



Identifying impediments to long-distance mammal migrations

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Abstract: *In much of the world, the persistence of long-distance migrations by mammals is threatened by development. Even where human population density is relatively low, there are roads, fencing, and energy development that present barriers to animal movement. If we are to conserve species that rely on long-distance migration, then it is critical that we identify existing migration impediments. To delineate stopover sites associated with anthropogenic development, we applied Brownian bridge movement models to high-frequency locations of pronghorn (*Antilocapra americana*) in the Greater Yellowstone Ecosystem. We then used resource utilization functions to assess the threats to long-distance migration of pronghorn that were due to fences and highways. Migrating pronghorn avoided dense developments of natural gas fields. Highways with relatively high volumes of traffic and woven-wire sheep fence acted as complete barriers. At crossings with known migration bottlenecks, use of high-quality forage and shrub habitat by pronghorn as they approached the highway was lower than expected based on availability of those resources. In contrast, pronghorn consistently utilized high-quality forage close to the highway at crossings with no known migration bottlenecks. Our findings demonstrate the importance of minimizing development in migration corridors in the future and of mitigating existing pressure on migratory animals by removing barriers, reducing the development footprint, or installing crossing structures.*

Keywords: Brownian bridge movement model, Greater Yellowstone, highway, long-distance migration, natural gas, pronghorn, resource utilization function, stopover

Identificación de los Impedimentos para las Migraciones de Larga Distancia de Mamíferos

Resumen: *En la mayor parte del mundo, la persistencia de las migraciones de larga distancia de los mamíferos está amenazada por el desarrollo. Incluso donde la densidad de población humana es relativamente baja existen caminos, cercas y desarrollo de energías que presentan barreras para el movimiento animal. Si deseamos conservar a las especies que dependen de la migración de larga distancia, entonces es crítico que identifiquemos los impedimentos que existen para que esta se lleve a cabo. Para delinear sitios de apeadero asociados con el desarrollo antropogénico aplicamos modelos de movimiento de puente browniano a las localidades con alta frecuencia de berrendos (*Antilocapra americana*) en el Ecosistema del Gran Yellowstone. Después utilizamos funciones de uso de recurso para evaluar las amenazas a la migración de larga distancia del berrendo que se debieran a las cercas y carreteras. Los berrendos en migración evitaron desarrollos densos de campos de gas natural. Las carreteras con volúmenes relativamente altos de tráfico y cercas de malla ciclón funcionaron como barreras completas. En los cruces con cuellos de botella migratorios conocidos, el uso de forraje de alta calidad y el hábitat arbustivo por parte de los berrendos conforme se aproximaban a la carretera fue más bajo de lo esperado con base en la disponibilidad de estos recursos. En contraste, los berrendos usaron constantemente el forraje de alta calidad cercano a la carretera en los cruces*

sin cuellos de botella migratorios conocidos. Nuestros hallazgos demuestran la importancia de minimizar el desarrollo en los corredores migratorios en el futuro y mitigar la presión existente sobre los animales migratorios al remover barreras, reducir la buella del desarrollo o al instalar estructuras de cruce.

Palabras Clave: apeadero, autopista, berrendo, función del uso de los recursos, gas natural, Gran Yellowstone, migración a larga distancia, modelo de movimiento de puente browniano

Introduction

Ungulate migrations have declined globally in response to overharvesting, anthropogenic barriers, and habitat loss (Bolger et al. 2008; Wilcove & Wikelski 2008). In addition, migrations are being affected by climate change (i.e., trophic mismatch [Post & Forchhammer 2008]) and the restoration of predators (Middleton et al. 2013). A recent summary of the status of worldwide migrations called for scientific investigation of extant pathways, an analysis of threats, and identification of conservation objectives (Harris et al. 2009). With the growing awareness of imperiled migrations and the urgency to protect migrating species, we are seeing rapid development of new techniques to identify remaining movement paths, in hopes of informing conservation and management decisions. Spatially explicit modeling has provided important information for site-specific management of migratory animals and for conservation of migration at a broad scale (e.g., Saher & Schmiegelow 2005; Horne et al. 2007; Sawyer et al. 2009a). We can use spatially explicit models to identify priorities for conservation on the basis of proportional levels of use and to provide a broader understanding of existing threats to migration and options for mitigation. Spatially explicit models also hold great potential for predicting the effects of future anthropogenic changes on migrating mammals.

Rapid and continued growth of the human population has precipitated an increased use of petroleum resources. Development of oil and gas reserves is expanding and causing conflict between corporations, land managers, and conservationists concerned with retaining intact ecosystems from arctic to desert to marine systems, including the Greater Yellowstone Ecosystem (GYE) (Joly et al. 2006; Sawyer et al. 2006; Copeland et al. 2009). Numerous studies have made it clear that migratory wildlife are detrimentally affected by the habitat loss and disturbance concomitant with oil and gas development (Sawyer et al. 2009b; Beckmann et al. 2012; Lendrum et al. 2012). Therefore, understanding migration patterns before developments are planned or approved would aid in protecting migration (Bolger et al. 2008; Wilcove & Wikelski 2008). However, developers are extracting petroleum without understanding the impacts on migratory species (Hebblewhite 2011). It is therefore important that we critically analyze the extent of these impacts and provide the information necessary for improved planning and mitigation.

