Influence of Well Pad Activity on Winter Habitat Selection Patterns of Mule Deer

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ABSTRACT Conversion of native winter range into producing gas fields can affect the habitat selection and distribution patterns of mule deer (Odocoileus hemionus). Understanding how levels of human activity influence mule deer is necessary to evaluate mitigation measures and reduce indirect habitat loss to mule deer on winter ranges with natural gas development. We examined how 3 types of well pads with varying levels of traffic influenced mule deer habitat selection in western Wyoming during the winters of 2005–2006 and 2006–2007. Well pad types included producing wells without a liquids gathering system (LGS), producing wells with a LGS, and well pads with active directional drilling. We used 36,699 Global Positioning System locations collected from a sample (n = 31) of adult (>1.5-yr-old) female mule deer to model probability of use as a function of traffic level and other habitat covariates. We treated each deer as the experimental unit and developed a population-level resource selection function for each winter by averaging coefficients among models for individual deer. Model coefficients and predictive maps for both winters suggested that mule deer avoided all types of well pads and selected areas further from well pads with high levels of traffic. Accordingly, impacts to mule deer could probably be reduced through technology and planning that minimizes the number of well pads and amount of human activity associated with them. Our results suggested that indirect habitat loss may be reduced by approximately 38–63% when condensate and produced water are collected in LGS pipelines rather than stored at well pads and removed via tanker trucks. The LGS seemed to reduce long-term (i.e., production phase) indirect habitat loss to wintering mule deer, whereas drilling in crucial winter range created a short-term (i.e., drilling phase) increase in deer disturbance and indirect habitat loss. Recognizing how mule deer respond to different types of well pads and traffic regimes may improve the ability of agencies and industry to estimate cumulative effects and quantify indirect habitat losses associated with different development scenarios. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1052–1061; 2009)

KEY WORDS gas development, habitat selection, liquids gathering system (LGS), mule deer, Odocoileus hemionus, predation risk, resource selection function, Wyoming.

Increased energy development on public lands has generated concern because of potential impacts to wildlife populations and their habitats (Lyon and Anderson 2003, Sawyer et al. 2006, Bergquist et al. 2007, Walker et al. 2007). Because many of the largest natural gas reserves in the Intermountain West, North America, occur in shrub-dominated basins (e.g., Powder River Basin, Piceance Basin, Green River Basin), management concerns have focused on native shrub communities and associated species, including mule deer (Odocoileus hemionus; Sawyer et al. 2006). Changes to mule deer habitat are often obvious and direct, such as replacement of native vegetation with well pads, access roads, and pipelines. More difficult to quantify, however, are indirect habitat losses that occur when animals avoid areas around infrastructure due to increased human activity.

Understanding effects of human activity on wildlife is key to successful management and conservation (Knight and Gutzwiller 1995, Gill et al. 1996, Taylor and Knight 2003). The influence of human-related disturbances on wildlife energetics, demography, and habitat selection is particularly important among temperate ungulates whose survival depends on minimizing energy expenditures during winter (Parker et al. 1984, Hobbs 1989). Across western North America, restricting human activity in crucial ungulate winter ranges has been a common management practice for decades (Lyon and Christensen 2002). However, limiting human activity on many native winter ranges has become complicated, as the dominant land use has shifted from agriculture to energy extraction (Bureau of Land Management [BLM] 2005) and recreation (Knight and Gutzwiller 1995). Although many wintering ungulate herds are exposed to human activities, our understanding of how ungulates react to such disturbances is limited.

It has been demonstrated that wintering mule deer respond to natural gas well pads by selecting habitats ≥3 km away (Sawyer et al. 2006), but we do not know how mule deer behavior changes with levels of human activity. For example, do well pads receiving 2 vehicle trips per day elicit a different behavioral response than those with 10 vehicle trips per day? Ungulates tend to avoid human disturbances such as roads (Rowland et al. 2000, Nelllemann et al. 2001, Dyer et al. 2002), energy development (Nelllemann and Cameron 1996, Bradshaw et al. 1997, Dyer et al. 2001, Nelllemann et al. 2003), bicyclists (Taylor and Knight 2003), hikers (Miller et al. 2001, Papouchis et al. 2001), and snowmobiles (Freddy et al. 1986, Seip et al. 2007). However, it remains unclear how behavioral responses scale with the level of human activity.

