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Migratory behavior can benefit wildlife populations by providing access to seasonal habitats. However, migrations are increasingly threatened by anthropogenic barriers such as fences, roads, and railways. Animal migrations can be severed by such barriers, and these linear features are projected to increase globally. In Wyoming, USA, pronghorn (*Antilocapra americana*) habitat has become fragmented by anthropogenic barriers, which have likely impacted pronghorn migrations and access to alternative habitats. Importantly for pronghorn movement, barriers are on a spectrum of permeability. Any management action to mitigate these anthropogenic linear features will need to assess the degree to which these different features are barriers to pronghorn movement. My first study objective (Chapter 1) was to quantify the degree to which fences, county roads, state roads, railways, and interstates inhibit pronghorn movement and their access to habitats. I used a large, collaborative GPS collar dataset (n = 1010 animal years) to study pronghorn movements across southern Wyoming relative to these barriers. My finding that Interstate 80 was the most severe barrier to pronghorn movement led to the question of how pronghorn migrations could be restored across Interstate 80 (Chapter 2). Using the same GPS collar dataset, I used habitat and connectivity models to visualize the most likely locations of migration corridors prior to the development of Interstate 80. My corridor predictions had high overlap with locations where pronghorn still attempt to cross. Overall, my thesis has applications for pronghorn management as well as broader implications for other migratory wildlife inhibited by barriers.

PRONGHORN MIGRATIONS AND BARRIERS:

PREDICTING CORRIDORS ACROSS WYOMING'S INTERSTATE 80 TO RESTORE MOVEMENT

By

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. Nowhere to run: semi-permeability of anthropogenic barriers influences effective habitat

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ABSTRACT

Animal movement can mediate the ecological consequences of fragmentation, however, barriers, such as fences, roads, and railways, are becoming a pervasive threat to wildlife. Barriers exist along a spectrum of permeability to movement, which has led to the prediction that less permeable barriers should lead to a larger effective loss of habitat than more permeable barriers. Advances in movement ecology have provided the tools for researchers to better understand the permeability of barriers to animal movement. Pronghorn (*Antilocapra americana*) habitat in western North America has been fragmented by anthropogenic linear networks. Although it is recognized that pronghorn are sensitive to barriers, neither the permeability of barriers nor their influence on effective habitat loss have been quantified. We used a large GPS collar dataset of pronghorn (n = 1010 animal years) in Wyoming, USA, to first quantify the permeability of five different anthropogenic barriers, including fences, county roads, railroads, state roads, and interstates. Next, we assessed how each barrier influenced pronghorn habitat use as indexed by i) the area used during winter, ii) the mean daily displacement during winter, iii) and the ability to avoid snow relative to the density of barriers on winter range. Pronghorn were over 300 times less likely to cross Interstate 80 than other major highways. Pronghorn winter range area and displacement were not influenced by barriers within their core winter range, however pronghorn were influenced by barriers on the periphery of their winter range. Yet, the density of the interstate and railroads, state roads, and fences all had similar effects on pronghorn winter range and daily displacements. Pronghorn avoidance of snow was not affected by the densities of barriers either within core or exploratory winter range. How pronghorn use their current habitat is likely influenced by the density of both semi-permeable and nearly impermeable barriers. Our results add to a growing body of literature on how movement behavior mediates the ecological consequences of semi-permeable barriers and their resulting fragmentation effects.

INTRODUCTION

Anthropogenic habitat fragmentation is one of the greatest threats to biodiversity and ecosystem function (Haddad et al. 2015, Crooks et al. 2017). Nonetheless, the ecological consequences of fragmentation per se — independent of habitat loss — remain challenging to identify (Hadley and Betts 2012, Fahrig 2017). This challenge exists, in part, because whether a landscape is considered to be fragmented depends on how species perceive and move through it (With et al. 1997). Within the same landscape, different species can be effectively connected or isolated from habitat patches due to their movement behavior (Wiens 1989, Ricketts 2001). Behavior, along with landscape structure, determine the degree to which a species' habitat is functionally connected (Taylor et al. 1993, Coulon et al. 2004, Broquet et al. 2006). As such, without first accounting for movement behavior, the patchiness of habitats does not necessarily imply habitat fragmentation. Meanwhile, the growing subdiscipline of movement ecology has contributed to our understanding of the interaction between an animal's movement and the landscape (Nathan et al. 2008, Cagnacci et al. 2010). Incorporating the methods of movement ecology into fragmentation research will improve quantification of the ecological consequences of anthropogenic disturbance.