We applied 2 spatially explicit modeling techniques to an extensive data set. We obtained our high-frequency location data by affixing global positioning system (GPS) collars on pronghorn (*Antilocapra americana*) in the GYE to identify threats to their long-distance migration. Currently there is only one remaining migration route that can be used effectively by pronghorn in the GYE to travel into Grand Teton National Park (GTNP) (Berger et al. 2006). Any complete obstruction of this route will likely extirpate the entire population from the park (Berger et al. 2006). Consequently, our objectives were 3-fold: to provide specific locations of existing threats and defined targeted areas for mitigation, to quantify behavioral responses to anthropogenic disturbance, and to identify important migration areas in need of protection for animals migrating to GTNP and other places in western Wyoming.

Previous literature demonstrates that ungulate stopovers during migration are correlated with resources (e.g., Weber et al. 1998; Alerstam et al. 2003; Sawyer & Kauffman 2011). We posit, however, that impediments to migration may induce stopovers that are indicative of deterrents to movement rather than phenology of forage and that resources and impediments may interact in their effects on ungulate migrations. For instance, areas with high-quality ecological resources or perceived hazardous impediments would end migration, either by meeting biological requirements of ungulates (e.g., when they reach summer range) or by creating a barrier to movement (e.g., an impenetrable highway). Thus disentangling the location, cause, and impacts of resource- and impediment-driven stopovers is key to understanding where and how best to protect migratory routes and mitigate anthropogenic impacts on movements of migratory ungulates.

We hypothesized that migrating pronghorn would slow their movement rate and reduce their use of high-quality forage when encountering impediments. We also hypothesized that movement behaviors would be influenced more by life-threatening impediments (e.g., highways) than by resources (e.g., high-quality forage). To test these hypotheses, we used Brownian bridge movement models (BBMMs) (Horne et al. 2007; Sawyer & Kauffman 2011) and resource utilization functions (RUFs) (Marzluff et al. 2004) to examine impacts of the anthropogenic landscape on long-distance migration of pronghorn in the GYE.

