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Human-mediated shifts in animal habitat use: Sequential changes in pronghorn use of a natural gas field in Greater Yellowstone

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ABSTRACT

To manage America's 991,479 km^2 (245 million acres) of public BLM lands for such mixed uses as natural resource extraction, wildlife, and recreation requires knowledge about effects of habitat alterations. Two of North America's largest natural gas fields occur in the southern region of the Greater Yellowstone Ecosystem (Wyoming), an area that contains >100,000 wintering ungulates. During a 5-year period (2005–2009), we concentrated on patterns of habitat selection of pronghorn (*Antilocapra americana*) to understand how winter weather and increasing habitat loss due to gas field development impact habitat selection. Since this population is held below a food ceiling (i.e., carrying capacity) by human harvest, we expected few habitat constraints on animal movements – hence we examined fine-scale habitat use in relationship to progressive energy footprints. We used mixed-effects resource selection function models on 125 GPS-collared female pronghorn, and analyzed a comprehensive set of factors that included habitat (*e.g.*, slope, plant cover type) and variables examining the impact of gas field infrastructure and human activity (*e.g.*, distance to nearest road and well pad, amount of habitat loss due to conversion to a road or well pad) inside gas fields. Our RSF models demonstrate: (1) a fivefold sequential decrease in habitat patches predicted to be of high use and (2) sequential fine-scale abandonment by pronghorn of areas with the greatest habitat loss and greatest industrial footprint. The ability to detect behavioral impacts may be a better sentinel and earlier warning for burgeoning impacts of resource extraction on wildlife populations than studies focused solely on demography. Nevertheless disentangling cause and effect through the use of behavior warrants further investigation.

1. Introduction

One of America's most vexing and polarizing challenges is how best to manage the 991,479 km^2 (245 million acres) of Bureau of Land Management (BLM) public lands established for multiple uses such as natural resource extraction, wildlife, and recreation. The intersection between energy development and biological conservation affords opportunities both to gather knowledge and to implement findings about how to mitigate impacts to wildlife. As the footprint of human development continues to expand globally into regions that have historically supported abundant wildlife resources, there will be even more pressing needs for long-term data sets, in conjunction with baseline data, to examine changes in life history parameters and behavioral processes.

Western North America contains abundant natural resources, including wildlife populations that still undergo spectacular processes like long-distance migration, a globally-imperiled ecological phenomenon (Berger et al., 2006). Unfortunately, conflicts often arise because the harvest of natural resources is not always compatible with maintaining wildlife populations, thus necessitating choices. These decisions are often contentious because interest groups have vastly different priorities. This puts policy-makers and wildlife managers in the position of needing to make informed decisions about trade-offs, as they attempt to balance the needs of wildlife against people's desire for energy independence. Ecological theory can guide policy-makers and wildlife managers. For instance, we know from studies based on carrying capacity theory, that a reduction in habitat will ultimately lead to a decline in population size, or when extreme a local extirpation. However, because carrying capacity is not static, and is determined by the complex interplay of many factors (*e.g.*, weather, human-footprints on the landscape), identifying thresholds is difficult. Often the challenge is further complicated by a lack of baseline data on wildlife populations' behavior or demography against which to assess short-term fluctuations.

Large-scale natural resource extraction has the potential to impact animal movements, habitat use and associated behavior, demography, and population trends (*e.g.*, Bradshaw et al., 1997;

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Joly et al., 2006; Sawyer et al., 2006; Vistnes and Nellemann, 2008), that includes such North American icons as, caribou (*Rangifer tarandus*; Bradshaw et al., 1997; Cameron et al., 2005; Noel et al., 2004), greater sage grouse (*Centrocercus urophasianus*; Copeland et al., 2009; Walker et al., 2007), and mule deer (*Odocoileus hemionus*; Sawyer et al., 2009). At a broader scale, effects of natural resource extraction span all continents and ecosystems and vary from deserts to tropical forests and polar regions (Contreras-Hermosilla, 1997; Joly et al., 2006; Peres and Lake, 2003).

How wildlife populations respond to increasing human-footprints and habitat loss in the form of energy infrastructure is oftentimes determined primarily by how close the population of concern is to its food ceiling (i.e., carrying capacity; see Stewart et al., 2005). If, for example, a population approaches its habitat's food ceiling, then impacts of habitat loss and fragmentation may be immediately revealed through either behavior (i.e., habitat or resource selection patterns) or demographic (*e.g.*, changes in survival) responses or both simultaneously. Further, if a population is maintained below its food supply by harvest but its' habitat is substantially squeezed or fragmented over time, it seems reasonable to expect changes in its spatial ecology even if sufficient food remains available. Mule deer, for example, respond to energy footprints although presumptively held below a given habitat's food resources (see Sawyer et al., 2009). With respect to the Upper Green River Basin (UGRB) in western Wyoming, we explored the extent to which increasing energy development affected several correlates of pronghorn (*Antilocapra americana*) biology with a specific emphasis on spatial ecology. Beyond habitat loss and human harvest however, weather exerts strong direct effects on animal movements (Hebblewhite et al., 2005). For species like pronghorn, deep snow may exacerbate risks brought on by habitat loss associated with energy field development.

Two of the largest gas fields in the lower 48 USA (i.e., the Pinedale Anticline Project Area (PAPA) and Jonah Fields, see Fig. 1) occur in the wintering home range of America's longest terrestrial migrant – pronghorn of the Greater Yellowstone Ecosystem (Berger et al., 2006). This is significant because Wyoming contains an estimated 400,000 of the world's approximately 700,000 pronghorn and the UGRB herd represents one of the largest in the state (Grogan and Lindzey, 2007; Hoffman et al., 2008).

Our primary study questions are therefore aimed at understanding the interplay of snow and industrial development on habitat selection by pronghorn in this area of extreme energy development. Given that pronghorn are likely kept below their food ceiling (see Stewart et al., 2005) through annual harvest of a mean of 2477 ± 701 pronghorn (*e.g.*, from 2001 to 2009 in Hunt Units 86–91 in the Sublette Herd in the Upper Green River Basin; Wyoming Game and Fish Department, unpub. data), we expected habitat to be a non-limiting factor. If true, then observed resource selection responses of pronghorn to gas field infrastructure may fall below detectable levels (Fig. 2). This annual level of harvest for these six hunt units is over a 4000 km^2 area where we conducted monthly distribution flights during the winters of 2005–2010 for which we never counted more than 6500 total animals (unpub. data). As a consequence, we assume that such relatively high human harvest maintained pronghorn below a point at which body condition would be affected by intra-specific competition for food. On the other hand, variation in snow depth in the UGRB and elsewhere (Martinka, 1967) is a key driver of winter movements and food availability. Consequently, we hypothesized that an increasing human-footprint from gas field development over time would sequentially lower the food ceiling through habitat loss independent of effects of snow depth. Our conceptualized interactions among snow, human harvest, and energy-induced habitat loss are depicted in Fig. 2.

There are two general predictions that stem from current BLM and industry proposals to reduce native habitats by 5–14% (BLM, 2006, 2008): (1) given the harvest-related limitations on population size, the UGRB landscape will retain enough crucial winter range and therefore pronghorn will respond in ways reflecting no biological impacts (i.e., patterns of resource selection will not vary), or (2) pronghorn will show heightened sensitivity to increasingly degraded habitats (i.e., pronghorn will avoid or select against areas in which density of well pads and roads have exceeded a threshold). These dual scenarios enable opportunities to examine fine-scale movements in relation to progressive habitat change while accounting for effects of snow and other variables.