Anthropogenic linear features (e.g., roads, railways, and fences) have become a ubiquitous disturbance for many wildlife species (Ibisch et al. 2016). For example, in the contiguous United States all landlocked habitats are within 35 km of a road (Watts et al. 2007). Globally, the length of road and railway networks are projected to expand 60% by 2050 (Dulac 2013), meanwhile fences are increasingly used to demarcate private property (Li et al. 2017, Løvschal et al. 2017, Mcinturff et al. 2020). Linear features can directly impact wildlife populations through vehicle collisions or fence entanglement (Jaeger et al. 2005). When linear features restrain animal movement, however, they can pose a more pervasive indirect threat to populations (Forman and Alexander 1998, Jaeger et al. 2005). By limiting movement, linear features fragment habitat, which can increase local extinction rates, reduce colonization rates, and reduce available habitat (Jaeger et al. 2005). Barrier effects cause an effective loss of habitat because wildlife underutilize otherwise available habitats (Dyer et al. 2002, Eigenbrod et al. 2008, Fahrig and Rytwinski 2009).

Linear features exist on a spectrum of permeability, and are rarely complete barriers to animal movement (Sawyer et al. 2013). The degree to which an animal can cross a linear feature is conditional on its movement behavior as well as the structure of the barrier, which together influence permeability. Given the tight links between movement and habitat use, less permeable (more severe) barriers should have a greater effect on habitat use than more permeable (less severe) barriers (Dyer et al. 2002, Beyer et al. 2016). Impermeable barriers reduce the habitat available to species; however, when barriers are semi-permeable, their effects on habitat availability are less clear (Kozakiewicz 1993, Beyer et al. 2016). At habitat edges, slight differences in permeability substantially alter larger-scale processes such as emigration and population dynamics (Stamps et al. 1987, Ries et al. 2004). Along barriers, differences in permeability may similarly alter larger-scale processes at a nonlinear rate. For instance, many species of mice avoid crossing gravel roads, yet enough individuals can still cross to facilitate gene flow (Merriam et al. 1989, Schtickzelle and Baguette 2003). By increasing the severity of fragmentation, semi-permeable barriers likely reduce habitat available to individuals (Beyer et al. 2016), yet this expectation has rarely been tested. Advances in movement ecology (e.g., Kranstauber et al. 2012, Thurfjell et al. 2014) provide the tools to quantify the species-specific effects of fragmentation by semi-permeable barriers on animal movement and habitat use.

Pronghorn (*Antilocapra americana*) habitat in the sagebrush steppe of western North America has been intersected by linear networks of roads and fences (Knick and Rotenberry 1997, Davies et al. 2011). Pronghorn have a low success rate of jumping over fences and often will either cross under the fence if the bottom wire is high enough from the ground, or forgo crossing them (Byers 1997, O’Gara and Yoakum 2004, Harrington and Conover 2006). When free to move, pronghorn are facultative migrants, where the distance and direction of movement is conditional on the severity of the winter (Bruns 1977, O’Gara and Yoakum 2004). Barriers that inhibit the migrations of pronghorn have contributed to population crashes by limiting access to available habitats (Martinka 1967, Oakley and Riddle 1974, Barrett 1982, Ryder et al. 1984). For example, in 1983 a winter storm in south-central Wyoming forced pronghorn to move to avoid snow, but a recently erected woven-wire fence severed access to alternative winter range. Winter mortality that year was estimated at 35–70% of the herd (Ryder et al. 1984). To mitigate such die-offs, management guidelines suggest modifying barriers to be more permeable (Yoakum et al. 2014). The implicit assumption is that improving the permeability of barriers will promote pronghorn use of surrounding habitat. It remains unclear, however, the degree to which improving permeability of barriers can facilitate habitat use on a larger-scale. Quantifying the relationship between barrier permeability and pronghorn habitat use is thus warranted to guide habitat management for pronghorn across its range.