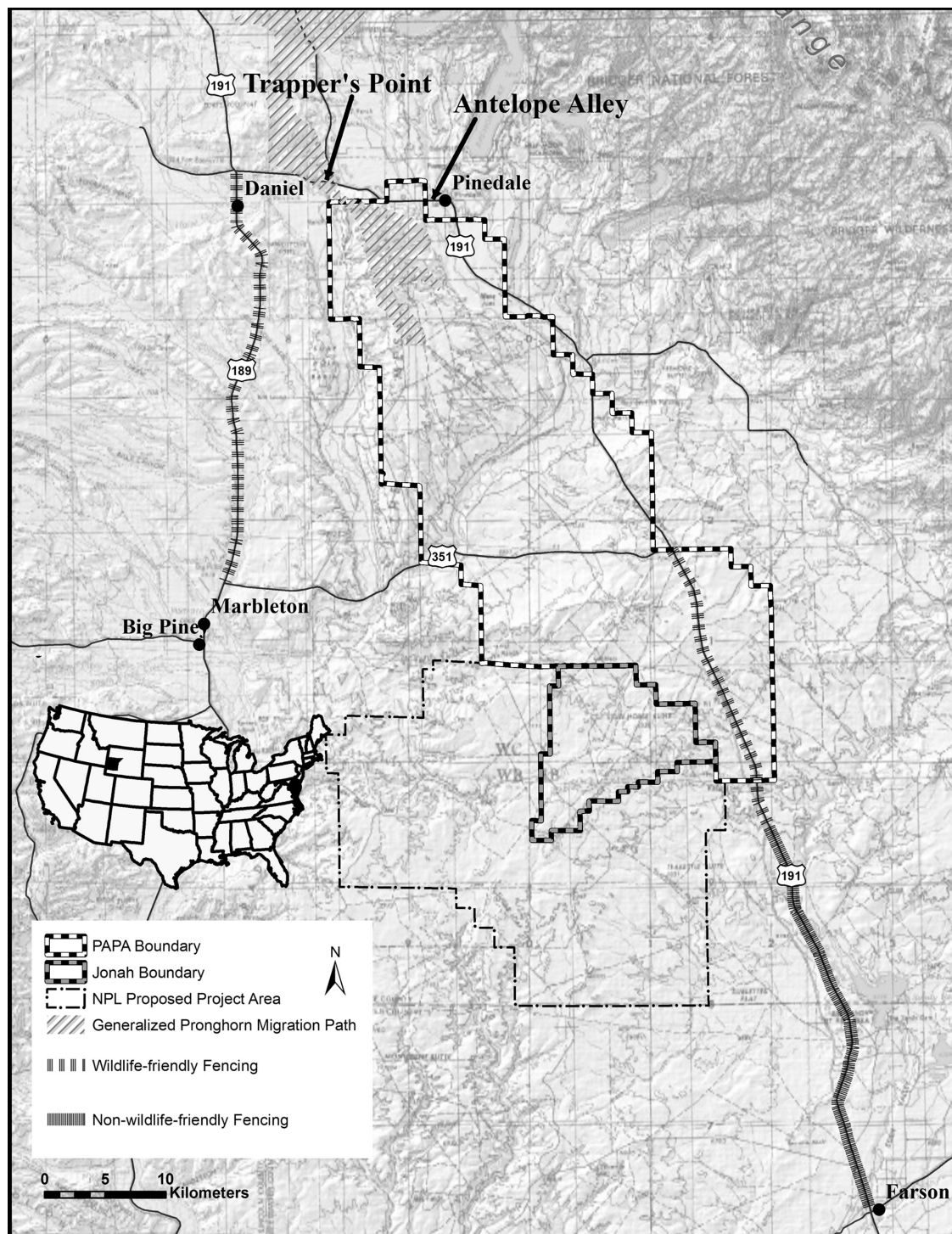


Figure 1. Upper Green River Basin, Wyoming, showing existing and proposed natural gas fields, major highways, and the general pronghorn migratory path through Trapper's Point. Existing natural gas fields are the Pinedale Anticline Project Area (PAPA) and the Jonah Field. The proposed natural gas field is the Normally Pressured Lance (NPL) formation. Trapper's Point and Antelope Alley are major highway crossing points and bottlenecks for migrating pronghorn. Highways analyzed for traffic level and fence type are highlighted either with diffuse crossbars or with dense crossbars.

Methods

Study Area

We focused on pronghorn of the upper Green River Basin of western Wyoming (Fig. 1). This area provides crucial winter range for an estimated 100,000 ungulates (Sawyer et al. 2005; Berger et al. 2006). Pronghorn and mule deer (*Odocoileus hemionus*) have historically migrated through areas, where 2 of the largest natural gas fields in the contiguous United States are currently being developed (Sawyer et al. 2005; Beckmann et al. 2012): the Pinedale Anticline Project Area (PAPA) (80,128 ha) and the Jonah Field (12,141 ha). This intensive gas field development has resulted in a 43% loss of mule deer over the past decade (Sawyer & Nielson 2011) and has caused abandonment of crucial winter range by pronghorn in the region (Beckmann et al. 2012). An additional natural gas field, the Normally Pressured Lance formation project (NPL) (57,093 ha), is slated for development adjacent to the Jonah Field (Fig. 1) (Beckmann et al. 2011; Encana Oil and Gas, Inc. 2011).

In the upper Green River Basin, pronghorn migration paths are intersected by multiple highways, including U.S. Highways 191 and 189 (US191 and US189), with different traffic levels (Fig. 1 & Supporting Information). At the southern end of the study area, woven-wire sheep fencing flanks US191 for approximately 33 km north of Farson (Fig. 1). Along US189 between Daniel Junction and the intersection with state highway 351, the fences have been modified to ease the passage of wildlife (Fig. 1). West of Pinedale, 2 historical migration bottlenecks coincide with highway crossings at Trapper's Point Monument and Antelope Alley, a colloquial name for the narrow pronghorn passage closest to Pinedale (Fig. 1 & Supporting Information) (Miller et al. 1999; Sawyer & Lindzey 2000; Berger et al. 2006). Since the completion of our study, a wildlife overpass structure has been erected at Trapper's Point (Supporting Information) (Gearino 2010).

Capture Methods

We fired a net gun from a helicopter to capture adult female pronghorn during the winters of 2005–2009. We equipped the animals with GPS collars with 8-hour mortality sensors and scheduled-release mechanisms (Advanced Telemetry Systems, Isanti, Minnesota). We placed collars on 50 adult female pronghorn annually over 5 years from February 2005 to February 2009 ($n = 250$). Each collar was programmed to collect 8 locations/day in 2005, 2007, 2008, and 2009 and 12 locations/day in 2006 during spring migration (1 January–15 May). Mean collar location error was <20 m (Di Orio et al. 2003), and fix rate accuracy exceeded 98% in all years (R.G.S. & J.P.B., unpublished data). All animal handling was in

accordance with Institutional Animal Care protocols established by the Wyoming Game and Fish Department and the American Society of Mammalogists (Animal Care and Use Committee 1998).

Spatial Data and Analyses

We used SPOT satellite imagery with 10-m resolution to plot habitat loss from construction of well pads and roads in the PAPA and the Jonah Field (Beckmann et al. 2012). We classified relevant sections of US191 and US189 according to traffic: low volume (<2000 vehicles/day) and high volume (≥ 2000 vehicles/day) on the basis of Wyoming Department of Transportation estimates for 2008 and 2009. Pertinent sections of highway had fencing that we classified as either wildlife friendly (4-strand barbed wire with or without a smooth bottom wire) or nonwildlife friendly (woven-wire fence).