As gas development expands across the Intermountain West (BLM 2005), identifying mitigation measures that reduce human disturbance and associated indirect habitat loss will become increasingly important, as will our ability to
understand and predict animal responses to disturbance. Levels of human activity vary across most developing gas fields, with higher levels of activity at well pads with active drilling operations and lower levels of activity at well pads with producing wells. This development scenario provides an excellent opportunity to quantify how behavioral responses of ungulates vary as a function of disturbance level. Our objective was to determine whether mule deer habitat selection in winter was influenced by well pads with varying levels of traffic in a developing gas field in western Wyoming. Our intent was to provide a quantitative assessment of how wintering mule deer respond to active drilling operations versus producing well pads with different traffic regimes, such that future development and mitigation strategies may be improved.

STUDY AREA

The Pinedale Anticline Project Area (PAPA) is located in the upper Green River Basin, approximately 5 km southwest of Pinedale, Wyoming, USA. The PAPA consisted primarily of federal lands (80%) administered by the BLM, with elevations of 2,070–2,400 m (BLM 2000). The PAPA supported livestock grazing and provided crucial winter range for 4,000 to 5,000 migratory mule deer that summer in portions of 4 mountain ranges 80–160 km away (Sawyer et al. 2005). Although the PAPA covered 799 km\(^2\), most mule deer spend winter in the northern third, an area locally known as the Mesa. The 260-km\(^2\) Mesa is bounded by the Green River on the west and the New Fork River on the north, south, and east, and it is vegetated primarily by Wyoming big sagebrush (*Artemisia tridentata*) and sagebrush–grassland communities. Our study was restricted to the Mesa portion of the PAPA, where we previously modeled predevelopment distribution patterns of mule deer during winters 1998–1999 and 1999–2000 (Fig. 1; Sawyer et al. 2006).

The PAPA also contains some of the largest natural gas reserves in the region, which the BLM approved for development in 2000 (BLM 2000). Due to a series of regulatory decisions (BLM 2000, 2004a, b), the PAPA contained 3 basic types of well pads during 2005 and 2006, including 1) active drilling pads, 2) producing well pads with liquids gathering systems (LGS), and 3) producing well pads without LGS. All active drilling pads implemented directional drilling, where multiple wells were drilled and completed from one pad. Most human activity in gas fields is vehicle traffic on unpaved roads and is highest at active drilling pads. However, once drilling is completed and wells are in production phase, traffic levels decline at well pads. Among producing well pads, those with LGS have the lowest levels of traffic because water and condensate by-products are collected in pipelines rather than by tanker trucks. During the 2005–2006 winter, our study area contained 6 active drilling pads and approximately 60 and 66 LGS and non-LGS well pads, respectively. During the 2006–2007 winter, our study area contained 5 active drilling pads and approximately 71 and 72 LGS and non-LGS well pads, respectively.

**METHODS**

We captured adult (≥1.5-yr-old) female mule deer using helicopter net-gunning in the northern portion of the PAPA, where deer congregate in early winter before moving to their individual winter ranges throughout the Mesa (Sawyer and Lindzey 2001). Previous work showed that capturing deer in this area during early winter provides the best opportunity to obtain a representative sample of the wintering population (Sawyer et al. 2006). We fitted deer with store-on-board Global Positioning System (GPS) radiocollars (Telonics, Inc., Mesa, AZ) equipped with remote-release mechanisms and programmed to attempt a location fix every 2 hours. Potential fix-rate bias (Frair et al. 2004, Nielson et al. 2009) was not a concern because of the high (99%) fix-rate success of the GPS collars in the open terrain of our study area.

We used active infrared sensors (Trailmaster\textsuperscript{®} TM 1550 sensor; Goodson and Associates, Inc., Lenexa, KS) to monitor vehicle traffic at a sample of 18 well pads during 13 January–27 March 2006 and 10 January–17 March 2007. We placed monitors approximately 1.2 m off the ground and set them at a sensitivity level that required the infrared beam to be broken for 0.30 seconds. We designed this configuration to minimize the sensor recording multiple hits for trucks pulling trailers. We estimated mean daily traffic volume for the 3 well pad types: those with LGS, those without LGS, and active drilling pads. We also observed 235 traffic (175 pickup trucks, 38 utility trucks, 18 tractor-trailers, 8 cars) crossings across the 18 sites to assess accuracy.
of the monitoring system. Of the 235 vehicle observations, 229 (97%) were accurately recorded. We used analysis of variance to test for differences in mean daily traffic volume among well pad types.