We sought to quantify the permeability of anthropogenic linear features — fences, county roads, state roads, railroads, and interstates — and to identify the most severe movement barriers to pronghorn. We expected that pronghorn near less permeable barriers should have less access to habitat than pronghorn near more permeable barriers. Thus, we expected that habitat use as measured by winter range area (E. 1) and daily displacement (E. 2) should increase as nearby barriers become more permeable. Additionally, because pronghorn avoid snow, the ability of pronghorn to avoid snow (E. 3) should be most constrained by the density of least permeable barriers. To test these predictions, we used a large, collaborative GPS movement dataset of thirteen years of pronghorn movements within seven different populations across southern Wyoming. Half of the world's pronghorn are found in Wyoming, and the herds in southern Wyoming are at the core of the species range (O'Gara and Yoakum 2004). Our barrier analysis thus assessed how fragmentation from semi-permeable barriers limits effective habitat use across a large swath of occupied pronghorn habitat.

METHODS

Study Area

We used a GPS dataset of movement from seven pronghorn populations found in southern Wyoming, USA: Red Desert, Bitter Creek, Sublette, Medicine Bow, Baggs, Uinta-Cedar, and Carter Lease herds (Fig. 1.1). The Medicine Bow and Baggs herds were in south-central Wyoming, an arid sagebrush-steppe that had Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) as the predominant vegetation cover, with mountains to the west characterized by alderleaf mountain mahogany (*Cercocarpus montanus*), aspen (*Populus tremuloides*), and limber pine (*Pinus flexilus*) (Taylor et al. 2016). The Bitter Creek, Sublette, Uinta-Cedar, and Carter Lease herds were located in south-central to south-western Wyoming, where Wyoming big sagebrush was the predominant vegetation with interspersed grassland. Low-lying areas had black greasewood (*Sarcobatus vermiculatus*) and Gardner's saltbush (*Atriplex gardneri*). High elevation areas were predominantly mountain big sagebrush (*A. tridentata vaseyana*), mixed shrubland, and aspen (Reinking et al. 2018). All pronghorn captures followed protocols in accordance with guidelines from the American Society of Mammologists (Sikes 2016), Wyoming Game and Fish Department (Chapter 33s-1104, 1162, 923, and 742), and University of Wyoming Institutional Animal Care and Use Committee (protocols 20170227MK00231-01, 20180306MK00297-03, 20131028JB00037, and 01012010).

GPS Data

We cleaned GPS collar data to remove any GPS point with a step greater than 20 m/s or exactly 0 m/s to the subsequent fix. Additionally, we removed erratic 'spike' points by removing any point with a median or mean distance greater than 25 km or cosine step angle correlation greater than 0.97 from the previous fix and the subsequent fix (Bjørneraas et al. 2010). These thresholds were visually verified and resulted in a 4.8% reduction in the dataset of points that were likely collar error.

To calculate permeability to anthropogenic features, we used a step-selection function to quantify the likelihood of crossing linear features. Because of the sensitivity of step-selection functions to different intervals in time between points, we subsampled the dataset to seven or eight hour fix rates (a 29.6% reduction in the dataset) (Thurfjell et al. 2014). Pronghorn in the Medicine Bow and Uinta-Cedar populations had seven-hour fix rates, all others had eight-hour fixes. To reduce pseudoreplication, we randomly sampled one step per day for every animal year. Additionally, we removed any animal years that had less than 90 GPS fixes to ensure convergence (loss of 14 animal years).