We used methods similar to Sawyer et al. (2009a) to select GPS locations associated with migration, defined as movement between spatially separate winter and summer ranges. However, winter and summer ranges were determined on an individual basis to account for temporal differences among individuals, and we did not include points from the 24 hours prior to and following migration. Migrations began and ended at midnight. Fall location data did not meet the high-frequency requirements of BBMM in any year except 2005 (Horne et al. 2007), so we only used fall data for comparing seasonal asymmetry of movement speeds on the approach and departure sides of an impediment. Animals that died before or during migration or whose migration began or ended outside of the high-frequency data collection period (1 January–15 May) were excluded from analyses. To evaluate independence of individuals in our data set, we compared migration initiation dates. When 2 or more individuals had the same initiation date, we visually inspected their utilization distributions for overlap in space and time. Results of this analysis indicated that all migrations in our study were spatially or temporally independent.

We used a BBMM (Horne et al. 2007; Sawyer et al. 2009a) to estimate utilization distributions for individual spring migrations. To process migration locations in R 2.14 (R Development Core Team 2013), we used an adapted script originally developed for mule deer migration (Sawyer et al. 2009a; Nielson et al. 2011) and modified it to accommodate the greater distances that pronghorn migrate relative to other fauna. Time between successive locations was <190 minutes >97% of the time and never exceeded 540 minutes. Less than 5% of our utilization distributions for individual pronghorn were estimated from datasets that included fewer than 20 locations, and the mean number of locations used to generate each utilization distribution was 197 (SE 12.06). The number of individual utilization distributions used to calculate population-level utilization distributions ranged

from 21 to 34 models per year. Prior to identification of stopovers, we converted each utilization distribution to a normally distributed random variable by log transforming raw probabilities from the BBMM (Willems & Hill 2009), and we eliminated values that were $< 1 \times 10^{-324}$. We mapped 100% probability contours of utilization distributions in ArcGIS 9.3 and overlaid each utilization distribution on a series of relevant GIS layers for subsequent modeling of resource use.

We quantified resource use during migration by estimating RUFs (Marzluff et al. 2004; Kertson & Marzluff 2010) that explained variation in the amount of resource use (i.e., relative concentration of use as quantified by the utilization distribution) by individual pronghorn. Predictor variables in RUFs included shrub habitat, the normalized difference vegetation index (NDVI) (a proxy for spatial variation in forage quality [Ryan et al. 2012; Long et al. 2014]), and distance to the highway. We did not include topographical variables in our models because the small extent of our analyses precluded any significant spatial variation in topography. Prior to analysis, we used the polycor package in the statistical program R to test for collinearity among predictor variables; no predictor variables were removed (all $|r| \leq 0.28$). We used the smallest resolution available for NDVI data to re-sample all variables to a resolution of 250 m, and we compared the date of each pronghorn highway crossing with NDVI values from that same week (Jenkerson et al. 2010; Lendrum et al. 2013).

We randomly selected ≤ 10 individual pronghorn utilization distributions (95% probability contour) per year ($n = 45$) to serve as the response variable in a series of RUFs. We used these RUFs to quantify differences when we compared use of space by migrating pronghorn. Specifically, we observed how several landscape attributes influenced the use of space as the pronghorn approached or departed from a major highway (either US191 or US189). We conducted our analyses of resource use within 7 km on either side of each highway because our primary goal was to characterize behavior of pronghorn near a potential impediment to migration. The 7 km-buffer corresponded to pronghorn's ability to detect movements as far away as 6.4 km and to make decisions about habitat use at large scales (Einarsen 1948; Kie et al. 2002).

For each individual pronghorn, we used the RUF analysis package to fit 7 a priori models (Table 1) (Marzluff et al. 2004). Each candidate model included a combination of a main effect and its associated interaction with a side of the highway (either US191 or US189). Models for each individual were ranked on the basis of Akaike's information criterion adjusted for small sample size (AICc), and model-averaged estimates of standardized parameters (based on Akaike weights) were used to evaluate significance of predictor variables (including interactions) at the individual level (Burnham & Ander-

son 2002). We then averaged standardized parameter estimates for each main effect and interaction term across individuals to estimate a final, population-level model for each of the 2 highways (Marzluff et al. 2004; Sawyer et al. 2006, 2007). We estimated the variance associated with each population-level parameter on the basis of the recommendations of Marzluff et al. (2004), and we determined statistical significance on the basis of whether the 95% CI for the parameter estimate overlapped 0 (Table 2). To add another measure of the relative importance of each predictor variable, we quantified the proportion of individuals with positive and significant, versus negative and significant, coefficients for each interaction term (Table 2) (Marzluff et al. 2004; Long et al. 2009).

To quantify use of stopovers around an impediment, we compared the number of GPS locations before and after the impediment within 1.6 km of the highway for each year in the spring (2005–2009) and for fall 2005. We used 1.6 km because this distance captured the stopover use on the side approaching the impediment in all years at Antelope Alley (Fig. 1). We expected that if highways were not important drivers of migratory stopovers, we would see symmetry in the number of locations on the approach and departure sides of the highway.