Resource Selection
Whereas traditional resource selection function methods (Manly et al. 2002) commonly use logistic regression to compare a discrete set of used units with a set of unused or available units (Thomas and Taylor 2006), our approach used multiple regression to model probability of use as a continuous variable (Marzluff et al. 2004; Sawyer et al. 2006, 2007). Our approach consisted of 5 basic steps in which we 1) measured predictor variables at 4,500 randomly selected circular sampling units, 2) estimated relative frequency of use in the sampling units for each radiocollared deer, 3) used relative frequency as the response variable in a generalized linear model (GLM) to estimate probability of use for each deer as a function of predictor variables, 4) averaged coefficients from models of each individual deer to develop a population-level model, and then 5) mapped predictions of the population-level model.

This method treats the marked animal as the experimental unit, thereby eliminating 2 of the most common problems with resource selection analyses: pooling data across individuals and ignoring spatial or temporal correlation in animal locations (Thomas and Taylor 2006). An additional benefit of treating each animal as the experimental unit is that interanimal variation can be examined (Thomas and Taylor 2006), while still providing population-level inference via averaging coefficients (Marzluff et al. 2004, Millspaugh et al. 2006, Sawyer et al. 2006). Finally, by modeling use as a continuous variable, we considered resource use in a probabilistic manner that relies on actual time spent by an animal in a sampling unit, rather than presence or absence of the animal (Marzluff et al. 2004, Millspaugh et al. 2006).

We used the study area of Sawyer et al. (2006), which was based on the distribution (i.e., min. convex polygon) of 39,641 locations from 77 mule deer over 6 years (1998–2003). Based on 7 years of previous modeling efforts, we identified 3 variables as potentially important predictors of winter mule deer distribution, including elevation, slope, and distance to well pad type (Sawyer et al. 2006). We did not include vegetation as a variable because the sagebrush-grassland was homogeneous across the study area, and vegetation maps that divide this habitat into finer classes did not exist. We used ArcView to calculate slope from a 26-m × 26-m digital elevation model (United States Geological Survey 1999). We digitized roads and well pads from high-resolution (10-m) satellite images provided by Spot Image Corporation (Chantilly, VA). Images were collected in September 2005 and 2006, after most annual construction activities (e.g., well pad and road building) were complete, but before snow accumulation. Images were geo-processed by SkyTruth (Sheperdstown, WV). We categorized well pads as active drilling, LGS, or non-LGS.

Our sampling units for measuring habitat variables consisted of 4,500 circular units with 100-m radii randomly distributed across the study area. Ideally, the sampling unit should be small enough to detect changes in animal movement or habitat selection (Millspaugh et al. 2006, Sawyer et al. 2006) but large enough to ensure the number of locations within the sampling units approximates a known error distribution (e.g., Poisson or negative binomial). Size of the sampling units may vary depending on mobility of the animal, frequency of GPS locations, and heterogeneity of the landscape. Previously, we evaluated units with 75-m, 100-m, and 150-m radii and found units with 100-m radii worked well for mule deer data collected at 2-hour intervals in the PAPA study area (Sawyer et al. 2006). Alternatively, we could have used square sampling units, but regardless of the shape or number, the sampling units cannot cover the entire study area because our modeling approach requires the total number of locations for each animal occurring in the sampling units be treated as a random variable. We took a simple random sample with replacement to ensure independence of sampling units. We counted the number of deer locations within each sampling unit and measured elevation, slope, and distance to well pad type at the center of each sampling unit.

Before modeling resource selection, we conducted a Pearson’s pairwise correlation analysis to identify possible multicollinearity issues and to determine whether we should exclude any variables from our modeling (|r| > 0.60). Among the well pad variables, distance to active drilling and non-LGS pads were correlated (r = 0.72) during the 2005–2006 winter. However, we retained both covariates because this made the models more interpretable, and the correlation did not seem to influence model stability (i.e., regression coefficient did not switch signs and SEs did not increase substantially as we added variables). During the 2006–2007 winter, distance to active drilling and non-LGS pads were highly correlated (r = 0.90); thus, we excluded distance to active drilling well pad as a covariate from the 2006–2007 model.