To assess habitat availability, we used pronghorn winter range as a proxy. We defined winter range between 31 December and 14 March, which were the respective 75% percentile of when autumn migrations ended and 25th percentile of when spring migrations began (visualized through net-squared displacement). We only calculated winter ranges for animals tracked for at least 7 days in a given year (loss of n = 38 animal years) and had more than 31 GPS points (loss of n = 2 animal years). We defined core winter ranges using a dynamic Brownian Bridge as the 95% contour of the utilization distribution (Kranstauber et al. 2012). Movement barriers can circumscribe the outer bounds of pronghorn home ranges (e.g., Sheldon 2005), which would often fail detection from our definition of core winter range. Therefore, we ran a separate analysis where the core winter range of pronghorn was buffered by the average weekly distance pronghorn moved, 22.86 km (hereafter, exploratory winter range). Differentiating between core and exploratory winter range provided insight to the differences between interior barriers and barriers at the border of each animal's winter range for a given year. Additionally, we calculated the mean daily displacement relative to the density of barriers within core and exploratory winter range. We first calculated the daily cumulative distance pronghorn moved for each year, then averaged daily distance within that year to get a mean daily displacement for each animal year. Only animal years with associated winter range estimates were included in the mean daily displacement analysis (loss of n = 40 animal years). Finally, to assess the ability of pronghorn to avoid negative features (high snow depth), we calculated the avoidance of snow while on winter range at the exploratory scale. Animal years were excluded if they were missing associated winter ranges or were collected before 2003, before which there are not snow estimates available through SNODAS (see Predictor Variables).

Predictor Variables

In the permeability analysis, barrier types were separated into five separate layers: fences, railroads, county roads, state roads, interstates, and railroads. Fence data were compiled by combining existing fence data from the Wyoming Cooperative Fish and Wildlife Research Unit (available through Wyoming GeoSpatial Hub), Wyoming Game and Fish Departments (Teal Cufaude, Laramie Region), and Bureau of Land Management (Robert Mathis, High Plains District). Since these data were compiled, there have likely been some changes as to fence presence; nonetheless, in our study area there have not been substantial changes in land ownership, a strong correlate to fence presence (Poor et al. 2014), so we are comfortable with the assumption that this fence data accurately represents fence locations throughout our study period with low bias. Road and railroad data were available from the Wyoming Department of Transportation. We categorized road layers as either county roads, state roads or interstates. We classified county roads as all roads with county administration that were two-lane paved roads without right-of-way fences. State roads were classified as two- or four-lane state highways with right-of-way fences. Interstates consisted of Interstate 80 and Interstate 25, four-lane roads with right-of-way fences or game-proof fences. Railroads consisted of the two major railroads in Wyoming. Because state roads and interstates often had right-of-way fencing, the fence data were cropped to remove any fences within 250 m of these linear features. Railroads and interstates were separate in the step-selection function, but the densities of each were summed for all further analysis because their densities were autocorrelated (variance inflation factor > 2; Zuur et al. 2009); the railroads were often next to interstates. To estimate snow experience we used the snow water equivalent, available through SNODAS (SWE; National Operational Hydrologic Remote Sensing Center 2004).

Statistics and Analysis

We used a step-selection function, with ten random steps for every observed step (the straight-line distance between consecutive GPS fixes), to assess the likelihood of crossing different barriers (Fortin et al. 2005, Thurfjell et al. 2014). Random steps were simultaneously drawn by identifying the used step between each source and target point, then using the distribution of observed step lengths and angles across the dataset, with a maximum length of 4741 m (the 99th percentile of empirical pronghorn step lengths for every 7–8 hours between GPS fixes). Movement outcomes were binary variables indicating whether a given barrier was crossed during a step. To reduce bias in estimated step selection function coefficients, we included step length to correct for bias (Forester et al. 2009). We used a mixed effects conditional Poisson model with a large, fixed variance of 10^3 to avoid shrinkage of the intercepts towards the overall mean, which would bias our results (Muff et al. 2020). We included random slopes for each of the five linear features relative to each animal year, nested by their population to account for the hierarchical structure of our dataset. When there are repeated measures within replicates then random intercept models alone often do not sufficiently correct for pseudoreplication (Schielzeth and Forstmeier 2009). Additionally, including random slopes for each of the five linear features provided the opportunity to assess whether there were differences in barrier permeability between individuals. Our final sample size for the step-selection function analysis was n = 1010.

