adult female mule deer to model relative frequency or probability of use as a function of habitat variables. Model coefficients and predictive maps suggested mule deer were less likely to occupy areas in close proximity to well pads than those farther away. Changes in habitat selection appeared to be immediate (i.e., year 1 of development), and no evidence of well-pad acclimation occurred through the course of the study; rather, mule deer selected areas farther from well pads as development progressed. Lower predicted probabilities of use within 2.7 to 3.7 km of well pads suggested indirect habitat losses may be substantially larger than direct habitat losses. Additionally, some areas classified as high probability of use by mule deer before gas field development changed to areas of low use following development, and others originally classified as low probability of use were used more frequently as the field developed. If areas with high probability of use before development were those preferred by the deer, observed shifts in their distribution as development progressed were toward less-preferred and presumably less-suitable habitats. (JOURNAL OF WILDLIFE MANAGEMENT 70(2):396–403; 2006)

Key words

generalized linear model (GLM), Global Positioning System (GPS), habitat selection, mule deer, natural gas development, negative binomial, *Odocoileus hemionus*, resource selection probability function (RSPF), Wyoming.

Natural gas development on public lands in Wyoming has steadily increased since 1984 (Bureau of Land Management 2002) and created much concern over potential impacts to wildlife. Public lands with high gas potential often coincide with regions of Wyoming that support large mule deer (*Odocoileus hemionus*) populations, such as the Green River Basin (Bureau of Land Management 2000a), Great Divide Basin (Bureau of Land Management 2000b), and Powder River Basin (Bureau of Land Management 2003). Impacts of natural gas development on mule deer may include the direct loss (i.e., surface disturbance) of habitat to well pad, access road, and pipeline construction. Additional indirect habitat losses may occur if increased human activity (e.g., traffic, noise) associated with infrastructure cause mule deer to be displaced or alter their habitat use patterns. Although it is relatively easy to quantify the direct habitat losses that result from conversion of native vegetation to infrastructure, it is much more difficult to document indirect habitat losses. Nonetheless, because indirect impacts can affect a substantially larger area than direct impacts, understanding them may be a key component to maintaining mule deer seasonal ranges and populations in regions with high levels of natural gas development. Accordingly, there is a need among land management and wildlife agencies to better understand how natural gas development can lead to indirect habitat loss to ensure informed land-use decisions are made, reasonable and effective mitigation measures identified, and appropriate monitoring programs implemented. Our objective was to determine whether natural gas development

affected the habitat selection patterns and, thus, distribution of wintering mule deer in western Wyoming.

Study Area

Beginning in 2000, the Bureau of Land Management (BLM) approved the construction of 700 producing well pads, 645 km of pipeline, and 444 km of roads to develop a natural gas field in the Pinedale Anticline Project Area (PAPA; Bureau of Land Management 2000a). The PAPA contains one of the largest and highest density (19 to 30 deer/km²) mule deer winter ranges in Wyoming (S. Smith, Wyoming Game and Fish Department, Cheyenne, Wyo., USA, unpublished data). The PAPA is located in the upper Green River Basin of western Wyoming, approximately 5 km southwest of Pinedale. The PAPA consists primarily of federal lands (80%) and minerals administered by the BLM (83%). The state of Wyoming owns 5% (39 km²) of the surface and another 15% (121 km²) is private (Bureau of Land Management 2000a). The study area contains abundant deep gas reserves, supports a variety of agricultural uses, and provides winter range for 4,000 to 5,000 migratory mule deer that summer in portions of 4 different mountain ranges 80 to 200 km away (Sawyer and Lindzey 2001). Although the PAPA covers 799 km², most mule deer wintered in the northern one-third, an area locally known as the Mesa. The Mesa is 260 km² in size, bounded by the Green River on the west and the New Fork River on the north, south, and east, and vegetated primarily by Wyoming big sagebrush (*Artemisia tridentata*) and sagebrush-grassland communities. Elevation ranges from 2,070 to 2,400 m. Our study was restricted to the Mesa portion of the PAPA.