To understand pronghorn use of winter range, we estimated both individual- and population-level resource selection responses to habitat loss, fragmentation, and human activity associated with gas field development and infrastructure using mixed-effects resource selection function (RSF) models to determine which factors influence pronghorn habitat use in gas fields during winter. Further, we examined pronghorn response to gas field development over a 5-year time frame to understand how varying and increasing densities and scale of development and infrastructure impact pronghorn habitat use on their crucial winter range.

2. Methods

2.1. Study area

The primary study area within the UGRB was the PAPA and Jonah gas fields (Fig. 1) where elevations range from 2100 to 2800 m. The larger of the two gas fields is the 80,127 hectare (198,000-acre) region designated as the PAPA, while the smaller 12,140 hectare (30,000-acre) Jonah Field is adjacent to the PAPA to the south (Fig. 1). At the end of 2009, 1713 wells had been drilled in the PAPA and 1623 wells had been drilled in the Jonah. However, less than 3% of the physical habitat in the PAPA and 14.3% of the habitat in the Jonah boundary areas are currently disturbed by roads and well pads (BLM, 2008). The BLM has approved the drilling of 1500 new wells inside the PAPA and 3100 additional new wells inside the Jonah (BLM, 2006, 2008). The infrastructure in the PAPA is projected to continue with expansion of well pads, roads, and pipelines through 2023, drilling through 2025, and production through 2065 (BLM, 2008). In the Jonah, 250 wells will be put into production each year over a period of 76 years up to a maximum of an additional 3100 wells (BLM, 2006).

The UGRB represents the southern reaches of the Greater Yellowstone Ecosystem, where species such as pronghorn migrate from summer range in areas as far away as Grand Teton National Park (150 km distance) to their winter range in the UGRB (Berger et al., 2006; Sawyer and Lindzey, 2000; Sawyer et al., 2005). This region consists primarily of sagebrush (*Artemisia* spp.) steppe communities in rolling hills punctuated by occasional plateaus. The sagebrush steppe in this region has a strong spatial pattern linked to topography (Burke et al., 1989). The topography also leads to snow being swept off of the higher elevation plateaus of the region by wind providing crucial winter range for some estimated 100,000 ungulates such as pronghorn, mule deer, and elk (*Cervus elaphus*) (Berger et al., 2006; Burke et al., 1989; Sawyer et al., 2009). Primary statutory authority for land and habitat management is the Bureau of Land Management (BLM), who also oversees access to minerals in the UGRB. The region around the New Fork River in the PAPA has been formally designated by the WGFD as crucial winter range for pronghorn for longer than the past 50 years (Fig. 3).

2.2. Animal capture and handling

Through our 5-year study duration, we captured and collared 125 adult (⩾1.5 years of age) female pronghorn inside the two gas fields

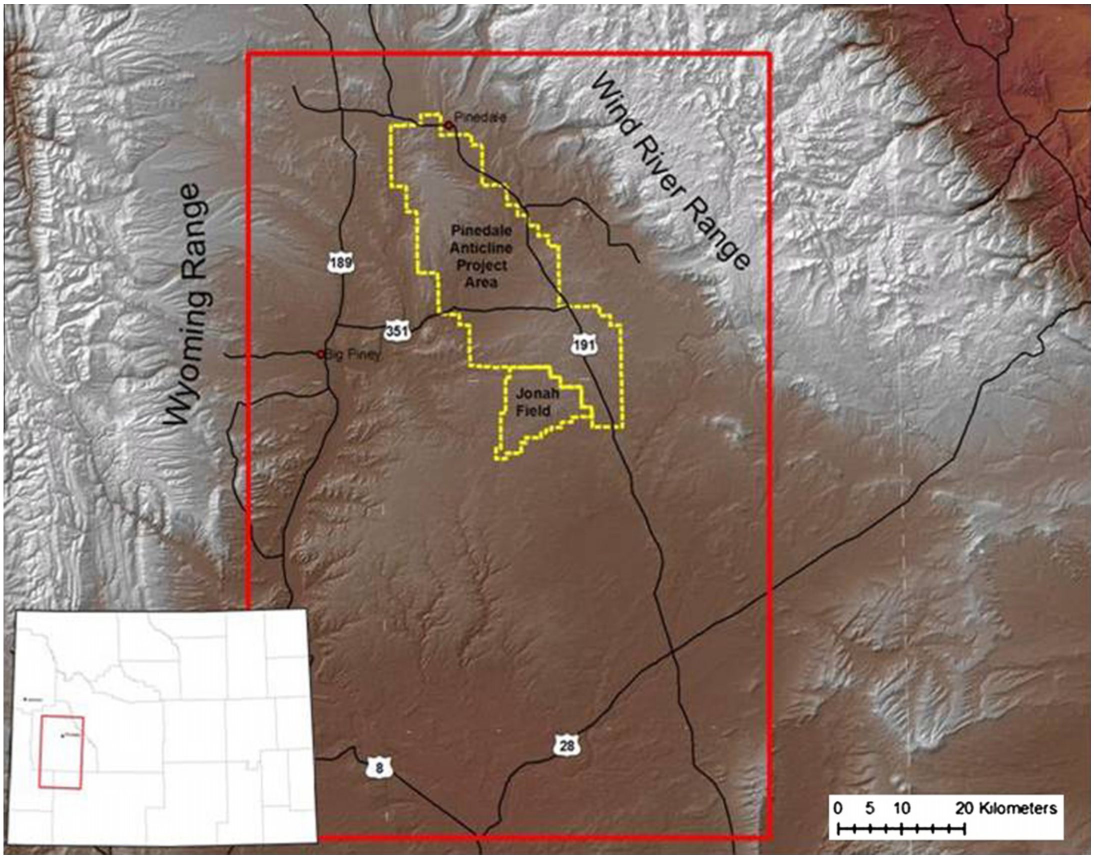

Fig. 1. Location of the Upper Green River Basin in the Greater Yellowstone Ecosystem of western Wyoming. The two largest natural gas fields in the lower 48 states of the USA, the PAPA (northern outline) and Jonah (southern outline) fields are highlighted.

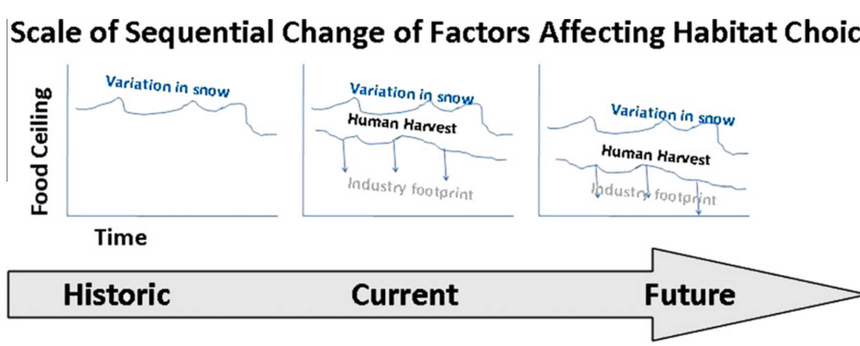

Fig. 2. Conceptual diagram demonstrating how carrying capacity (i.e., food ceiling) for pronghorn during winter might be affected by varying snow depth. Habitat loss and fragmentation by an increasing human-footprint due to natural gas field development over time lowers the food ceiling. However, relatively high levels of human harvest of pronghorn that keeps the population below the food ceiling may potentially mask the true impacts of a further lowering of the food ceiling due to energy infrastructure.

using a net-gun fired from a helicopter. We manually restrained females and fitted each female with a global positioning system (GPS) collar with 8-h mortality sensors and remote release mechanisms (Advanced Telemetry Systems, Isanti, MN). The GPS collars were programmed to collect eight locations per day during winter and migratory periods (1 January–15 May; 16 October–November 15), and a single location per day during summer and early fall (16 May–15 October). All handling was in accordance with Institutional Animal care protocols established by the Wyoming Game and Fish Department and the American Society of Mammalogists.