We used multiple regression to compare the area of winter range against the densities of barriers within core and exploratory winter ranges. Barrier densities were estimated as the density (km/km^2) of each barrier within each animal core or exploratory winter ranges for each year, while the response variable was the 95% contour area of the utilization distribution. We fit a generalized mixed effects model with a gamma distribution and population as a random intercept to the core and exploratory winter range models. In the winter range analysis, sample sizes were n = 682 animal years.

Similar to the winter range analysis, we regressed mean daily displacement against the density of each barrier at the core and exploratory winter range. We applied a generalized linear mixed effect model with a gamma distribution to predict the mean displacement, given the barrier density from the core or exploratory winter ranges. Each model had population as a random intercept. In this analysis, sample size was n = 682 animal years.

To assess if the density of barriers affected the ability of pronghorn to avoid snow while on winter range, we calculated the selection ratio (Manly et al. 2002) of snow that pronghorn experienced relative to the available snow for each day. We defined availability as the exploratory winter range for each animal year. For each animal year, and for each day during the winter, we extracted the snow water equivalent of all GPS points on winter range (used) and each snow water equivalent pixel within the winter range contour (available). We then divided mean snow water equivalent for all used points within that day by the mean available snow water equivalent of that day to get daily selection ratios. Selection ratios were then averaged by animal year. We removed all sampled days with no available snow cover. We used a linear mixed effects regression with population as a random intercept to evaluate selection ratios as a function of barrier density. In the snow avoidance analysis, sample size was n =584 animal years.

For each model (step selection function, winter range regression, displacement regression, and snow avoidance regression), we compared model fit of the full model with all fixed effects against a null model with only the random intercept. For each analysis, if the full model was within 3 AIC of the null model then the model was considered not explanatory.

All statistics and analysis used R-3.6.2 (R Core Team 2016); packages used included ‘glmmTMB’ for the mixed effects conditional Poisson regression and mixed beta regression (Brooks et al. 2017), and ‘lme4’ for linear and generalized linear mixed effects models (Bates et al. 2015).

RESULTS

All five anthropogenic linear features were significant barriers to pronghorn movement, as demonstrated by negative coefficients from the step selection function with 95% confidence intervals that did not overlap 0 (Table 1.1). The interstate was the most severe barrier to pronghorn movement (Fig. 1.2). Pronghorn were over 300 times less likely to cross the interstate than state roads, the second most severe barrier. Pronghorn were four times less likely to cross state roads than railroads, the third most severe barrier. Pronghorn were two times less likely to cross railroads than fences. Finally, pronghorn were almost two times less likely to cross a fence than county roads. Although the interstate was the most severe barrier, only a quarter of the sampled pronghorn ever encountered the barrier (i.e., were within a step length of the interstate; Table S1.1).

Pronghorn occupied less area when there was a higher density of fences (Fig. 1.3). Pronghorn lost 104 m^2 of core winter range for every 1 km/km^2 increase in fence density (Table 1.2). The effects of barriers on exploratory winter range were stronger than on core winter range. Pronghorn with a higher density of fences, railroads and interstate within their exploratory winter range occupied less area (Fig. 1.3). Pronghorn lost 187 m^2 of their exploratory winter range for every 1 km/km^2 increase in fence density, 74 m^2 for every 1 km/km^2 increase in state road density, and 244 m^2 for every 1 km/km^2 increase in railroad and interstate density (Table 1.2). Pronghorn gained 63 m^2 of winter range for every 1 km/km^2 increase in county road density within exploratory winter range.