The relative frequency of locations from each radiocollared deer found in each sampling unit was an empirical estimate of probability of use by that deer, and we used it as a continuous response variable in a GLM. We used an offset term (McCulagh 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. We preferred the negative binomial distribution over the Poisson because the negative binomial allows for overdispersion (White and Bennett 1996), which in this application is due to many sampling units with zero locations. We began our modeling by first estimating coefficients for each radiocollared deer with the following equation:

\[
\ln(E[|i|]) = \ln(\text{total}) + \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \tag{1}
\]

which is equivalent to
where \( l_i \) is number of locations for a radiocollared deer within sampling unit \( i (i = 1, 2, \ldots, 4,500) \), \( total \) is total number of locations for the deer within the study area, \( \beta_0 \) is an intercept term, \( \beta_1, \ldots, \beta_p \) are unknown coefficients for habitat variables \( X_1, \ldots, X_p \), and \( E[\cdot] \) denotes the expected value. The offset term, \( \ln(\text{total}) \), converts the response variable from an integer count (e.g., 0, 1, 2) to a frequency (e.g., 0, 0.003, 0.005) by dividing the number of deer locations in each sampling unit \( (l) \) by the total number of locations for the individual deer \( (\text{total}) \); Fig. 2). At the level of an individual animal, this approach estimates true probability of use for each sampling unit as a function of predictor variables and is referred to as a resource selection probability function (RSPF; Manly et al. 2002). However, it is important to note that if we average coefficients from individual deer RSPFs to obtain a population-level model, the predictions reflect geometric means of individual probabilities rather than true probabilities. Also, because our sampling units may overlap, they are not mutually exclusive and thus predictions from equation 1 are not subject to a unit-sum constraint.

We followed the Marzluff et al. (2004) approach by fitting one model with all variables to each animal. Next, we treated the estimated coefficients as random variables, because they represent independent, replicated measures of resource use (Marzluff et al. 2004, Millspaugh et al. 2006). This approach quantifies the resource selection of individuals and provides a valid method of assessing population-level use by averaging coefficients among marked individuals (Marzluff et al. 2004, Millspaugh et al. 2006). We considered quadratic terms for distance to well pad and slope variables (Sawyer et al. 2006), and following convention, we also included the linear form of each variable. We did not use an information theoretic approach such as Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) for model selection because there is no standard method by which AIC can be properly applied to retain the animal as the experimental unit and build a population-level model with a common set of predictor variables. To evaluate population-level resource selection we assumed GLM coefficients for predictor variable \( t \) for each deer were a random sample from an approximate normal distribution (Seber 1984), with the mean of the distribution representing the population-level effect of predictor variable \( t \) on probability of use (Marzluff et al. 2004; Millspaugh et al. 2006; Sawyer et al. 2006, 2007). This approach implicitly assumes that population-level effects are accurately reflected by averaging coefficients among animals, which yields predictions that are equivalent to the geometric mean of predictions made from individual RSPFs. Importantly, the geometric mean of a set of numbers is always less than or equal to the arithmetic mean, with the difference between the two increasing with increasing variance in the numbers being averaged (Morris and Doak 2002). We recognize that an alternative approach for estimating population-level effects is to calculate the arithmetic mean, cell by cell, from the mapped predictions of individual RSPFs; however, this approach only produces a population-level predictive map, not a population-level model. Given that predictions from both approaches were highly correlated \( (r_s = 0.65 \text{ in } 2005–2006 \text{ and } r_s = 0.80 \text{ in } 2006–2007) \) and our goal was to produce a population-level model, we averaged coefficients of the \( s \) individual deer RSPFs, using

\[
\tilde{\beta}_t = \frac{1}{n} \sum_{i=1}^{n} \beta_{i,t},
\]

where \( \tilde{\beta}_t \) was the estimate of coefficient \( t (t = 1, 2, \ldots, p) \) for individual \( s (s = 1, 2, \ldots, n). \) We estimated the variance of each coefficient in the population-level model using the variation among individual deer and the equation

\[
\text{var} \left( \tilde{\beta}_t \right) = \frac{1}{n-1} \sum_{i=1}^{n} \left( \beta_{i,t} - \beta_t \right)^2.
\]

Population-level inferences using equations 3 and 4 are unaffected by biases in estimated coefficients caused by potential spatial autocorrelation because we selected sampling units at random with replacement (Thompson 1992). Similarly, temporal autocorrelation is not an issue in this analysis because the response variable is the count of relocations within each sampling unit and does not have an associated time stamp other than the study period. To evaluate significance of explanatory variables, we used univariate analyses (i.e., \( t \)-tests) with each coefficient as the response variable (Marzluff et al. 2004, Millspaugh et al. 2006, Sawyer et al. 2006). This approach to evaluating ecological significance is considered conservative because the interanimal variation is included in the calculation of

![Figure 2](image-url)
In winter 2006–2007, traffic levels varied from 2 to 6 vehicle passes per day at LGS well pads, from 6 to 12 at non-LGS well pads, and from 86 to 90 at active drill pads. Mean daily traffic volumes at LGS, non-LGS, and active drill pads were 3.6 (SE = 0.50, n = 8), 8.4 (SE = 1.16, n = 7), and 85.3 (SE = 2.91, n = 3) detections per day, respectively. Mean daily traffic volumes differed across well pad types \((F_2 = 981.31, P \leq 0.001)\) and 95% confidence intervals did not overlap.