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Methods

Capture

We captured adult (≥ 1 year) female mule deer using helicopter net-gunning in the northern portion of the PAPA where deer congregated in early winter before moving to their individual winter ranges throughout the Mesa (Sawyer and Lindzey 2001). We believed attempting to randomly capture deer in this area during early winter provided the best opportunity to achieve a representative sample from the wintering population. In years before development (winters 1998–1999 and 1999–2000), we fitted deer with standard, very high frequency (VHF) radio collars (Advanced Telemetry Systems, Isanti, Minnesota). We located radio-collared deer from the ground or air every 7 to 10 days during the 1998–1999 and 1999–2000 winters (1 Dec to 31 Mar). During years of gas field development (winters 2000–2001, 2001–2002, and 2002–2003), we fitted deer with store-on-board global positioning system (GPS) radio collars (Telonics, Inc., Mesa, Arizona) equipped with VHF transmitters and remote-release mechanisms programmed to release at specified dates and times. We fitted GPS radio collars to a sample of different deer each winter; however, 3 deer had collars that collected GPS locations for both the 2001–2002 and 2002–2003 winters. We programmed GPS radio collars to attempt location fixes every 1 or 2 hrs, depending on model type. We did not differentially correct GPS locations because 3-dimensional fixes typically have < 20 m error (Di Orio et al. 2003), and previous work in the study area indicated 99% fix-rate success with 80% of successful fixes 3-dimensional locations (Sawyer et al. 2002). Potential fix-rate bias was not a concern because of the high fix-rate success of the GPS collars.

Modeling Procedures

Defining availability.—We defined the study area by mapping 39,641 locations from 77 mule deer over a 6-year period (1998 to 2003), creating a minimum convex polygon (MCP), and then clipping the MCP to the boundary of the PAPA. This was consistent with the McClean et al. (1998) recommendation that the study-area level of habitat availability should be based on the distribution of radio-collared animals.

Habitat variables.—We identified 5 variables as potentially important predictors of winter mule deer distribution, including elevation, slope, aspect, road density, and distance to well pad. We did not include vegetation as a variable because the sagebrush-grassland was relatively homogeneous across the study area and difficult to divide into finer vegetation classes. Further, we believed differences in sagebrush characteristics could be largely explained by elevation, slope, and aspect. We used the SPATIAL ANALYST extension for ArcView (Environmental Systems Research Institute, Redlands, California) to calculate slope and aspect from a 26×26 -m digital elevation model (U.S. Geologic Survey 1999). Grid cells with slopes > 2 degrees were assigned to 1 of 4 aspect categories: northeast, northwest, southeast, or southwest. Grid cells with slopes of ≤ 2 degrees were considered flat and assigned to a fifth category that was used as the reference (Neter et al. 1996) during habitat modeling. We obtained elevation, slope, and aspect values for each of the sampled units using the GET GRID extension for ArcView. The sample units consisted of approximately 4,500 circular units with 100-m radii

distributed across the study area. We annually digitized roads and well pads from LANDSAT thematic satellite images acquired from the U.S. Geologic Survey and processed by SkyTruth (Shepherdstown, West Virginia). The LANDSAT images were obtained every fall, before snow accumulation, but after most annual development activities were complete. We calculated road density by placing a circular buffer with a 0.5-km radius on the center of the sample unit and measuring the length of road within the buffer. We used the NEAREST NEIGHBOR extension for ArcView to measure the distance from the center of each sampled unit to the edge of the nearest well pad. We did not distinguish between developing and producing well pads. We assumed habitat loss was similar among all well pads because development of the field was in its early stages (i.e., < 5 years), and there was no evidence of successful shrub reclamation. Additionally, there was no evidence that suggested the type of well pad was an accurate indicator of the amount of human activity (e.g., traffic) that occurred at each site. Without an accurate measure of human activity, we believed it was inappropriate to distinguish between producing and developing well pads.

Statistical analyses.—Our approach to modeling winter habitat use consisted of 4 basic steps: 1) estimate the relative frequency of use (i.e., an empirical estimate of probability of use) for a large sample of habitat units for each radiocollared deer, during each winter; 2) use the relative frequency as the response variable in a multiple regression analysis to model the probability of use for each deer as a function of predictor variables; 3) develop a population-level model from the individual deer models, for each winter; and 4) map predictions of population-level models from each winter. Our analysis treated each winter period separately to allow mule deer habitat use and environmental characteristics (e.g., road density or number of well pads) to change through time. We treated radiocollared deer as the experimental unit to avoid pseudo-replication (i.e., spatial and temporal autocorrelation) and to accommodate population-level inference (Otis and White 1999, Johnson et al. 2000, Erickson et al. 2001).