2.3. Habitat loss

During the 5-year study, sequential changes in the proliferation of roads, well pads and surface disturbance inside the gas fields in the UGRB occurred as natural gas wells were drilled (see Fig. 4 for example). We used 10 m resolution SPOT satellite imagery to calculate habitat loss from construction of well pads and roads in the PAPA and Jonah Field. The satellite image was displayed on-screen and roads and well pads were hand-digitized. The base data layer of roads and well pads from 2005 to 2009 was obtained from the Pinedale, Wyoming, office of the BLM. The BLM's dataset was digitized from 0.6 m resolution imagery at a scale of 1:2000. New roads and well pads constructed each year since the BLM's data were last updated were then added to the existing shapefile for each year's modeling effort. New roads consisted of any identifiable two-tracks, improved dirt, or paved surfaces. Any two-track that was not apparent from the satellite image was not digitized. Well pads were denuded areas used to house gas field structures of any kind that had identifiable roads leading to them. Well pads

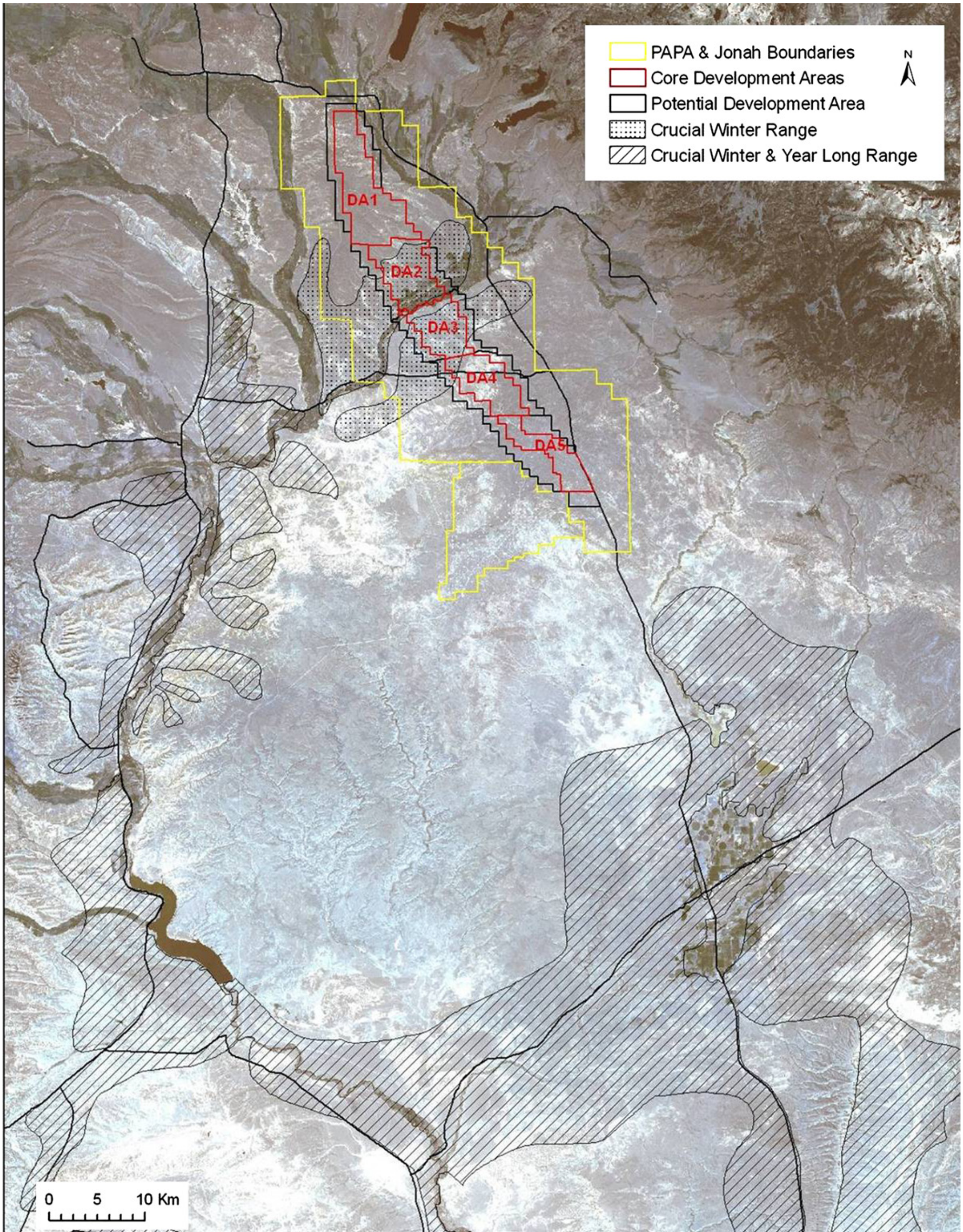

Fig. 3. Wyoming Game and Fish Department crucial winter and year long range designations for pronghorn of the UGRB. PAPA Core Development Areas 2 and 3 (DA2 and DA3) and the proposed Potential Development Area overlap extensively with designated crucial winter range.

were treated the same as pumping stations, equipment storage facilities, etc. ArcMap 9.3 (Environmental Systems Research Institute, Redlands, CA) was then used to calculate the total area of habitat loss from construction of roads and well pads for all years.

We utilized a grid-based method to assess habitat loss associated with construction of roads and well pads for each year from 2005 to 2009. To determine the proportion of disturbed habitat, we first overlaid the boundaries of the PAPA and Jonah Field with a grid comprised of 300 m × 300 m cells. We used 300 m because this was the median distance between pronghorn locations and well pads in winter 2005–2006 based on location data collected using GPS collars; thus, 300 m appeared to be a plausible distance at which pronghorn responded to objects in their environment. Similarly other species, such as mule deer, likely respond and make