**Resource Selection**

We used 24,955 locations from 20 GPS-collared mule deer to estimate individual models during the 2005–2006 winter (1 Dec–15 Apr). Most deer (17 of 20) had positive coefficients for elevation, indicating a preference for higher elevations. Based on the relationship between linear and quadratic terms for slope, distance to LGS pad, distance to non-LGS pad, and distance to active drill pad, most deer selected for areas with moderate slopes (14 of 20), away from non-LGS well pads (16 of 20), away from LGS well pads (13 of 20), and away from active drill pads (13 of 20).

Coefficients from the population-level model and associated \(P\)-values suggested that most deer selected for areas with higher elevations, moderate slopes, and away from all well pad types (Table 1). Areas with the highest predicted level of use had an average elevation of 2,239 m; a slope of 4.98; and were 2.61 km from LGS well pads, 4.30 km from non-LGS well pads, and 7.49 km from active drill pads (Table 2). In contrast, areas with the lowest predicted level of use had an average elevation of 2,183 m; a slope of 3.07; and were 4.03 km, 1.44 km, and 2.78 km from LGS, non-LGS, and active drill well pads, respectively (Table 2). The predictive map indicated that deer use was lowest in areas at low elevation and near clusters of non-LGS and active drill pads (Fig. 3). Predicted levels of mule deer use were noticeably different than those observed prior to development (Fig. 1).

Using the predicted high-use areas as a reference, mule deer distanced themselves from all types of well pads and tended to select areas progressively further from well pads with higher levels of traffic. Specifically, areas with the highest predicted deer use were 2.61 km, 4.30 km, and 7.49 km away from LGS, non-LGS, and active drill pads, respectively. We used these avoidance distances as a metric variance, thereby making rejection of the null hypothesis \((\beta = 0)\) less likely (Marzluff et al. 2004). Nevertheless, ecological significance of explanatory variables is based on the consistency of selection coefficients among collared deer; our sample size was the number of marked mule deer, not sampling units or GPS locations.

We mapped predictions of population-level models for each winter on a 104-m × 104-m grid that covered the study area. We checked predictions to ensure all values were in the interval \([0,1]\), to verify that we would not extrapolate outside the range of model data (Neter et al. 1996). We then assigned the model prediction for each grid cell a value of 1 to 4 based on the quartiles of the distribution of predictions for each map, and we classified areas as high use, medium-high use, medium-low use, or low use. We calculated the mean value of model variables for each of the 4 categories and used high-use values as a reference for assessing how mule deer responded to well pad types. As a predevelopment reference, we developed a map depicting predicted levels of mule deer use before gas development, as presented by Sawyer et al. (2006).

To evaluate predictive ability of the population-level models we developed for 2005–2006 and 2006–2007 we applied each of them to the 2007–2008 winter landscape. We then used 7,578 GPS locations collected from an independent sample \((n = 9)\) of mule deer during the 2007–2008 winter to calculate a Spearman rank correlation \((r_s)\) characterizing the number of GPS locations that occurred in 10 equal-sized prediction bins based on each of the population-level models (Boyce et al. 2002). We performed all statistical analyses in R language and environment for statistical computing (R Development Core Team 2006).

**RESULTS**

In winter 2005–2006, traffic levels varied from 2 to 5 vehicle passes per day at LGS well pads, from 4 to 9 at non-LGS well pads, and from 86 to 145 at active drill pads. Mean daily traffic volumes at LGS, non-LGS, and active drill pads were 3.3 (SE = 0.30, \(n = 9\)), 7.3 (SE = 0.62, \(n = 6\)), and 112.4 (SE = 17.3, \(n = 3\)) vehicle passes per day, respectively. Mean daily traffic volumes differed across well pad types \((F_2 = 119.38, P \leq 0.001)\) and 95% confidence intervals did not overlap.