Pronghorn moved less when there was a higher density of fences and state roads within core winter range (Fig. 1.4). The daily distance pronghorn moved was 66 m shorter for every 1 km/km^2 increase in fence density and 35 m shorter for every 1 km/km^2 in state road density within core winter range (Table 1.3). Within exploratory winter range, the daily distance pronghorn moved was 78 m shorter for every 1 km/km^2 increase in fence density, 54 m shorter for every 1 km/km^2 in state road density, and 63 m shorter for every 1 km/km^2 in interstate and railroad density (Table 1.3).

Pronghorn avoided snow across populations (mean selection ratio = 0.768, 95% confidence interval 0.744 – 0.792). Contrary to our predictions, however, the model with barrier density fixed effects was no more explanatory than the null model with only random intercepts as including the fixed effects raised the AIC greater than 3 from the null model.

DISCUSSION

Pronghorn in southern Wyoming rarely crossed five different anthropogenic linear features, with the interstate being the most severe barrier by several orders of magnitude. Semi-permeable barriers have been hypothesized to exacerbate habitat loss (Dyer et al. 2002, Beyer et al. 2016), which was supported by our findings that the density of barriers caused pronghorn to occupy smaller winter ranges and move shorter distances. Pronghorn habitat use was constrained by movement barriers, but the larger-scale barrier effects on habitat use were not proportional to permeability. In particular, the interstate's influence on pronghorn winter range size and displacement was no greater than the influence of fences, and had no effect at the core winter range scale. Contrary to our predictions, barrier density on winter range did not influence the ability of pronghorn to avoid snow. Overall, our results indicate that pronghorn movements were severely constrained by barriers, with cascading (but noisy) effects on habitat use.

Pronghorn avoided crossing interstates more than any other barrier, but living close to the interstate did not reduce winter range size more than living close to fences. Rather, pronghorn winter ranges decreased at a similar rate for an increasing density of fences, and interstates and railroads. Despite lower foraging times and increased vigilance along roads (Gavin and Komers 2006), pronghorn have been observed to follow along major highways for up to 10.5 km (Dodd et al. 2011, Gates et al. 2012). Without ever crossing, pronghorn can partially compensate for the barrier effects of roads by elongating their winter range along the barrier. In contrast, pronghorn may be boxed in by the higher density of fences, despite such barriers being easier to cross. Within the rural US, the linear extent of fences can be up to 16 times greater than paved roads (Jakes et al. 2018). Even barriers that are relatively permeable to animal movement can cause an effective loss of habitat if they occur at high density. For example, elk (*Cervus canadensis*) are unable to access habitat unaffected by roads when the density of the road network exceeds 1.6 km/km^2 (Frair et al. 2008). In a study similar to ours, Jones et al. (2019) found that doubling the prevalence of fences can cause pronghorn to lose access of up to 11% of high-quality habitat. Wildlife have been hypothesized to lose their ability to access habitats at a nonlinear rate, as thresholds in disturbance disrupt connectivity (With and Crist 1995). Our results suggest that the permeability and density of barriers may similarly interact to disrupt pronghorn habitat use, although we did not attempt to identify threshold levels.

We were surprised to not find an effect of barriers on snow avoidance, since there are fairly consistent case studies documenting this effect (Oakley and Riddle 1974, Bruns 1977, Ryder et al. 1984). It is possible that none of the 12 years in our dataset were high snow years. However, pronghorn still avoided snow, which indicates that snow levels were high enough to detect an avoidance, just not relative to barriers. The lack of an effect of barrier density on snow avoidance may be explained by snow-free refuges created by high grade roads (Bruns 1977). Our snow data were too coarse of a scale to observe snow refuges that occur on the leeward side of large roads, which could minimize the snow pronghorn experience precisely because those barriers intersect their winter range. Increased use of habitat along high grade roads and railways has likewise been identified in the behavior of mule deer (*Odocoileus hemionus*) and elk (Rost and Bailey 1979), Mongolian gazelles (*Procapra gutturosa*) and onager (*Equus hemionus*) (Ito et al. 2013). Linear anthropogenic barriers can cause a heterogeneous distribution of snow, so that the accumulation of snow may depend on the arrangement of barriers. The degree to which barriers affect the ability of pronghorn to avoid snow thus may also be confounded by their orientation on the landscape. Although snow cover data was not available at a scale fine enough to test, snow refuges may explain our result that barriers had seemingly no effect on snow avoidance.