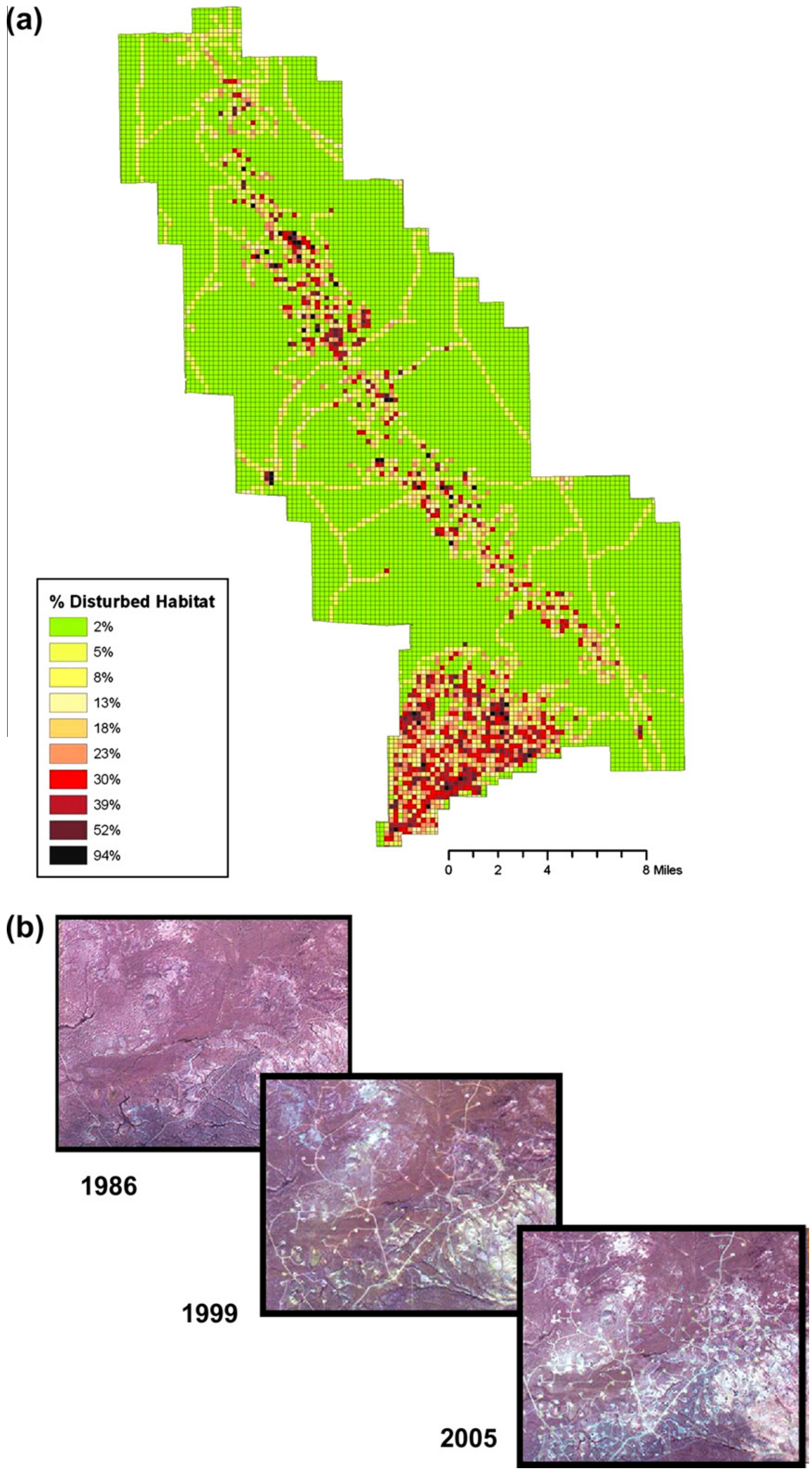

Fig. 4. (a) A 300 m × 300 m polygon grid was used to standardize our analysis of habitat loss. Total proportion of surface disturbance from construction of wells pads and roads was calculated for each cell. Data shown are for 2009 as an example. (b) Roads and well pads in one region of the Upper Green River Basin gas fields via satellite images from 1986 to 2005 showing habitat loss and fragmentation (images are of the same region of the UGRB, at the same spatial scale across each year and are used with permission from SkyTruth).

decisions about habitat selection at large spatial scales (see Kie et al., 2002). The total area within the hand-digitized road and well polygons was then summed and divided by the area of each grid cell (900 m^2) to determine the proportion of habitat disturbed within each 900 m^2 cell (see Fig. 4a as an example).

2.4. Snow depth modeling

We sampled snow depths each year with a 2-m probe at 81 fixed locations throughout the UGRB (see Beckmann et al., 2011 for snow depth survey locations) on a monthly basis during winter when snow was present. All measures were taken at least 10 m from the road in a randomized direction. The snow models were only applied in the RSF models (see below) within the PAPA and Jonah gas field boundaries. To model the patterns of variation given the uneven distribution of snow across the study area, we used an inverse distance weighted (IDW) technique, which determines cell values using a linear weighted combination of a set of sample points (Philip and Watson, 1982; Watson and Philip, 1985). We used the IDW tool from Arc Toolbox in ArcView 9.3 (Environmental Systems Research Institute, Redlands, CA) to interpolate snow depth. The output cell size and resolution grid was set to 30 m.

2.5. Habitat selection by pronghorn in gas fields

2.5.1. Habitat characteristics

We restricted the analysis to areas within the boundaries of the PAPA and Jonah Fields as these are the areas consistent with the extent of available GIS layers on habitat loss from development (Figs. 1 and 4). We identified nine habitat characteristics as potentially important factors influencing pronghorn distribution during winter: elevation, slope, aspect, distance to nearest road, distance to nearest well pad, well-pad status, habitat loss (labeled disturbance), vegetation, and snow depth. Vegetation was classified as sagebrush, irrigated crops, riparian, or a category labeled "other" that included desert shrub, mixed grasslands, and exposed rock/soil (Reiners et al., 1999). As a surrogate for human activity and traffic volume, well pads were classified based on their phase in the production cycles as: active (i.e., wells on which active drilling was occurring, wells that transitioned from drilling to production during the current winter, and wells in production prior to the start of the current winter), inactive (i.e., wells that were either abandoned or on which drilling did not begin until after March 31st of the current year), or unknown (i.e., generally cleared areas/structures that were visible on the satellite image but for which information was not available in the Wyoming Oil and Gas Conservation Commission database [http://wogcc.state.wy.us/] because they were infrastructure other than wells). We calculated slope and aspect from a 26-m digital elevation model using the Spatial Analyst extension in ArcInfo 9.3. We assigned grid cells with slopes $\geqslant 2^\circ$ to one of four aspect categories: northeast, southeast, southwest, or northwest. Grid cells with slopes <2° were classified as flat and included in the analysis as a reference category. We measured direct habitat loss as the proportion of disturbed habitat based on our grid cell analysis. We considered quadratic terms for elevation, snow depth, distance to nearest well pad, distance to nearest road, and slope to allow for non-linear relationships in pronghorn response. Following convention, a linear term for each variable was included along with the quadratic term (Zar, 1999). In addition, we tested interaction terms for distance to nearest well and snow depth, distance to nearest road and snow depth, disturbance (i.e., habitat loss) and snow depth, and well distance and well status, to allow pronghorn response to vary with increasing snow depth and increasing levels of human activity.

2.5.2. Mixed effects model development

We used mixed-effects resource selection function models (Zuur et al., 2009) to identify factors influencing habitat use by pronghorn. Mixed-effects models offer two important advantages over the traditional fixed-effects methods; random intercepts account for unbalanced sample designs (*e.g.*, the number of GPS locations differs among animals) and random intercepts and coefficients improve model fit given variation in selection among individuals and functional responses in selection (Gillies et al., 2006). In addition, mixed-effects models provide information on both population-level (represented by the fixed-effects) and individual-level (represented by the random effects) resource selection patterns (Hebblewhite and Merrill, 2008).

The analysis was performed separately for each year, which allowed for comparisons of factors influencing habitat selection both within and across years. Following Hebblewhite and Merrill (2008), we incorporated random effects into the traditional use-availability RSF design (Manly et al., 2002), in which covariates that may influence selection are compared at used and available locations. To measure resource availability, we generated a set of random points within the study area for each animal defined by boundaries of the PAPA and the Jonah (i.e., availability was assessed at the scale of the gas fields), with replacement, equivalent to the actual number of GPS locations recorded for the animal ($n_{\text{total}} = 48{,}622$ across all animals and all years; see number of GPS locations below for breakdown of number of random points each year). The random points were generated using the Hawth's Tools extension in ArcInfo 9.3 (Beyer, 2004). The random points were then randomly assigned to months in proportion to the actual GPS locations recorded for each animal. We measured the elevation, slope, aspect, vegetation, road distance, well distance, habitat loss, well status, and snow depth attributes associated with each random point using Hawth's Tools and Spatial Analyst in ArcInfo 9.3.