We estimated relative frequency of use for each radio-collared deer using a simple technique that involved counting the number of deer locations in each of approximately 4,500 randomly sampled, circular habitat units across the study area. We took a simple random sample with replacement for each winter to ensure independence of the habitat units (Thompson 1992:51). We chose circular habitat units that had a 100-m radii; an area small enough to detect changes in animal movements but large enough to ensure multiple locations could occur in each unit. Previous analyses suggested model coefficients were similar across a variety of unit sizes, including 50, 75, and 150-m radii (R. Nielson, Western Ecosystems Technology, Inc., Cheyenne, Wyo., USA, unpublished data). We measured predictor variables on each of the sampled habitat units and conducted a Pearson's pairwise correlation analysis (PROC CORR; SAS 2000) before modeling to identify multicollinearities and to determine whether any variables should be excluded from the modeling ($|\tau| > 0.60$).

The relative frequency of locations from a radio-collared deer found in each habitat unit was an empirical estimate of the probability of use by that deer and was used as a continuous response variable in a generalized linear model (GLM). We used

an offset term (McCullagh and Nelder 1989) in the GLM to estimate probability of use for each radiocollared deer as a function of a linear combination of predictor variables, plus or minus an error term assumed to have a negative binomial distribution (McCullagh and Nelder 1989, White and Bennetts 1996). We preferred the negative binomial distribution over the more commonly used Poisson because it allows for overdispersion (White and Bennetts 1996).

We obtained a population-level model for each winter by first estimating coefficients for each radiocollared deer. We used PROC GENMOD (SAS 2000) and the negative binomial distribution to fit the following GLM for each radiocollared deer during each winter period:

$$\ln[E(r_i)] = \ln(total) + \beta_0 + \beta_1 X_1 + \dots + \beta_p X_p, \quad (1)$$

which is equivalent to

$$\ln[E(r_i/total)] = \ln[E(\text{Relative frequency}_i)] = \beta_0 + \beta_1 X_1 + \dots + \beta_p X_p \quad (2)$$

where r_i is the number of locations for a radio-collared deer within habitat unit i ($i = 1, 2, \dots, 4,500$), $total$ is the total number of locations for the deer within the study area, β_0 was an intercept term, β_1, \dots, β_p are unknown coefficients for habitat variables X_1, \dots, X_p , and $E(\cdot)$ denotes the expected value. We used the same offset term for all sampled habitat units of a given deer, thus the term $\ln(total)$ was absorbed into the estimate of β_0 and ensured we were modeling relative frequency of use (e.g., 0, 0.003, 0.0034, ...) instead of integer counts (e.g., 0, 1, 2, ...). Because some locations for each deer were not within a sampled habitat unit, inclusion of the offset term in Eq. (1) was not equivalent to conditioning on the total number of observed locations (i.e., multinomial distribution). In fact, one could drop the offset term and simply scale the resulting estimates of frequency of use by the total number of observed locations to obtain predictions of relative frequency identical to those obtained by Eq. (1). This approach to modeling resource selection estimates the relative frequency or absolute probability of use as a function of predictor variables, so we refer to it as a resource selection probability function (RSPF; Manly et al. 2002).

We assumed GLM coefficients for predictor variable k , for each deer, were a random sample from a normal distribution (Seber 1984, Littell et al. 1996), with the mean of the distribution representing the average or population-level effect of predictor variable k on probability of use. We estimated coefficients for the population-level RSPF for each winter using

$$\hat{\beta}_k = \frac{1}{n} \sum_{j=1}^n \hat{\beta}_{kj}, \quad (3)$$

Where $\hat{\beta}_{kj}$ was the estimate of coefficient k for individual j ($j = 1, \dots, n$). We estimated the variance of each population-level model coefficient using the variation between radiocollared deer and the equation

$$\text{var}(\hat{\beta}_k) = \frac{1}{n-1} \sum_{j=1}^n (\hat{\beta}_{kj} - \bar{\beta}_k)^2. \quad (4)$$

This method of estimating population-level coefficients using Eqs. (3) and (4) was used by Marzluff et al. (2004) and Glenn et

al. (2004) for evaluating habitat selection of Steller's jays (*Cyanocitta stelleri*) and northern spotted owls (*Strix occidentalis caurina*), respectively. Population-level inferences using Eqs. (3) and (4) are unaffected by potential autocorrelation because temporal autocorrelation between deer locations or spatial autocorrelation between habitat units do not bias model coefficients for the individual radiocollared deer models (McCullagh and Nelder 1989, Neter et al. 1996).