Pronghorn space use was more obstructed by barriers that occur within their exploratory winter range compared to the core winter range. Pronghorn home ranges are often circumscribed by barriers (Sheldon 2005), which could explain why we observed a stronger relationship between habitat use and barrier density at the larger-scale of the exploratory winter range. Within core winter range, pronghorn are likely capable of adjusting their home range behavior to minimize exposure to barriers. When pronghorn need access to habitats outside their core areas, however, barriers likely restricted such movements. Notably, for species such as pronghorn, movement to alternative habitats is fundamental to their survival (Barrett 1982). For example, pronghorn population declines are often attributed to severe winters when high snowpack at a large-scale limits access to alternative habitats (Christie et al. 2015, Reinking et al. 2018). Pronghorn winter distributions are often a result of snow conditions (Barrett 1982, Deblinger and Alldredge 1984, Collins 2016), which suggests that to optimally exploit resources, pronghorn depend on a connected landscape to access ephemeral winter habitats. In unpredictable environments, the population-level benefits of migration and nomadism outweigh more restricted movement tactics so long as the landscape remains connected (Teitelbaum and Mueller 2019). For example, during a high-snowpack winter in Mongolia, a spatially confined population of Przewalski’s horses (*Equus ferus przewalskii*) experienced greater mortalities than a nearby population of onager, which were more exploratory and able to relocate to alternative habitats (Kaczensky et al. 2011). Because the benefits of nomadism depend on landscape connectivity, highly mobile nomadic species should be more threatened by movement barriers than residents or migrants (Teitelbaum and Mueller 2019). By limiting movements to alternative habitats, fragmentation created by barriers can lower carrying capacity (Boone and Hobbs 2004), and the severity of this lower carrying capacity is likely determined by movement behavior. The causal link we have identified between movement barriers and habitat use suggests that movement barriers fundamentally influence the ability of pronghorn to access critical seasonal habitats.

Our step selection function to estimate permeability assumed that the permeability of barriers would not be confounded by different habitat types on the other side. The propensity to cross barriers can vary depending on habitat type or quality. Red deer (*Cervus elaphus*), for example, were more likely to cross roads when motivated by access to nutritious pastures (Meisingset et al. 2013). Additionally, we assumed that likelihood of crossing did not change throughout the year. Snow can complicate the barrier effects of fencing, where intermediate snow levels prevent pronghorn from crawling under fences, and high snow levels can allow pronghorn passage over fences or onto exit ramps of roads (O'Gara and Yoakum 2004). Additionally, our analysis required the assumption that barrier permeability did not change with availability (i.e., there were no functional responses to barriers; Mysterud and Ims 1998). Our study included a large sample size across a large swath of land, all of which gives us confidence that any bias in our approach resulting from snow cover or habitat effects should still represent the general permeability of these barriers.

For pronghorn, a highly mobile ungulate, barriers of different permeability and prevalence constrict winter range size and limit movement. Anthropogenic linear features are expanding globally (Forman and Alexander 1998), and our findings illustrate for one species how movement barriers scale up to influence habitat use. As the amount of habitat available is diminished by barriers, the effects of barriers will likely threaten population viability and carrying capacity (Boone and Hobbs 2004, Fahrig and Rytwinski 2009). Improving the permeability of barriers will be necessary to maintain existing patterns of wildlife movement. Whether, where, and how to mitigate barriers will be conditional on the system and the species life history. Crossing structures (e.g., McDonald and St. Clair 2004, Clevenger and Waltho 2005, Xia et al. 2007, Gagnon et al. 2011, Seidler et al. 2018), fence modifications (e.g., Knight et al. 1997, Burkholder et al. 2018, Jones et al. 2020), and mobile protected areas (Rayfield et al. 2008, Bull et al. 2013) can all be effective conservation measures for mobile species across diverse systems. In fragmented landscapes, restoring connectivity across semi-permeable barriers holds promise to conserve animal movement and enhance fragmented habitats.