Random effects were incorporated in the RSF model (Manly et al., 2002) following Gillies et al. (2006), wherein resource covariates are compared at used and available locations using:

$$\hat{w}(x) = \exp(\mathbf{X\beta})$$

where $\hat{w}(x)$ is the relative probability of use as a function of covariates x_n, and $\mathbf{X\beta}$ is the vector of fixed-effects resource selection coefficients estimated from the fixed-effects logistic regression (Manly et al., 2002).

In addition to the fixed effects, we incorporated random effects in the RSF model to test for differences in selection among animals by including both a random intercept and random coefficients. Random effects were only considered for factors with four or more levels to avoid imprecise estimates (Bolker et al., 2008). Maximum-likelihood estimates were derived using generalized linear models with Laplace approximation (Bates and Maechler, 2009). To avoid including collinear variables which can produce unstable and misleading results, we screened all explanatory variables for correlation using a Spearman's pairwise correlation analysis with $r \geqslant 0.6$ as the threshold cut-off value. When the threshold was exceeded, only a single variable of the correlated pair was included in the model and alternate models were tested to identify the variable that best explained the data. Model-selection was performed by first identifying the covariates and interaction terms in the top-ranked fixed-effects model and then incorporating random effects to test for variation among individuals (Zuur et al., 2009). Akaike's Information Criterion (AIC) was used to rank models and evaluate model fit (Burnham and Anderson, 2002). We validated our models using area under the receiver operating characteristic curve (ROC) analyses. We used 10% of all GPS locations that were randomly pulled out each year prior to model development to assess validity of each year's model. All analyses were performed in R 2.9.1 using glm (R Development Core Team, 2009) or lmer in the lme4 package (Bates and Maechler, 2009).

Based on the population-level mixed-effects model, we mapped the predicted probability of use across the PAPA and Jonah Field using a 104 m × 104 m grid that covered the study area to be consistent with resource selection models for mule deer in the region (see Sawyer et al., 2006). Attributes associated with each grid cell were identified with the Spatial Analyst extension in ArcInfo 9.3. Predicted probability of use was estimated for each grid cell by applying the coefficients from the final population-level model using the raster calculator tool in Spatial Analyst. Grid cells (i.e., 104 m × 104 m) were assigned to one of four relative use categories (very high – 76–100%, high – 51–75%, medium – 26–50%, and low – 0–25%) based on quartiles of the distribution of predicted values.

3. Results

3.1. Habitat loss

Disturbance due to development in the gas fields has increased annually. In 2005, habitat loss due to construction of well pads was 9.9 km^2 in the PAPA and 11.0 km^2 in the Jonah. In 2009, habitat loss due to construction of well pads in the PAPA and Jonah had increased to 12.7 km^2 and 14.8 km^2, respectively. Over this 5-year span, the total amount of habitat loss due to well pad construction in the PAPA increased by 28.7% and in the Jonah by 34.1%.

Habitat loss in the PAPA from 2005 to 2009 due to road construction increased from 6.6 km^2 to 7.6 km^2. From 2005 to 2009, habitat loss in the Jonah Field due to road construction increased from 1.9 km^2 to 2.5 km^2. Total length of road constructed in the PAPA over the years has increased from 455 km to 510 km in 2009. In the Jonah, total length of road constructed increased during 2005–2009 from 213 km to 258 km. Between 2005 and 2009, the total length of roads increased in the PAPA by 12.1% and the Jonah by 20.7%. In 2007–2008, more road length was added in the PAPA than for all other years combined.

3.2. Snow depth

Snow in the PAPA and Jonah was typically deepest in February (Fig. 5). Highest average monthly snow depths were measured in February 2005 (25.9 cm) and February 2008 (26.6 cm), but average snow depths dropped in March 2005 to 7.0 cm. The lowest average monthly snow depths were measured in 2007 when both the maximum average monthly snow depth (14.5 cm in January) as well as the February average snow depth (10.0 cm) for 2007 were lower than any other year.

3.3. Habitat selection by pronghorn in gas fields

Of the 125 adult, female pronghorn captured inside gas fields, 117 were used to construct our RSF models. The remaining 8 collars were not recovered. Sample sizes to construct our RSF models by year were as follows: 2004–2005 – 5319 GPS locations for 20 pronghorn collected between 2/26/05 and 3/31/05 (Fig. 6a); winter 2005–2006 – 8826 GPS locations for 18 pronghorn collected between 1/24/06 and 3/31/06 (Fig. 6b); winter 2006–2007 – 15,186 GPS locations for 30 pronghorn collected between 1/1/07 and 3/31/07 (Fig. 6c); winter 2007–2008 – 10,792 GPS locations for 25 pronghorn collected between 1/7/08 and 3/31/08 (Fig. 6d); winter 2008–2009 – 8499 GPS locations for 24 pronghorn collected between 2/3/09 and 3/31/09 (Fig. 6e).

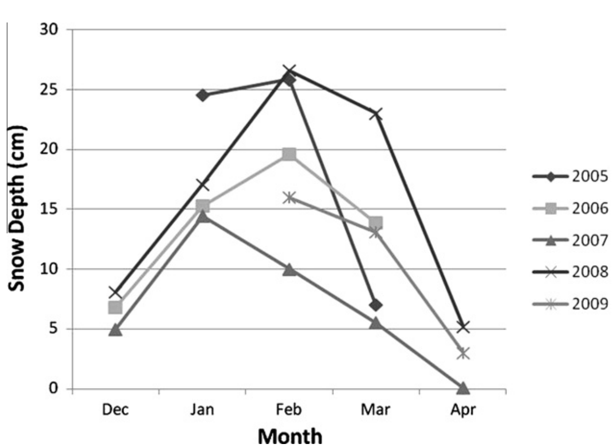

Fig. 5. Average monthly snow depths (cm) for each year (2005–2009) in the Upper Green River Basin of western Wyoming.

Among the habitat variables, there were high levels of correlation in all years between the slope and aspect variables ($r > 0.75$). Among the variables for gas-field development, there were high levels of correlation in all years between the variables for well-distance and road-distance ($r > 0.65$), and road-distance and habitat loss ($r > 0.70$). The variables for aspect, well-distance, and habitat loss (i.e., disturbance) produced models that better fit the data than those for slope or road-distance, so these three explanatory variables were retained in the final analysis.

Not surprisingly, pronghorn showed consistent selection across all winters for sagebrush areas relative to crops, riparian areas, and other types of vegetation. Irrigated crops were generally used more frequently than riparian areas in all years except the winters of 2006–2007 (when there was no significant difference) and 2007–2008. Relative to flat areas, pronghorn showed consistent selection for northeast, southeast, and southwest aspects. Habitat with a northwest aspect was used no differently than flat areas, or less frequently than flat areas, depending upon the year (Tables 1 and 2).

Across all winters, pronghorn consistently selected for habitat at lower elevation (Table 3). On average, habitat patches (i.e., 104 m × 104 m grid) with the highest probability of use were located 55 m lower than patches with the lowest probability of use (mean elevation = 2156 versus 2211 m). Pronghorn also consistently selected for habitat with less accumulated snow except in winter 2004–2005, which represented the highest snow year in the study (Table 3 and Fig. 5). These two factors appear to largely account for the reduced use by pronghorn of the northern and eastern portions of the gas fields, as elevation tends to decline along a north–south gradient, and snow depth along both a north–south and east–west gradient.