Standard criteria for model selection such as Akaike's Information Criterion (Burnham and Anderson 2002) might be appropriate for individual deer but do not apply for building a model for population-level effects because the same model (i.e., predictor variables) is required for each deer within a winter. Therefore, we used a forward-stepwise model-building procedure (Neter et al. 1996) to estimate population-level RSPFs for winters 2000–2001, 2001–2002, and 2002–2003. The forward-stepwise model-building process required fitting the same models to each deer within a winter and using Eqs. (3) and (4) to estimate population-level model coefficients. We used a t -statistic to determine variable entry ($\alpha \leq 0.15$) and exit ($\alpha > 0.20$; Hosmer and Lemeshow 2000). We considered quadratic terms for road density, distance to nearest well pad, and slope during the model-building process and following convention, the linear form of each variable was included if the model contained a quadratic form.

We conducted stepwise model building for all winters except for the predevelopment period that included winters 1998–1999 and 1999–2000. The limited number of locations recorded for radiocollared deer during that period precluded fitting individual models. Rather, we estimated a population-level model for the predevelopment period by pooling location data across 45 deer that had a minimum of 10 locations. We took simple random samples of 30 locations from deer with >30 locations to ensure that approximately equal weight was given to each deer in the analysis. We fit a model containing slope, elevation, distance to roads, and aspect for the predevelopment period. Distance to well pad was not included as a variable in the predevelopment model because there were only 11 existing well pads on the Mesa before development, and most were >10 years old, with little or no human activity associated with them. We used bootstrapping to estimate the standard errors and P values of the predevelopment population-level model coefficients.

We mapped predictions of population-level RSPFs for each winter on 104×104 -m grids that covered the study area. We checked predictions to ensure all values were in the $[0,1]$ interval, such that we were not extrapolating outside the range of the model data (Neter et al. 1996). The estimated probability of use for each grid cell was assigned a value of 1 to 4 based on the quartiles of the distribution of predictions for each map. We assigned grid cells with the highest 25% of predicted probabilities of use a value of 1 and classified them as high-use areas, assigned grid cells in the 51 to 75 percentiles a value of 2 and classified them as medium- to high-use areas, assigned grid cells in the 26 to 50 percentiles a value of 3 and classified them as medium- to low-use areas, and assigned grid cells in the 0 to 25 percentiles a values of 4 and classified them as low-use areas. We used contingency tables to identify changes in the 4 habitat-use categories across the 4 winter periods.

Results

Predevelopment: Winters 1998–1999 and 1999–2000

The population-level RSPF was estimated from 953 VHF deer locations collected from 45 adult female mule deer during the winters (1 Dec to 15 Apr) of 1998–1999 and 1999–2000 (Table 1). Units with the highest probability of use (Fig. 1) had an average elevation of 2,275 m, an average slope of 5 degrees, and an average road density of 0.14 km/km². Aspects with the highest probability of use were northwest and southwest.

Year 1 of Development: Winter 2000–2001

Individual models were estimated for 10 radiocollared deer during the winter (1 Jan to 15 Apr) of 2000–2001. Eight of the 10 deer had positive coefficients for elevation and negative coefficients for road density, indicating selection for higher elevations and low road densities. Based on the relationship between the linear and quadratic terms for slope and distance-to-well-pad variables, all 10 deer selected for moderate slopes, and 7 of 10 deer selected areas away from well pads.

The population-level RSPF was estimated from 18,706 GPS locations collected from 10 radiocollared deer during the winter of 2000–2001 (Table 1). The RSPF included elevation, slope, road density, and distance to well pad (Table 1). Deer selected for areas with higher elevations, moderate slopes, low road densities, and away from well pads. Habitat units with the highest probability of use (Fig. 2) had an average elevation of 2,266 m, slope of 5 degrees, road density of 0.16 km/km², and were 2.7 km away from the nearest well pad. Predictive maps indicate probability of deer use was lowest in areas close to well pads and access roads (Fig. 2). Shifts in deer distribution between predevelopment and year 1 of development were evident through the changes in the 4 deer use categories (Table 2). Of the habitat units classified as high deer use before development, only 60% were classified as high deer use during year 1 of development (Table 2). Of the areas classified as low deer use before development, 58% remained classified as low deer use during year 1 of development (Table 2).

Year 2 of Development: Winter 2001–2002

Individual models were developed for 15 radiocollared deer during the winter (4 Jan to 15 Apr) of 2001–2002. Fourteen of the 15

deer had positive coefficients for elevation, indicating selection of higher elevations. Based on the relationship between the linear and quadratic terms for slope and distance-to-well-pad variables, all 15 deer selected for moderate slopes, and 12 of 15 deer selected areas away from well pads.