Results

We found that 71–84% of radio-collared pronghorn migrated each year, and the average migration length was 52.83 km (SE 2.89) over 22 days (1). Pronghorn spent 78% (SE 2) of their time in stopovers (the highest 25% quartile of the utilization distribution) during spring migration. In all years, probability of use during migration was high outside the areas of densest gas field development and low inside the densest gas field development (Fig. 2). In contrast, pronghorn used the undeveloped area of the proposed NPL project in all 5 years.

Highways appeared to represent obstacles to pronghorn in some locations but be permeable in others. These results were associated with varying traffic levels and fence types. Average traffic levels on US191 north of Farson were 2 times higher than on US189 in January–May 2008 and 1.7 times higher in January–May 2009 (WYDOT 2010, 2011). Where nonwildlife-friendly fencing occurred along US191 north of Farson, migrating pronghorn traveled along the east side of the highway for > 30 km, but no animals crossed the highway. The BBMMs demonstrated that this section of US191 and its associated fencing formed a complete barrier to migration (Fig. 3a). In contrast, where wildlife-friendly fencing ran parallel to US191 north of Farson, 11% (2/19) of radio-collared pronghorn migrated across the road.

The BBMM results across all 5 years (2005–2009) indicated relatively high levels of permeability for pronghorn movement across US189. All animals (33/33)

Table 1. Resource utilization models used to compare pronghorn movements within 7 km of U.S. Highways 191 and 189 with landscape attributes in the upper Green River Basin, Wyoming, 2005–2009.

| <i>Model number</i> | <i>Model name</i> | <i>Number of parameters</i> |
|---------------------|--|-----------------------------|
| 1 | NDVI ^a + depart side ^b + (NDVI*depart side) | 5 |
| 2 | Distance to highway + depart side + (distance to highway* depart side) | 5 |
| 3 | Shrub ^c + depart side + (shrub*depart side) | 6 |
| 4 | NDVI + distance to highway + depart side + (NDVI*depart side) + (distance to highway*depart side) | 6 |
| 5 | NDVI + shrub + depart side + (NDVI*depart side) + (shrub*depart side) | 8 |
| 6 | Distance to highway + shrub + depart side + (distance to highway*depart side) + (shrub*depart side) | 8 |
| 7 | NDVI + distance to highway + shrub + depart side + (NDVI*depart side) + (distance to highway*depart side) + (shrub*depart side) | 10 |

^aNormalized difference vegetation index, a proxy of spatial variation in forage quality.

^bThe departing side of the highway, i.e., after an animal crosses.

^cShrub habitat.

that wintered east of US189 migrated across the road in the spring, some crossing multiple times (Fig. 3b). In fact, BBMM estimates indicated that the probability of pronghorn use during spring migration was highest across some parts of US189 (Fig. 3b). This highway was flanked by wildlife-friendly fencing.

Across all 5 years, during spring migration 55% (22/40) of pronghorn moving through Trapper's Point used a stopover (>1 location in a high-probability utilization distribution) on ridge tops or north-facing slopes (Fig. 3c). At Antelope Alley, an area with expanded municipal and private development that restricts animal movement to a bottleneck <1500 m wide, 100% ($n = 17$) of pronghorn used a stopover roughly 3 km before the impediment. The mean number of GPS locations within 1.6 km of the highway was significantly higher on the approach side (21.4 [SE 8.5]) than on the depart side (3.0 [SE 1.2]) ($p \leq 0.05$) during spring migration. During fall, the pattern was the same for pronghorn migrating in the opposite direction; the mean number of GPS locations within 1.6 km of the highway was 11.5 (SE 7.5) on the approach side and 2.0 (SE 0) on the departure side.

There appeared to be 2 predominant strategies among pronghorn crossing US191 at either Trapper's Point or Antelope Alley during spring migration in relation to their distance to the highway. Nine individuals increased use of areas close to the highway both before and after crossing ($n = 9/23$; Table 2). Eight other individuals increased use of areas farther from the highway ($n = 8/23$; Table 2). The other 6 individuals showed no significant pattern of use relative to distance to the highway. Because of this

variation in strategies, a consistent influence of distance to the highway was not evident at the population level for pronghorn crossing US191, despite the fact that this variable was statistically significant for 74% of pronghorn at the individual level (Table 2). In contrast, patterns of use relative to both NDVI values and shrub cover appeared to differ between the approach and departure sides of US191, as evidenced by the greater degree of consistency among individuals in direction and significance of the interaction terms for those variables (Table 2). A more detailed evaluation of those interaction terms revealed that pronghorn crossing US191 did not select areas with higher NDVI values (and thus, presumably, did not select higher-quality forage) that were available to them on either side of the highway. This pattern was stronger on the departure than on the approach side of the highway. When pronghorn approached US191 during spring migration, they avoided shrub habitat, whereas on the departure side of the highway they increased their use of shrubs.