The impact of gas field development on pronghorn habitat use is determined by the interplay between a complex series of factors. Overall, probability of use declines as the distance to the nearest well pad increases, which is likely an indication that the most suitable winter habitat for pronghorn tends to be located above richer pockets of natural gas, which is clustered in the Jonah and along the spine of the Anticline (Figs. 4 and 6). Patches (i.e., 104 m × 104 m) with the highest probability of use were located an average of 504 m from the nearest gas well, versus 2777 m for patches with the lowest probability of use (Table 3). Within these preferred areas, the probability of use declines with increasing levels of habitat loss resulting from surface disturbance (Fig. 4 and Tables 1 and 2), which can likely be attributed to the lack of available forage since distance to nearest well and well status do not show conclusive associations. On average, habitat patches (i.e., 104 m × 104 m grid) with the highest probability of use have 3.8% surface disturbance due to construction of roads and well-pads versus 5.3% and 5.2% surface disturbance for patches with high to medium use, respectively (Table 3).

Among the three well-status classifications (active, inactive, unknown), there were no clear patterns of influence on habitat selection preferences. Although at least one of the well-status variables was significant in all years, the directionality of coefficients (positive or negative) varied annually, and the overall impact on the model was negligible (Tables 1 and 2). Thus, it appears that either: (1) human activity associated with different well-types has little impact on pronghorn habitat selection; (2) the well-status classifications did a poor job of characterizing fine-scale human activity levels associated with different well-types; or (3) the close proximity of various

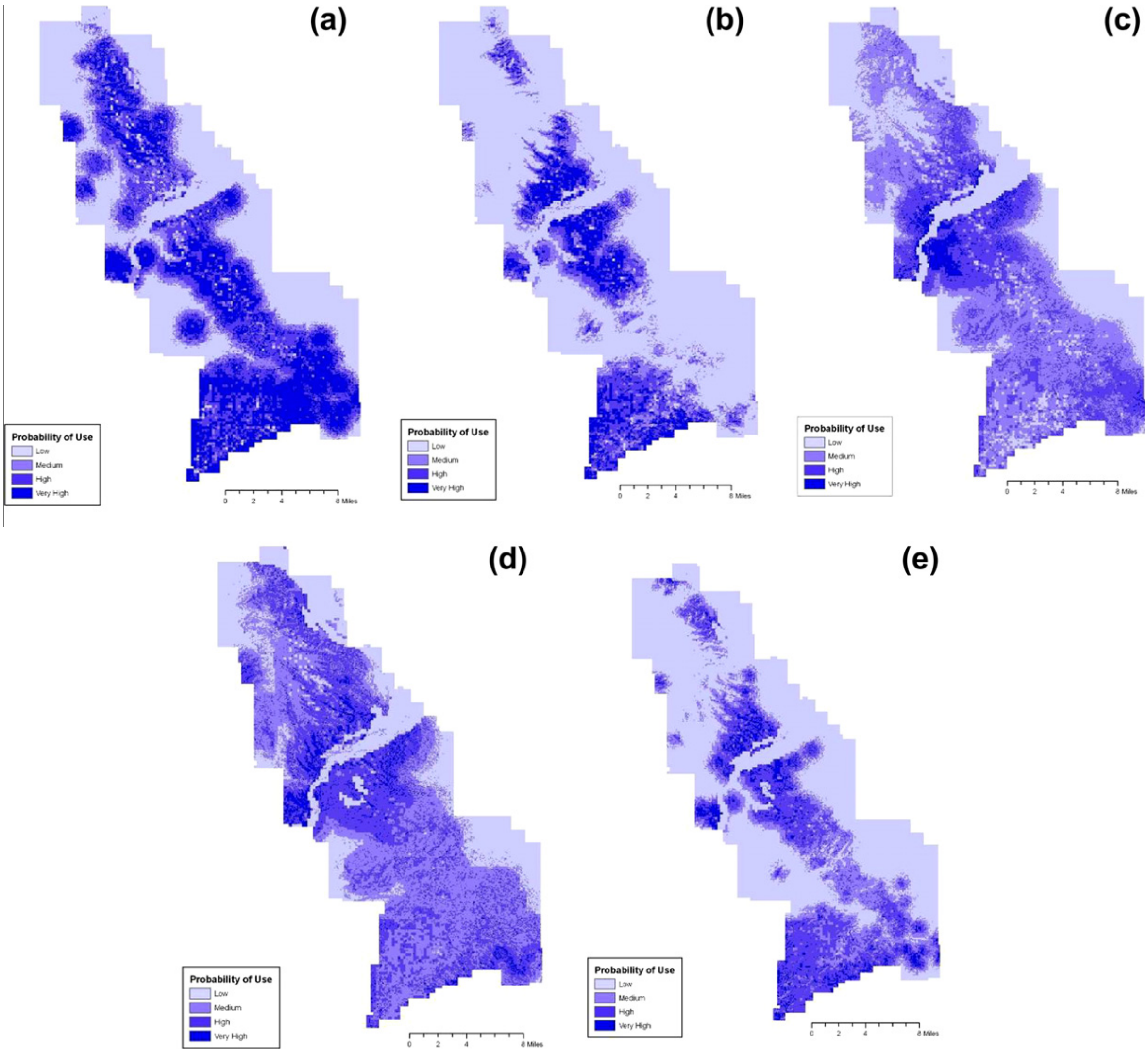

Fig. 6. Predicted probabilities and associated categories of pronghorn use of winter habitat as determined by mixed-effects resource selection function models in the Pinedale Anticline Project Area (PAPA) and Jonah gas fields in the Upper Green River Basin, Wyoming during the winters of (a) 2004–2005; (b) 2005–2006; (c) 2006–2007; (d) 2007–2008; and (e) 2008–2009. Darker shades correspond to higher predicted probabilities of use.

types of gas-field infrastructure with differing activity levels means that the status of the nearest well is not indicative of human activity levels at a coarser scale at which pronghorn may respond.

Similarly, there were no clear patterns of influence among the interaction terms between snow depth and well distance, snow depth and disturbance, or well distance and well status. The exception was the interaction between well distance and unknown wells which was negative (i.e., the probability of habitat use declined more rapidly with increasing distance from wells of unknown status compared to active wells) in the 4 years that the term was significant in the final model (Tables 1 and 2). In some years, pronghorn were more likely to use disturbed areas as snow depth increased (*e.g.*, 2007 and 2008), whereas in other years the use of disturbed areas declined with increasing snow depth (*e.g.*, 2005; Tables 1 and 2). As snow depth increased, the probability of use declined with increasing distance from the nearest gas well in 2005, 2006, and 2009, but increased with increasing distance to the nearest well in 2007, which represented the lowest snow year in the study (Tables 1 and 2 and Fig. 5). These results likely demonstrate the complex interactions and resulting interpretations between snow depth and gas field infrastructure on historic, pronghorn crucial winter range.

Nevertheless, there has been a 5-fold decline over the course of the study in the percentage of patches (i.e., 104 m × 104 m grid) classified as having a very high probability of use (from 28% in 2005 to 5% in 2009), and an increase in the percentage of patches classified as having a low probability of use (from 34% in 2005 to 53% in 2009; Fig. 7 and Table 3). These results indicate a general decline in the availability of high-quality habitat for pronghorn due to habitat alteration associated with gas field development (Figs. 6 and 7). In the absence of gas field development (i.e., we removed variables associated with gas field development), our 2009 model predicted that 17% of habitat patches (i.e., 104 m × 104 m grid) would be classified as having a very high probability of use, 46% as a high probability of use, 29% as a medium probability of use, and just 8% as a low probability of use as compared to the metrics calculated which include gas field development (Table 3).

The inclusion of random effects, which allow for variation in selection among individuals, resulted in a marked increase in model performance (Table 4). Although models that included a random intercept by animal performed only marginally better than the top-ranked fixed-effects models, the incorporation of random effects for distance to nearest well or habitat loss resulted in dramatic improvements in model fit, with the random coefficient for well-

Table 1
Parameter estimates for population-level resource selection function for pronghorn during three winters.