The population-level RSPF was estimated from 14,851 GPS locations collected from 15 radiocollared deer during the winter of 2001–2002 (Table 1). The RSPF included elevation, slope, and distance to well pad (Table 1). Deer selected for areas with higher elevations, moderate slopes, and away from well pads. Habitat units with the highest probability of use (Fig. 3) had an average elevation of 2,255 m, slope of 5 degrees, and were 3.1 km away from the nearest well pad. Predictive maps indicate probability of deer use was lowest in areas close to well pads (Fig. 3). Shifts in deer distribution between predevelopment, year 1, and year 2 of development were evident through the changes in the 4 deer-use categories (Table 2). Of the habitat units classified as high deer use before development, only 49% were classified as high deer use during year 2 of development (Table 2). Of the areas classified as low deer use before development, 48% remained classified as low deer use during year 2 of development (Table 2).

Year 3 of Development: Winter 2002–2003

Individual models were developed for 7 radiocollared deer during the winter (20 Dec to 15 Apr) of 2002–2003. All 7 deer had positive coefficients for elevation, indicating selection of higher elevations. Based on the relationship between the linear and quadratic terms for slope and distance-to-well-pad variables, 6 of 7 deer selected for moderate slopes, and 6 of 7 deer selected areas away from well pads.

The population-level RSPF was estimated from 4,904 GPS locations collected from 7 radiocollared deer during the winter of 2002–2003 (Table 1). Our target sample of 10 marked animals was not met because 3 deer died early in the season. The RSPF included elevation, slope, and distance to well pad (Table 1). Deer selected areas with high elevations, moderate slopes, and away from well pads. Habitat units with the highest probability of use (Fig. 4) had an average elevation of 2,233 m, slope of 5 degrees, and were 3.7 km away from the nearest well pad. Predictive maps indicate probability of deer use was lowest in areas close to well

Table 1. Coefficients for population-level winter mule deer resource selection probability functions (RSPF) before and during 3 years of natural gas development in western Wyo., USA, 1998–2003.

	Predevelopment			Year 1			Year 2			Year 3		
	β	SE	P	β	SE	P	β	SE	P	β	SE	P
Intercept	-29.649	6.637	<0.001	-84.560	21.124	0.003	-75.712	12.931	<0.001	-104.295	11.316	<0.001
Elevation	0.009	0.001	<0.001	0.031	0.008	0.005	0.027	0.005	<0.001	0.036	0.004	<0.001
Slope	0.098	0.010	<0.001	0.391	0.073	<0.001	0.258	0.046	<0.001	0.342	0.128	0.036
Slope ²	-0.004	0.001	<0.001	-0.022	0.004	<0.001	-0.017	0.003	<0.001	-0.019	0.007	0.042
Well distance	na ^a			3.129	1.899	0.134	3.375	1.264	0.018	6.712	2.394	0.031
Well distance ²	na			-0.465	0.229	0.073	-0.416	0.156	0.019	-0.719	0.289	0.047
Road density	-0.249	0.027	<0.001	-0.827	0.387	0.061	ns ^b			ns		
Aspect =↖NE	0.012	0.051	0.818	ns			ns			ns		
Aspect =↖NW	0.399	0.025	<0.001	ns			ns			ns		
Aspect =↖SE	-0.301	0.022	<0.001	ns			ns			ns		
Aspect =↖SW	0.194	0.028	<0.001	ns			ns			ns		

^a Not applicable.

^b Not significant.

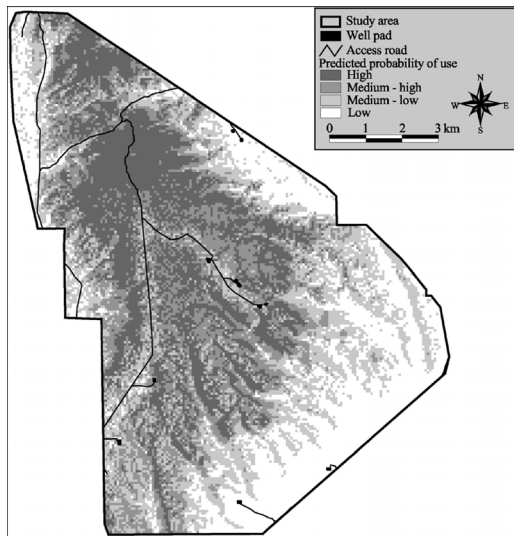


Figure 1. Predicted probabilities and associated categories of mule deer habitat use during 1998–1999 and 1999–2000 winters, before natural gas field development in western Wyo., USA.