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>(-60.089)</td>
<td>12.640</td>
<td>&lt;0.001</td>
<td>(-73.969)</td>
<td>15.364</td>
<td>&lt;0.001</td>
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<tr>
<td>Elevation (m)</td>
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<td>0.004</td>
<td>0.010</td>
<td>0.020</td>
<td>0.007</td>
<td>0.012</td>
</tr>
<tr>
<td>Slope (°)</td>
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<td>0.052</td>
<td>0.004</td>
<td>0.359</td>
<td>0.052</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Slope² (°)</td>
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<td>0.003</td>
<td>0.001</td>
<td>(-0.024)</td>
<td>0.003</td>
<td>&lt;0.001</td>
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<tr>
<td>Non-LGS well pad (m)</td>
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<td>0.001</td>
<td>5.748</td>
<td>1.545</td>
<td>0.004</td>
</tr>
<tr>
<td>LGS well pad (m)</td>
<td>1.316</td>
<td>0.880</td>
<td>0.151</td>
<td>3.397</td>
<td>1.013</td>
<td>0.007</td>
</tr>
<tr>
<td>LGS well pad² (m)</td>
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<td>0.109</td>
<td>&lt;0.001</td>
<td>(-0.421)</td>
<td>0.126</td>
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<td>Active drilling pad (m)</td>
<td>3.121</td>
<td>1.204</td>
<td>0.178</td>
<td>na²</td>
<td>na²</td>
<td>na²</td>
</tr>
<tr>
<td>Active drilling pad² (m)</td>
<td>(-0.197)</td>
<td>0.073</td>
<td>0.014</td>
<td>na²</td>
<td>na²</td>
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</tr>
</tbody>
</table>

\(a\) LGS = liquids gathering system.

\(b\) na = not applicable.
to assess indirect habitat loss associated with well pad types. Using a straight line distance, mule deer avoidance of LGS pads was approximately 40% less than that of non-LGS pads (i.e., 1 – \[2.6/4.3\] = 0.40; Fig. 4). However, assuming a circular area of behavioral response from the point of disturbance (well pad), the indirect habitat loss was reduced by 63% (i.e., 1 – [21/58] = 0.63; Fig. 4) relative to non-LGS pads. Conversely, the straight line distance mule deer selected away from active drill pads was approximately 2.8 times greater than LGS pads and 1.7 times greater than non-LGS pads. Assuming a circular area of behavioral response, indirect habitat loss associated with active drill pads was approximately 3.0 times more than non-LGS pads and 8.4 times more than LGS pads.

We used 11,744 locations collected from 11 GPS-collared mule deer to estimate individual models during the 2006–2007 winter. Most deer (9 of 11) had positive coefficients for elevation, indicating a preference for higher elevations. All deer selected for areas with moderate slopes and most selected for areas away from non-LGS well pads (9 of 11) and LGS well pads (9 of 11). We did not include distance to active drill pad as a variable during this winter because it was strongly correlated with distance to non-LGS well pads.

Coefficients from the population-level model and associated P-values suggested that deer selected for areas with higher elevations, moderate slopes, and away from LGS and non-LGS well pads (Table 1). Areas with the highest predicted level of use had an average elevation of 2,243 m; slope of 4.55°; and were 3.46 km and 4.35 km from LGS and non-LGS well pads, respectively (Table 2). In contrast, areas with the lowest predicted level of use had an average elevation of 2,206 m; slope of 3.27°; and were 2.12 km and 0.69 km from LGS and non-LGS well pads, respectively (Table 2). Within high use habitats, deer used areas closer to LGS pads compared with non-LGS. The predictive map indicated that deer use was lowest in areas with low elevations and clusters of non-LGS well pads (Fig. 5). Predicted levels of mule deer use were noticeably different than those observed before development (Fig. 1).

**Figure 3.** Population-level model predictions and associated categories of mule deer habitat use during winter 2005–2006 in western Wyoming, USA. LGS = liquids gathering system, GPS = Global Positioning System.

**Figure 4.** Relationship between straight-line avoidance distances and circular area of impact as a measure of indirect mule deer habitat loss associated with liquids gathering system (LGS) and non-LGS well pads during the 2005–2006 winter in western Wyoming, USA.

<table>
<thead>
<tr>
<th>Model variables</th>
<th>Predicted mule deer use</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2,239 2,243 2,224 2,203 2,238 2,233 2,183 2,206</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>4.98 4.55 3.64 3.61 3.26 3.52 3.07 3.27</td>
</tr>
<tr>
<td>Distance to LGS pad (km)</td>
<td>2.61 3.46 3.33 3.43 2.87 2.53 4.03 2.12</td>
</tr>
<tr>
<td>Distance to non-LGS pad (km)</td>
<td>4.30 4.35 3.53 3.97 2.50 2.83 1.44 0.69</td>
</tr>
<tr>
<td>Distance to active drill pad (km)</td>
<td>7.49 na 5.47 na 3.93 na 2.78 na</td>
</tr>
</tbody>
</table>

* LGS = liquids gathering system.