Along US189, substantial variation among individuals in use of shrub habitat resulted in nonsignificant population-level effects of that variable (Table 2). However, the sign and significance of interactions between side of the highway and NDVI and between side of the highway and distance to the highway were much more consistent among individual pronghorn along US189 (Table 2). Further evaluation of those interaction terms revealed that pronghorn crossing US189 were increasing their use of areas close to the highway, but the magnitude of this relation was much stronger on the approach side of the

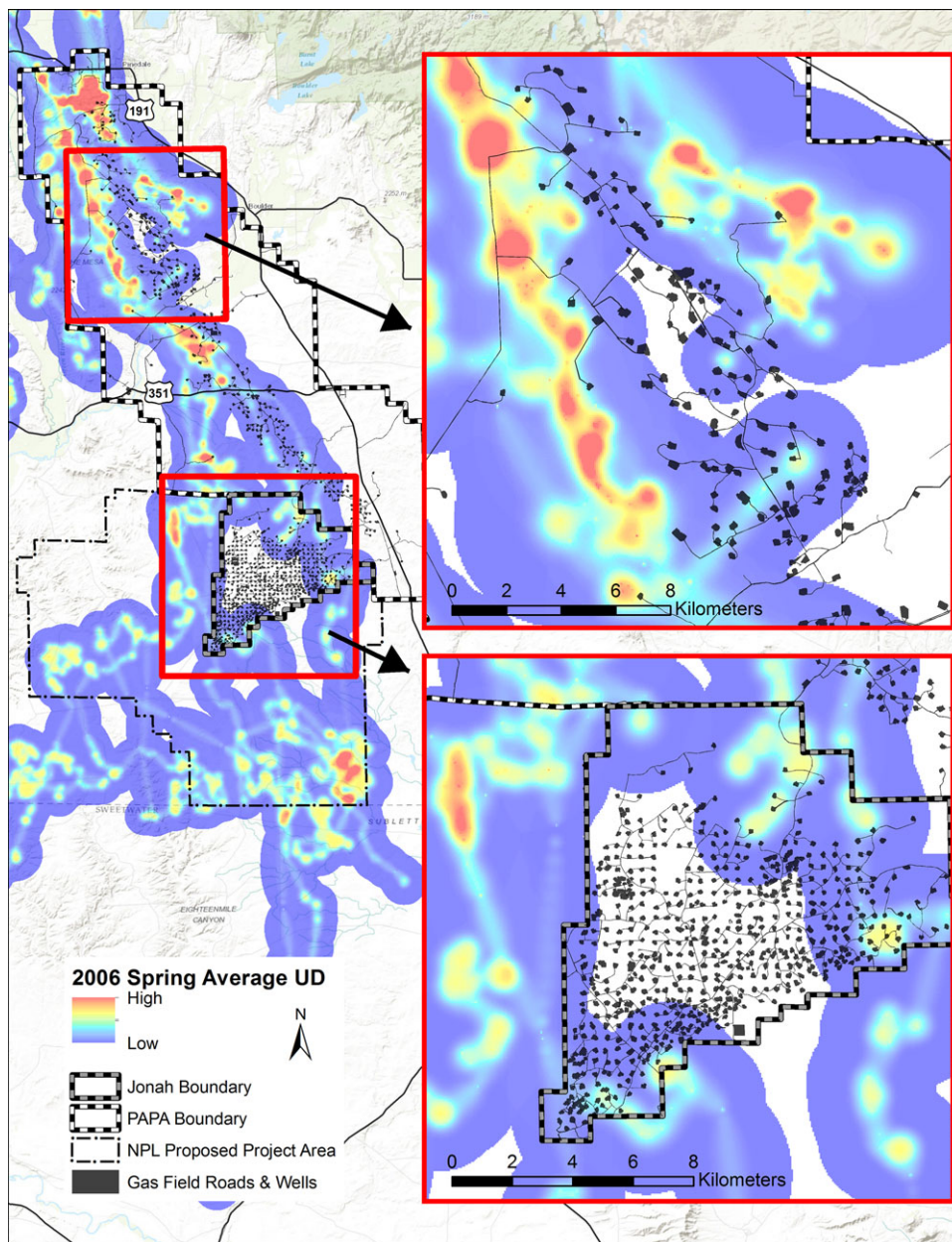


Figure 2. Population-level pronghorn utilization distribution (UD) for 2006 from Brownian bridge movement models overlaid with natural gas field development and the proposed normally pressured lance (NPL) natural gas field. Insets are enlargements of the spine of the Pinedale Anticline Project Area (PAPA) and the Jonah Field.

highway (Table 2). These animals also increased their use of high-quality forage (i.e., higher NDVI) on both sides of the highway, but this relation was slightly stronger on the approach side (Table 2).

Discussion

As development of petroleum resources continues to expand globally, the displacement of migratory wildlife and the threats to long-distance migration increase. In the GYE, migrating pronghorn reduced their use of the most intensively developed areas in 2 natural gas fields. This pattern of use is similar to winter resource selection patterns seen in pronghorn in the same system

(Beckmann et al. 2012). Although pronghorn showed low levels of use of developed gas fields, they exhibited high use of the still-undeveloped proposed NPL gas field (Fig. 2). We also detected stopover locations directly outside the more densely developed areas. These results suggest that pronghorn found sufficient resources to warrant stopovers in alternative locations, that stopovers outside gas fields were due to the perception of impediments, or both. Given that stopovers near migration bottlenecks (i.e., Trapper's Point on US191) were not associated with resources, we propose that stopovers outside developed gas fields were at least partly impediment driven.