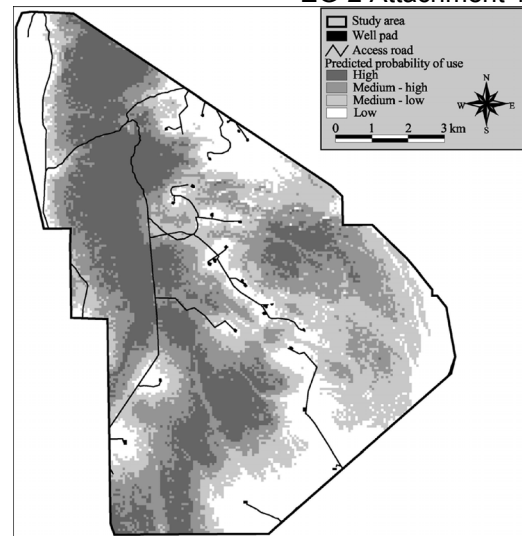


Figure 2. Predicted probabilities and associated categories of mule deer habitat use during year 1 (winter of 2000–2001) of natural gas development in western Wyo., USA.

pads (Fig. 4). Shifts in deer distribution between predevelopment, year 1, year 2, and year 3 of development were evident through the changes in the 4 deer-use categories (Table 2). Of the habitat units classified as high deer use before development, only 37% were classified as high deer use during year 3 of development (Table 2). Of the areas classified as low deer use before development, 41% remained classified as low deer use during year 3 of development (Table 2).

Discussion

Our statistical analysis differs from the typical methods used in the study of habitat selection (Manly et al. 2002) in several important ways. First, our sample size was the number of radiocollared deer during each winter, and our objective was to make statistical inferences to the corresponding population in the study area. Thus, we assumed that our radiocollared deer represented a simple random sample from the population each winter. Second, our response variable was an empirical estimate of the probability of use of a habitat unit, or the volume under an animal's utilization distribution surface. And third, we used a stepwise model-building procedure to develop a population-level model from individual deer models, where the average of the coefficients across deer comprised the population-level model for each winter period.

We recognize that other techniques may be used to estimate population-level models. Random-coefficients or hierarchical models (Littell et al. 1996) can estimate individual and population-level coefficients; however, model convergence can be problematic. To date, we believe the most appropriate method to obtain a population-level model is to fit a GLM with negative binomial errors to each radiocollared deer and average the coefficients. Seber (1984:486) describes this estimator and notes that identical population-level coefficients can be obtained if one averages the relative frequency of use in each of the sampled habitat units and fits a single model. We prefer to estimate individual models because the variation among individuals is often of biological interest.

We would have preferred the use of GPS radio collars during all years of this study because they can systematically collect thousands of accurate deer locations, regardless of weather conditions or time of day. Although the VHF radio collar locations used for the predevelopment model were collected at irregular intervals and during daylight hours, we believe the resulting model provides a reasonable comparison to models estimated during years of development with GPS radio collar locations. Hayes and Krausman (1993) suggested diurnal use of habitats by female mule deer were representative of overall patterns of habitat use, except in areas with high levels of human disturbance. Because human activity was exceptionally low on the Mesa before development, we believe the 953 VHF locations collected from 45 radiocollared deer accurately reflect overall deer use during that time period.

We view our resource selection analysis as an objective means to document mule deer response to natural gas development and quantify indirect habitat losses through time. Although indirect impacts associated with human activity or development have been documented in elk (*Cervus elaphus*; Lyon 1983, Morrison et al. 1995, Rowland et al. 2000), data that suggest similar behavior in mule deer (Rost and Bailey 1979, Yarmaloy et al. 1988, Merrill et al. 1994) are limited and largely observational in nature. Specific knowledge of how, or whether, mule deer respond to natural gas development does not exist in the literature. Our results suggest winter habitat selection and distribution patterns of mule deer were affected by well pad development. Changes in habitat selection by mule deer appeared to be immediate (i.e., year 1 of development), and through 3 years of development, we found no evidence they acclimated or habituated to well pads. Rather, mule deer had progressively higher probability of use in areas farther away from well pads as development progressed. The nonlinear relationship between probability of deer use and distance to well pad indicates deer selected areas away from well pads, but only up to a certain distance. We believe this reflects the ability of mule

Table 2. Percent change in the 4 predevelopment deer-use categories through 3 years (2001–2003) of natural gas development in western Wyo., USA.