* na = not applicable.
Mule deer distanced themselves from LGS and non-LGS well pads and tended to select areas progressively further from well pads that received higher levels of traffic. Areas with the highest predicted deer use were 3.46 km and 4.35 km away from LGS and non-LGS well pads, respectively. Mule deer avoidance of LGS pads was approximately 21% less than that of non-LGS pads. However, assuming a circular area of avoidance from the point of disturbance (well pad), the indirect habitat loss was reduced by 38% relative to non-LGS pads.

When the 2005–2006 and 2006–2007 population-level models were applied to the 2007–2008 landscape, which included new well pad development, their predictions produced Spearman rank correlations ($r_s$) of 0.903 and 0.939, respectively. The high $r_s$ values indicated that both models effectively predicted the distribution of an independent set of locations ($l = 7,578$) collected from 9 mule deer.

**DISCUSSION**

Consistent with our previous work on this mule deer population, we found that deer habitat selection was influenced by well pads (Sawyer et al. 2006). Mule deer avoided all types of well pads but tended to select areas farther from well pads with higher levels of traffic. The reduced response of mule deer to low traffic levels suggests that impacts of gas development on mule deer may be reduced by minimizing traffic. Avoidance distances calculated from predicted high-use areas provided a useful metric to estimate indirect habitat loss associated with different types of well pads. Indirect habitat loss associated with LGS well pads was 38–63% less than with non-LGS well pads, which is noteworthy given that the expected production life of gas wells in the PAPA is 40 years (BLM 2006). Indirect habitat loss associated with active drilling pads was much higher than that at producing well pads; however, all active drill pads in our study were used for directional drilling, which is generally a short-term (6 months–2 yr) disturbance, whereas producing well pads represent a long-term (i.e., decades) disturbance. Recognizing how mule deer respond to different types of well pads and traffic regimes may improve the ability of agencies and industry to estimate cumulative effects and quantify indirect habitat losses associated with different development scenarios (e.g., clustered development; Theobald et al. 1997).

Evaluating wildlife responses to disturbance is conceptually similar to how ecologists have evaluated prey response to predation risk (Lima and Dill 1990, Lima 1998). Like predation risk, human-related disturbances can divert time and energy away from foraging, resting, and other activities that improve fitness (Gill et al. 1996, Frid and Dill 2002), which could be important to wintering ungulates whose nutritional condition is closely linked to survival. Similar to Gavin and Komers (2006) and Haskell and Ballard (2008), we found it useful to evaluate our findings in relation to predation risk theory. Predation risk (Lima and Dill 1990) predicts that antipredator behavior has a cost to other activities (e.g., foraging, resting) and that the trade-off is optimized when the antipredator behavior (e.g., fleeing, vigilance, habitat selection) tracks short-term changes in predation risk (Frid and Dill 2002). Given that risk of predation can vary across seasons, days, or even hours, antipredator behaviors of prey species should be sensitive to the current risk of predation (Lima and Dill 1990) or level of disturbance. Our results suggested that reducing traffic from 7 to 8 (non-LGS well pads) vehicle passes per day to 3 (LGS well pads) was sufficient for mule deer to perceive less risk and alter their habitat selection behavior such that LGS well pads were avoided less than non-LGS well pads, effectively reducing indirect habitat loss associated with producing well pads.

The trade-offs associated with maximizing foraging opportunities and minimizing predation have been well studied (e.g., Lima and Dill 1990, Bleich et al. 1997, Brown and Kotler 2004). Importantly, however, trade-offs can only occur if foraging benefits and predation risks are positively correlated (Bowyer et al. 1998, Pierce et al. 2004). If the most energetically profitable foraging areas are not perceived as the most dangerous, then there is no trade-off between maximizing foraging and minimizing predation (Lima 1998). Because many of the well pads were constructed in habitats identified as highly preferred by mule deer before development (Fig. 1; Sawyer et al. 2006), we believe that tangible trade-offs existed and that mule deer reduced foraging opportunities by avoiding well pads. High levels of predation risk may indirectly affect survival and reproduction by reducing the amount of time, energy, and resources needed to maintain healthy body condition (Frid and Dill 2002). Furthermore, animals displaced from disturbed sites...
may experience greater intraspecific competition or density-dependent effects when congregating into smaller areas of undisturbed or suboptimal habitat (Gill and Sutherland 2000). However, the link between antipredator behavior and reduced population performance is difficult to demonstrate (Lima 1998) and has not yet been documented for mule deer and energy development.