Parameter	2004–2005		2005–2006		2006–2007	
	β	*P*	*β*	*P*	*β*	*P*
Intercept	−213.492	<0.001	−1107.129	<0.001	283.250	<0.001
Vegetation-other		ns	−0.692	0.05	2.986	<0.001
Riparian	−1.065	0.001	−1.731	<0.001		ns
Sagebrush	1.879	<0.001	1.249	<0.001	3.428	<0.001
Well distance		ns	−1.144	0.01	0.291	0.10
Well distance^2	−0.422	<0.001		ns	−0.292	<0.001
Disturbance	−1.730	<0.001	−5.637	<0.001	−4.765	<0.001
NE aspect	1.001	<0.001		ns	0.506	<0.001
SE aspect	1.166	<0.001	1.225	<0.001	0.688	<0.001
SW aspect	0.791	<0.001	0.888	<0.001	0.285	<0.001
NW aspect		ns	−0.819	<0.001	−0.305	<0.001
Elevation	1979.599	<0.001	10373.946	<0.001	−2521.148	<0.001
Elevation^2	−4619.821	<0.001	−24320.571	<0.001	5535.838	<0.001
Snow depth	−13.552	<0.001	32.681	<0.001		ns
Snowdepth^2	67.640	<0.001	−133.536	<0.001	−18.824	<0.001
Inactive well		ns	−0.679	<0.001	0.093	0.05
Unknown well	0.600	<0.001	−0.183	0.05	−0.499	<0.001
Well distance:inactive well		ns	−0.143	0.05	0.057	0.10
Well distance:unknown well	−0.646	<0.001	−0.424	<0.001		ns
Well distance:snow depth	−2.308	<0.001	−3.530	<0.001	1.561	<0.001
Disturbance:snow depth	−22.467	<0.001		ns	6.273	0.10

Table 2
Parameter estimates for population-level resource selection function for pronghorn during the winters of 2007–2008 and 2008–2009.

Parameter	2007–2008		2008–2009	
	β	*P*	*β*	*P*
Intercept	14.962	<0.001	−351.316	<0.001
Vegetation-other		ns		ns
Riparian	1.092	<0.001	−1.287	<0.001
Sagebrush	3.583	<0.001	2.286	<0.001
Well distance		ns	−1.597	0.01
Well distance^2	−0.154	<0.001		ns
Disturbance	−5.280	<0.001	−4.180	<0.001
NE aspect	1.004	<0.001	0.733	<0.001
SE aspect	0.937	<0.001	0.807	<0.001
SW aspect	0.616	<0.001	0.561	<0.001
NW aspect		ns	−0.752	<0.001
Elevation	−85.766	<0.001	3347.365	<0.001
Elevation^2		ns	−7991.814	<0.001
Snow depth	8.545	<0.001		ns
Snow depth^2	−40.719	<0.001		ns
Inactive well	−0.229	<0.001	0.080	ns
Unknown well	0.327	<0.001	0.558	<0.001
Well Distance:inactive well	0.102	0.01		ns
Well Distance:unknown well	−0.263	<0.001	−0.382	<0.001
Well distance:snow depth		ns	−1.663	<0.001
Disturbance:snow depth	21.311	<0.001		ns

distance out-performing the coefficient for habitat loss in all years, accounting for more of the variation in the data (Table 4). The five final models had area under the receiver operating characteristic curve (ROC) values ranging from 0.82 to 0.90 ($AUC_{2005} = 0.86$, $AUC_{2006} = 0.82$, $AUC_{2007} = 0.89$, $AUC_{2008} = 0.86$, $AUC_{2009} = 0.90$) using the independent validity test data, indicating useful and accurate models (Swets, 1988).

4. Discussion and conclusions

True impacts of increasing infrastructure, habitat loss, and fragmentation to extract natural resources may be masked or dampened for populations held below a region's ecological food ceiling by hunting. However, if populations maintained below a food ceiling respond to habitat loss and fragmentation, then we can infer impacts from development for resource extraction can be substantial. When impacts from natural resource extraction on such populations are masked or delayed, then threshold levels may be crossed before negative impacts are identified and too late for appropriate adaptive management responses to be initiated in a timely manner. Determining if behavioral impacts are realized by wildlife populations prior to demographic responses to a sequentially increasing human-footprint from natural resource extraction would allow those concerned with conserving or managing wildlife the ability to identify impacts before thresholds of demographic responses are crossed. Alternatively, behavioral shifts in resource selection and habitat use in response to human activity or habitat loss may reduce or preclude long term demographic impacts, an issue that awaits further investigation in developing gas fields.

In the case of pronghorn of the Upper Green River Basin, we demonstrated significant changes in behavioral responses and resource selection patterns at both the population and individual-level during a relatively short 5-year period. These shifts due to energy development were detected despite the fact that this population is held below the food ceiling of the region due to high human harvest. On average, more than 2450 pronghorn/year are removed from the six hunt units in our 4000 km^2 study site (Wyoming Game and Fish, unpub. data). Nevertheless, shifts in pronghorn resource selection in relation to a sequentially increasing industry footprint in the UGRB were detectable. Behavioral responses by species to habitat loss may be a precursor to population impacts, such as lower reproduction and survival rates in subsequent years in regions rapidly and sequentially increasing in natural resource extraction infrastructure. The ability to detect behavioral responses prior to demographic responses would allow land and wildlife management agencies to appropriately adjust both spatial and temporal parameters of development to avoid potential demographic effects. The competing hypothesis is that shifts in behavior may preclude any demographic responses to development.

Our data reveal that by focusing on habitat use and behavioral shifts, we detected fine-scale avoidance of patches with high levels of disturbance. Notably, this included an 82% decline in the number of patches classified as highest quality. Such behavioral impacts may serve as a caution to pending negative demographic impacts in this population as the human-footprint grows in the UGRB.

Table 3
Average metrics associated with habitat patches (i.e., 104 m × 104 m grid) based on relative probability of use by pronghorn during the winters of 2004–2005 through 2008–2009.

Use category	Patches %	Elevation (m)	Habitat loss (%)	Snow (cm)	Well distance (m)
2008–2009					
Low	53	2210	1.40	17	2252
Medium	19	2199	5.70	15.3	565
High	23	2173	9.50	14.9	274
Very high	5	2155	7.90	14.2	206
2007–2008					
Low	18	2213	2.20	15.6	3556
Medium	40	2210	5.80	15.1	1142
High	36	2179	3.60	14.7	783
Very high	5	2154	2.60	14	657
2006–2007					
Low	28	2218	5.45	15.4	2809
Medium	42	2208	4.13	12.5	1056
High	26	2168	1.51	10.1	890
Very high	4	2121	0.88	8.5	917
2005–2006					
Low	62	2212	1.80	18.7	2139
Medium	13	2183	5.60	15	772
High	14	2171	7.40	13.4	429
Very high	11	2158	4.90	12.4	288
2004–2005					
Low	34	2200	1.61	26	3129
Medium	14	2201	4.95	25.4	1188
High	24	2197	4.52	26.2	692
Very high	28	2190	2.95	28.3	452

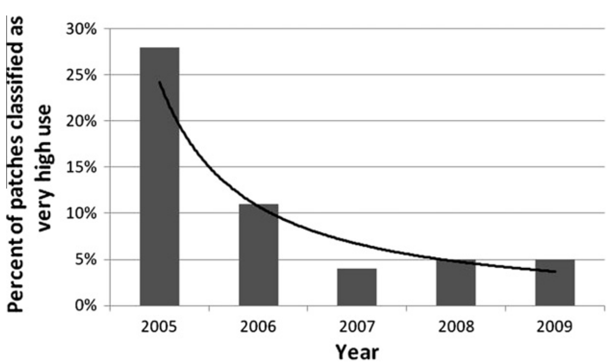

Fig. 7. Percent of patches classified as very high use for pronghorn in winter in the PAPA and Jonah gas fields in the Upper Green River Basin, Wyoming using mixed-effects resource selection function models developed from 125 GPS-collared adult female pronghorn from 2005 to 2009. Patches classified as very high use for pronghorn have declined by 82% over the 5-year period of 2005–2009. The line represents a line-of-best-fit.