Predevelopment category ^a	Year of development	Deer use category			
		High	Medium-high	Medium-low	Low
High	Year 1	60%	23%	13%	4%
	Year 2	49%	19%	23%	9%
	Year 3	37%	22%	27%	14%
Medium-high	Year 1	31%	36%	22%	11%
	Year 2	34%	23%	25%	18%
	Year 3	27%	22%	28%	22%
Medium-low	Year 1	9%	34%	31%	26%
	Year 2	16%	35%	25%	25%
	Year 3	25%	27%	25%	23%
Low	Year 1	0%	7%	34%	58%
	Year 2	1%	23%	27%	48%
	Year 3	11%	29%	20%	41%

^a Category rows may not sum to exactly 100% because of rounding error.

deer to avoid localized disturbances and habitat perturbations without completely abandoning their home ranges.

Population-level RSPFs and associated predictive maps were useful tools for illustrating changes in habitat selection patterns through time. We recognize the 4 levels of habitat use were subjectively defined and could vary depending on study objectives or species information. Nonetheless, we believe RSPFs and associated predictive maps can provide a useful framework for quantifying indirect habitat losses by measuring the changes (e.g., percentage or area) in habitat use categories through time. Predictive maps suggest that some areas categorized as high use before development, changed to low use as development progressed, and other areas initially categorized as low use changed to high use. For example, following year 1 of development, 17% of units classified as high use before development had changed to medium-low or low use, and by year 3 of development, 41% of those areas classified as high use before development had changed to medium-low or low use. Conversely, by year 3 of development, 40% of low-use areas had changed to medium-high

or high-use areas. Assuming habitats with high probability of use before development were more suitable than habitats with lower probability of use, these results suggest natural gas development on the Mesa displaced mule deer to less-suitable habitats.

Winter severity and forage availability can influence the distribution patterns of mule deer (Garrott et al. 1987, Brown 1992). However, winter conditions on the Mesa were considered relatively mild during the course of this study (1998–2003) and were unlikely to have precluded deer from using their entire winter range. Gilbert et al. (1970) reported snow depths >61 cm were required to preclude use of an area by mule deer. With the exception of isolated drifts, snow depths were <61 cm across the Mesa during all years of study. If the observed changes in deer distribution were due to severe winter conditions, we would expect deer use to shift to areas with lower elevations and south-facing slopes. Instead, deer always selected for high elevations, and aspect was never a significant predictor variable during years of development, further suggesting the observed shifts in deer distribution

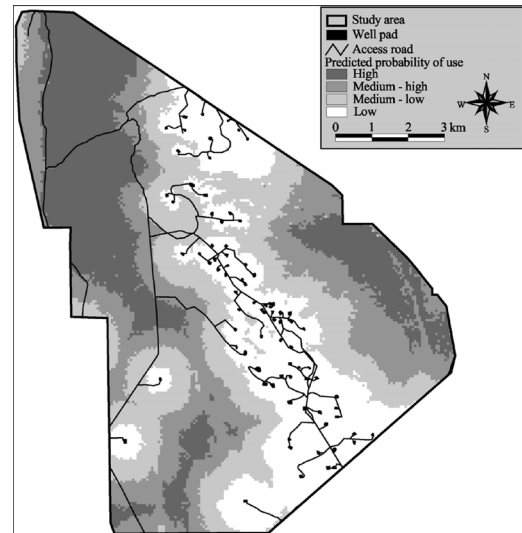
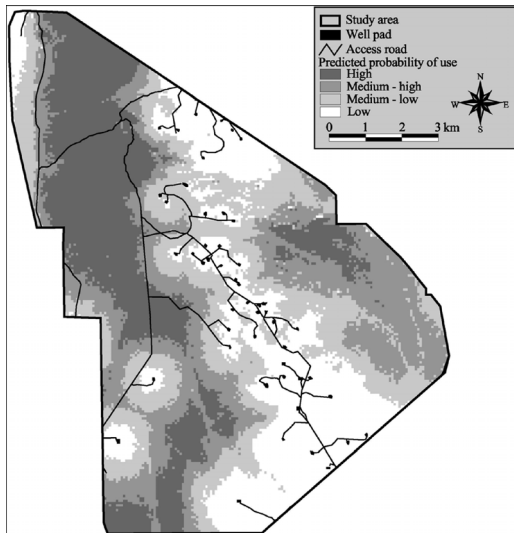


Figure 3. Predicted probabilities and associated categories of mule deer habitat use during year 2 (winter of 2001–2002) of natural gas development in western Wyo., USA.