Drilling during winter (15 Nov–30 Apr) in areas designated as crucial winter range is a recent phenomenon. Traditionally, seasonal timing restrictions have limited development activities (e.g., construction, drilling, well completion) to nonwinter months and represent the most common, and sometimes the only, mitigation measure required by the BLM for reducing disturbance to wintering ungulates on federal lands. Because of seasonal timing restrictions, the energy industry typically was not allowed to drill during the winter in crucial winter ranges. However, winter drilling will likely become a more common practice across the Intermountain West, as evidenced by recent National Environmental Policy Act decisions in western Wyoming, where stakeholders identified year-round directional drilling as the preferred method to develop the necessary number of wells to recover natural gas reserves, regardless of winter range designation (BLM 2004a, b, 2006). Wildlife managers have expressed concerns about year-round drilling in crucial winter range because seasonal timing restrictions would be waived and levels of human disturbance would increase substantially during winter (BLM 2004a), when mule deer are most vulnerable (Parker et al. 1984, Hobbs 1989). Although significant indirect habitat loss may occur with seasonal timing restrictions in place (Sawyer et al. 2006), our results suggest that wintering mule deer are sensitive to varying levels of disturbance and that indirect habitat loss may increase by a factor of >2 when seasonal restrictions are waived.

Both directional drilling and construction of the LGS were large-scale, multimillion dollar decisions that involved an assortment of local, state, and national stakeholders (BLM 2004a). Although Wyoming currently produces the most natural gas in the contiguous United States, the scale and intensity of gas development is predicted to increase elsewhere in the Intermountain West, especially in Colorado, Utah, New Mexico, and Montana (BLM 2005). As gas development becomes more widespread, wildlife and development conflicts will be inevitable. Although the wildlife species of concern (e.g., mule deer, greater sage grouse [Centrocercus urophasianus], pronghorn [Antilocapra americana]) may differ across states or regions, the available development strategies (e.g., directional drilling, LGS) will probably be similar. If human disturbances such as vehicle traffic are analogous to predation risk (Gill et al. 1996, Frid and Dill 2002, Gavin and Komers 2006), then mule deer responses to directional drilling and LGS development strategies should be qualitatively similar in other areas across the Intermountain West.

The conceptual framework of predation risk provides a useful context for interpreting responses of ungulates to human disturbances (e.g., Rowland et al. 2000, Nellmann et al. 2003, Taylor and Knight 2003, Gavin and Komers 2006). However, given the rapid and widespread energy exploration and development across the Intermountain West (BLM 2005), manipulative studies will be necessary to advance our understanding of wildlife responses to human disturbance and habitat perturbations. Unfortunately, many of the systems we study are too large or too expensive to manipulate (Macnab 1983). In addition, when experiments are conducted at large spatial scales, such as the 799-km² PAPA, replication and randomization are rarely options (Nichols 1991, Sinclair 1991). When the treatment or manipulation is commodity driven, such as mineral extraction or gas development, randomization becomes especially difficult to achieve. Recognizing the constraints that limit our ability to conduct large-scale manipulative studies, researchers have been encouraged to treat management prescriptions, such as fire or harvest regimes, as a form of experimentation (Macnab 1983, Nichols 1991, Sinclair 1991) and as an opportunity for adaptive management (Walters and Holling 1990). Gas development will probably continue to be a dominant activity on federal lands across the Intermountain West. As such, we encourage researchers to consider energy development strategies and mitigation measures as large-scale experimentation that, if properly monitored, can improve our knowledge of energy development impacts to wildlife.

MANAGEMENT IMPLICATIONS

Because mule deer selected for habitats progressively further from well pads with higher levels of traffic, our results suggest that potential impacts of gas development on mule deer may be reduced by technology and planning that minimizes the number of well pads (e.g., directional drilling) and the level of human activity associated with them (e.g., LGS). Our results suggest indirect habitat loss to mule deer could potentially be reduced by 38–63% when condensate products are collected in LGS pipelines rather than being stored at well pads and removed via tanker trucks. In addition, because a LGS can be installed underground and usually in existing roadway or pipeline corridors, associated direct habitat losses are minimal. The LGS seemed to be an effective means for reducing long-term (i.e., production phase) indirect habitat loss to wintering mule deer, whereas drilling in crucial winter range created a short-term (i.e., drilling phase) increase in deer disturbance and indirect habitat loss.

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