Pronghorn show relatively high fidelity to migration routes (Sawyer & Lindzey 2000; Berger et al. 2006). Pronghorn behavior changed during migration in the

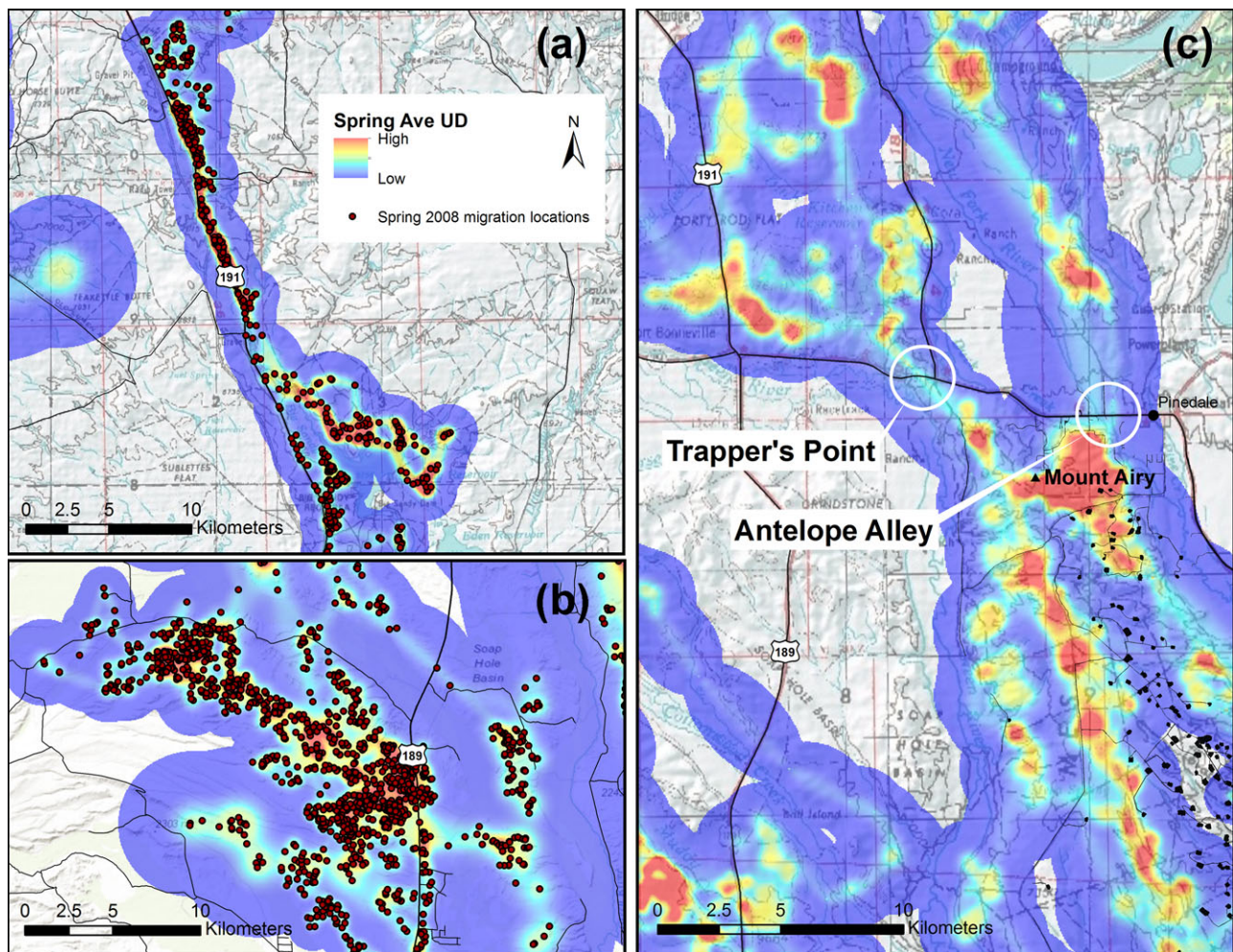


Figure 3. Results of population-level Brownian bridge movement models (BBMMs) for pronghorn in the upper Green River Basin, Wyoming: (a) high-volume traffic section of US191 in the southern Greater Yellowstone Ecosystem in 2008 (points represent animal locations used to calculate the BBMM [direction of pronghorn migration is from south to north]); nonwildlife-friendly fence surrounded the southern 33 km of this highway, (b) low-volume traffic section of US189 in 2008 (points represent animal locations used to calculate the BBMM [direction of pronghorn migration is from east to west]); wildlife-friendly fence surrounded this stretch of highway, and (c) bazard-induced stopovers, that is areas where migrating animals slow their progression from south to north on the landscape but are not using available high-quality resources (white circles encompass the associated bazard).

face of impediments such as roads, fences, and natural gas fields. The implication is that if pronghorn move more rapidly across impediments and select lower-quality forage along traditional migration routes because of impediments, there may be important fitness consequences (Gavin & Komers 2006).