The ability to detect behavioral impacts through avoidance at a fine spatial scale may be important even where demographic impacts are not the primary current. Further efforts will reveal if such nuanced behavior is an important precursor for understanding whether energy-related impacts will lead to population declines.

Ungulate winter resource selection is complicated, influenced by many factors, and varies among individuals, area, and conditions. Modeling these interactions requires a careful balance between accounting for influential factors and reducing variation in the models. In general, wintering pronghorn in the gas fields of the UGRB select for sagebrush dominated areas with shallow snow. The fact that pronghorn use of disturbed areas declined with increasing snow depths in the winter of 2005—a trend that was reversed in other years—may reflect the early peak (January and February) in snow depths in 2005 making adequate forage in disturbed areas inaccessible during the most critical months for energy retention. Across all winters except 2005, pronghorn utilized areas closer to gas wells when snow depths were greater, perhaps using associated roads to facilitate movement. In general, barring 2005, the interactive snow depth parameters suggest that when snow is deeper, pronghorn are more likely to use areas closer to disturbance and wells. This is likely because those disturbed areas are situated in the most crucial pronghorn winter habitat that becomes necessary during winters of high snowfall, especially in DA2 and DA3 in the PAPA. This spatial relationship is likely a result of the Anticline (uplift below the surface) that trapped the gas being located directly beneath the Mesa, the high plateau inside the PAPA that is wind swept during winter and which provides key crucial winter range for pronghorn and other ungulates in the region (Burke et al., 1989; BLM, 2006; Sawyer et al., 2006; Sawyer and Nielson, 2010). Pronghorn are likely constrained in their response to gas field infrastructure because it is being developed in areas that pronghorn have historically used as crucial winter range in the UGRB. In fact, the Wyoming Game and Fish Department has identified the Mesa region inside the PAPA natural gas field as crucial winter range for pronghorn for more than 50 years prior to gas field development.

Over time, our models demonstrate that gas field development is leading to a significant decrease in the number and amount of highest quality habitat patches (very high probability of use) and an increase in the number and amount of marginal/poor habitat patches (low probability of use). When we look at data from winter 2008–2009 without including natural gas development as variables in our models, the ratio of habitat patches that are predicted to be of highest quality are similar to the ratios predicted in both 2004–2005 and 2005–2006, when habitat disturbance across the gas fields was lower. In other words, when variables related to impacts of gas fields (*e.g.*, well pads, roads, distance to well pads, distance to roads, habitat loss) are removed from our resource selection models in 2009, the amount of high quality habitat on the landscape returns to 2004–2005 levels. This together with the fact that the parameter estimate for level of disturbance showed a consistent negative relationship with habitat use, demonstrates that habitat disturbance/loss appears to be the principal factor in determining pronghorn winter habitat use in the gas fields at both the individual- and population-level. Because this

Table 4
Comparison of top-ranked fixed-effects model with models containing a random intercept and random coefficient for well-distance and disturbance, 2005–2009.

Model structure	Variance		
	AIC	Intercept	Coefficient
2005			
Top-ranked fixed-effects model	11,767		
Top-ranked fixed-effects model with random intercept by animal	11,769	0.002	
Top-ranked fixed-effects model with random coefficient for well-distance by animal	11,202	0.580	0.777
Top-ranked fixed-effects model with random coefficient for disturbance by animal	11,716	0.017	10.207
2006			
Top-ranked fixed-effects model	15,961		
Top-ranked fixed-effects model with random intercept by animal	15,940	0.018	
Top-ranked fixed-effects model with random coefficient for well-distance by animal	15,019	0.674	3.224
Top-ranked fixed-effects model with random coefficient for disturbance by animal	15,580	0.195	56.916
2007			
Top-ranked fixed-effects model	36,293		
Top-ranked fixed-effects model with random intercept by animal	36,251	0.019	
Top-ranked fixed-effects model with random coefficient for well-distance by animal	34,167	0.737	0.811
Top-ranked fixed-effects model with random coefficient for disturbance by animal	35,692	0.054	79.615
2008			
Top-ranked fixed-effects model	26,071		
Top-ranked fixed-effects model with random intercept by animal	26,051	0.012	
Top-ranked fixed-effects model with random coefficient for well-distance by animal	24,582	0.629	3.053
Top-ranked fixed-effects model with random coefficient for disturbance by animal	25,314	0.094	50.481
2009			
Top-ranked fixed-effects model	19,531		
Top-ranked fixed-effects model with random intercept by animal	19,494	0.026	
Top-ranked fixed-effects model with random coefficient for well-distance by animal	17,974	0.873	7.97
Top-ranked fixed-effects model with random coefficient for disturbance by animal	18,776	0.262	68.208

is the case, over time as more habitat disturbance and loss has occurred due to gas field infrastructure, we have continued to see further shifts in pronghorn behavior and resource selection patterns resulting in a loss of high quality habitat patches due to behavioral avoidance of the areas most intensively developed in the gas fields.

In fact, patches of habitat which were predicted to be of very high use by pronghorn during winter inside the PAPA and Jonah gas fields have declined in abundance over the 5 year period from 2005 to 2009 by 82%. This trend indicates a fivefold loss in percentage of very high use patches (i.e., 104 m × 104 m) and represents a significant loss of high value winter habitat for pronghorn in the PAPA and Jonah gas fields over a very short period of time due to gas field development and infrastructure. There was a precipitous decline (61%) in the amount of highest quality habitat patches (very high probability of use patches; 104 m × 104 m grid) from year one (winter 2004–2005) to year two (winter 2005–2006), followed by a leveling off in the decline in subsequent years (Fig. 7). However, between year two (winter 2005–2006) and year three (winter 2006–2007) there was an additional loss of half (10% down to 5%) of the remaining habitat patches (i.e., 104 m × 104 m grid) classified as highest quality. In total, between the second and fifth years of our study there was an additional 20% loss of highest quality habitat patches following the precipitous 61% loss in the first year suggesting a sequential loss of high quality habitat over the course of our 5-year study.

It could be argued that this leveling off in the rate of decline is more representative of annual variation rather than further decline. Pronghorn are tolerant of some level of human activity and behavioral modifications to human activity may preclude future demographic impacts. However, there is the possibility that pronghorn responses to gas field development may lead to declines in highest quality habitat patches in a manner reflecting thresholds, where the decline takes the form of steps and at this time the first big step was shown from 2005 to 2007. This is an idea that warrants further investigation as these gas fields develop.

Wildlife populations can only withstand a certain level of loss of crucial wintering habitat and resulting shifts in behavior, locations, and use before demographic impacts are realized. Here we demonstrated that the ability to detect behavioral impacts before demographic impacts suggests that at least for some species, behavior may be a better sentinel and earlier warning for negative impacts of natural resource extraction on wildlife populations than studies focused solely on demography. Nevertheless, disentangling cause and effect through the use of behavior and resource selection patterns will be an important consideration.

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