Figure 4. Predicted probabilities and associated categories of mule deer habitat use during year 3 (winter of 2002–2003) of natural gas development in western Wyo., USA.

were due to increased well-pad development and associated human activity rather than winter conditions.

A single well pad typically disturbs 3 to 4 acres of habitat; however, areas with the highest probability of deer use were 2.7, 3.1, and 3.7 km away from well pads during the first 3 years of development, respectively. There are 2 potential concerns with the apparent avoidance of well pads by mule deer. First, the avoidance or lower probability of use of areas near wells creates indirect habitat losses of winter range that are substantially larger in size than the direct habitat losses incurred when native vegetation is removed during construction of the well pad. Habitat losses, whether direct or indirect, have the potential to reduce carrying capacity of the range and result in population-level effects (i.e., survival or reproduction). Second, if deer do not respond by vacating winter ranges, distribution shifts will result in increased density in remaining portions of the winter range, exposing the population to greater risks of density-dependent effects. Consistent with Bartmann et al. (1992), we would expect fawn mortality to be the primary density-dependent population-regulation process because of their high susceptibility to over-winter mortality (White et al. 1987, Hobbs 1989).

Monitoring shifts in distribution or habitat use allows for mitigation measures aimed at reducing impacts to be evaluated and for timely, site-specific strategies to be developed. The current mitigation measure is focused on seasonal-timing restrictions, where drilling activity is limited to nonwinter months. This type of mitigation is common across federal lands and intended to reduce human activity and, presumably, the associated stress to big game during the winter months, typically 15 November to 30 April. Major shifts in the distribution of mule deer on the Mesa occurred even though drilling on federal lands was largely restricted to nonwinter months. Our findings suggest current mitigation measures may not be achieving desired results. Winter-timing restrictions are only imposed on leases that occur in areas designated as crucial winter range, and then, only through the development phase of the well. Consequently, variable levels of human activity may occur throughout the field during winter as producing wells are serviced, and despite the recognition of the uniqueness of crucial winter range, roads may cross or abut these areas, exposing them to human disturbances as well.

Management Implications

In deep-gas fields like the PAPA, where well densities range from 4 to 16 pads per section (2.58 km²), the number of producing well pads and associated human activity may negate the potential effectiveness of timing restrictions on drilling activities as a means of reducing disturbance to wintering deer. Mitigation measures designed to minimize disturbance to wintering mule deer in natural gas fields should consider all human activity across the

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entire project area and not be restricted to the development of wells or to crucial winter ranges. Reducing disturbance to wintering mule deer may require restrictions or approaches that limit the level of human activity during both production and development phases of the wells. Directional-drilling technology offers promising new methods for reducing surface disturbance and human activity. Limiting public access and developing road management strategies may also be a necessary part of mitigation plans. Future research and monitoring efforts should evaluate how different levels of human activity (e.g., traffic or noise) at developing and producing well pads influence mule deer distribution. Understanding mule deer response to different levels of human activity and types of well pads would allow mitigation measures to be properly evaluated and improved.

Assuming there is some level of increased energy expenditure required for deer to alter their winter habitat-selection patterns (Parker et al. 1984, Freddy et al. 1986, Hobbs 1989), the apparent displacement of deer from high-use to low-use areas has the potential to influence survival and reproduction. This relationship, however, needs to be documented. Accordingly, we recommend appropriate population parameters (i.e., adult female survival, overwinter fawn survival, recruitment) be monitored in areas with large-scale gas development so that changes in reproduction or survival can be detected. The major shortcoming of efforts to evaluate the impacts of disturbances on wildlife populations is that they seldom are addressed in an experimental framework but, rather, tend to be short-term and observational. Brief, postdevelopment monitoring plans associated with regulatory work generally result in little or no information that allow agencies and industry to assess impacts on wildlife or to improve mitigation measures. We encourage long-term (>5 years) studies that identify habitat-selection patterns and that measure population characteristics in control and treatment areas before and during gas-development projects that occur in sensitive mule deer ranges.

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