The different roads, fences, and traffic volumes we considered resulted in a spectrum of behavioral responses by migrating pronghorn. At one extreme, the section of US191 in the southern region of the study site represented a complete barrier and appeared to be impassable to pronghorn. Conversely, animals from the same wintering herd had little trouble crossing other sections of the

same or a similar highway <40 km away. Fencing associated with these highways appeared to be an important contributing factor to the level of permeability. Barriers of this sort can effect dramatic changes in wildlife movements, resulting in genetic isolation and increased mortality rates (Beckmann & Hilty 2010; Dodd et al. 2011). Additionally, highways that increase stopover behavior may reduce animal fitness by reducing body condition (Gavin & Komers 2006).

Migrations can be restored if anthropogenic barriers, such as impermeable fences, are identified and removed or modified. Where the barrier itself cannot be changed, as in the case of a highway, construction of wildlife

Table 2. Estimates of standardized resource utilization function coefficients for interactive resource attributes for 45 migrating pronghorn in the upper Green River Basin, Wyoming, 2005–2009.

| Interactive resource attribute | Highway 191 | | | Highway 189 | | | | |
|---|--------------------------------------|------------------|--|--------------------------------------|---------|--|----|----|
| | mean standardized parameter estimate | 95% CI | number of pronghorn with use significantly associated with attribute | mean standardized parameter estimate | 95% CI | number of pronghorn with use significantly associated with attribute | | |
| | | | + | | | – | + | – |
| NDVI ^a *depart from highway | –0.0052 | –4.6713 – 4.6608 | 6 | 15 | –0.8114 | –16.5553 – 14.9326 | 5 | 16 |
| Distance to highway*depart from highway | 0.3033 | –2.5748 – 3.1814 | 9 | 8 | 8.6723 | –35.5817 – 52.9263 | 18 | 3 |
| Shrub habitat*depart from highway | 0.2030 | –1.7743 – 2.1802 | 10 | 5 | –0.3770 | –4.4364 – 3.6823 | 11 | 9 |

^aNormalized difference vegetation index, a proxy of spatial variation in forage quality.

over- and underpasses should be considered. BBMMs provide managers with the tools to target where road mitigation could occur. We acknowledge that these models will continue to be challenged and improved (e.g., Pozdnyakov et al. 2014), but even current models have successfully described ungulate migration for multiple species in the GYE and around the globe (Horne et al. 2007; Sawyer et al. 2009a; Bischof et al. 2012). It is not entirely clear how well RUFs approximate more traditional resource selection functions based on a use-availability design (Long et al. 2009; Kertson & Marzluff 2010; Hooten et al. 2013). However, for explicitly modeling utilization distribution as a response variable, while controlling for the spatial autocorrelation induced by the smoothing procedures used to estimate the utilization distribution, RUFs are the best available option (Marzluff et al. 2004; Millspaugh et al. 2006).

We found evidence that hazards along migration routes can be associated with stopover areas. Moreover, forage quality did not adequately explain pronghorn stopover behavior at certain sites. Therefore, relying on a resource-focused interpretation of stopovers may lead to inappropriate or unsuccessful management responses (e.g., appropriate candidate areas for road mitigation may not be recognized). The implications of our results are that migrating pronghorn may experience trophic mismatch leading to reduced fitness of summering herds (Post & Forchhammer 2008; Monteith et al. 2011).

The fact that we observed a reversed seasonal trend in stopover areas surrounding some US191 crossing locations further supports the idea that these areas are associated with the impediment rather than resources. These data on hazard-induced stopovers contribute to the understanding of migration behavior along a path. Ultimately, this knowledge contributes to conservation of long-distance migration by revealing key risk areas along routes. In future studies, adding snow measures may enhance understanding of the drivers of pronghorn migration. In addition, evaluating the effects of NDVI across entire population-level migration routes will facilitate assessment of plant phenology as an overall driver of pronghorn migration and contribute to the understanding of potential trophic mismatch.

Two possibilities should be considered with regard to the movement corridors between stopovers, where animals travel quickly. These areas may represent the limited capacity of local resources to support large numbers of animals. Alternatively, they may contain stressful or distracting localized hazards that cause animals to forgo use of their high-quality resources. In either case, an unmitigated migration impediment could eventually extirpate such a route and lead to loss of migration.

Our results demonstrate that stopovers during ungulate migration sometimes indicate impediments to movement, rather than the presence of important energetic resources. Unless stopovers associated with

hazards are mitigated, migrating ungulate populations may be negatively affected by stressful behavioral changes, trophic mismatches, or genetic isolation. By using appropriate modeling approaches to disentangle the causes of stopovers, managers can target efforts to achieve great conservation success.

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Supporting Information

An aerial photograph of the Trapper's Point bottleneck in the Upper Green River Basin, Wyoming, 2013 (Appendix S1), is available online. The authors are solely responsible for the content and functionality of this material. Queries (other than absence of the material) should be directed to the corresponding author.

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