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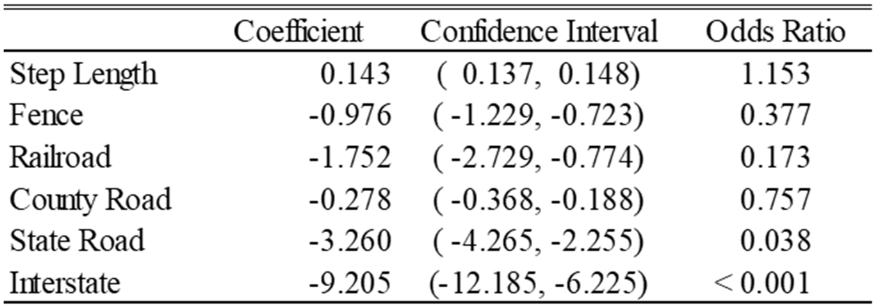
CHAPTER 1 TABLES

Table 1.1. Population odds ratios of crossing. Step length (km) was included as a predictor to account for availability. Beta coefficients are the calculated effect of each predictor on crossing different linear features using a step-selection function. Population and animal year were included as nested random intercepts with each barrier a random slope. Confidence intervals of the beta coefficient are at the 95% confidence level. None of the confidence intervals overlapped zero. Odds ratios are the exponentiated beta coefficients, where less than 1 indicates higher likelihood of avoidance to crossing.



	Coefficient	Confidence Interval	Odds Ratio
Step Length	0.143	(0.137, 0.148)	1.153
Fence	-0.976	(-1.229, -0.723)	0.377
Railroad	-1.752	(-2.729, -0.774)	0.173
County Road	-0.278	(-0.368, -0.188)	0.757
State Road	-3.260	(-4.265, -2.255)	0.038
Interstate	-9.205	(-12.185, -6.225)	< 0.001

Table 1.2. Coefficients with 95% confidence intervals of the effect of barrier density on winter range area within core and exploratory winter range. Coefficients are from a generalized linear mixed effects model with population as a random intercept. Bold coefficients have 95% confidence intervals that do not overlap 0.Coefficents are in km/km^2, n = 682 animal years.

	Core Winter Range		Exploratory Winter Range	
	Coefficient	Confidence Interval	Coefficient	Confidence Interval
Fence	**-0.104**	**(-0.172, -0.036)**	**-0.187**	**(-0.262, -0.111)**
County Road	-0.020	(-0.085, 0.045)	**0.063**	**(0.008, 0.118)**
State Road	-0.040	(-0.105, 0.025)	**-0.074**	**(-0.138, -0.010)**
Interstate and Railroad	0.018	(-0.051, 0.087)	**-0.244**	**(-0.303, -0.184)**

Table 1.3. Coefficients with 95% confidence intervals of the effect of barrier density on mean daily displacements within core and exploratory winter range. Coefficients are from a generalized linear mixed effects model with population as a random intercept. Bold coefficients have 95% confidence intervals that do not overlap 0. Coefficients are in km, n = 682 animal years.

	Core Winter Range		Exploratory Winter Range	
	Coefficient	Confidence Interval	Coefficient	Confidence Interval
Fence	**-0.066**	**(-0.086, -0.046)**	**-0.078**	**(-0.101, -0.054)**
County Road	0.006	(-0.013, 0.025)	0.013	(-0.005, 0.032)
State Road	**-0.035**	**(-0.052, -0.018)**	**-0.054**	**(-0.075, -0.033)**
Interstate and Railroad	0.005	(-0.013, 0.024)	**-0.063**	**(-0.081, -0.044)**

CHAPTER 1 FIGURES

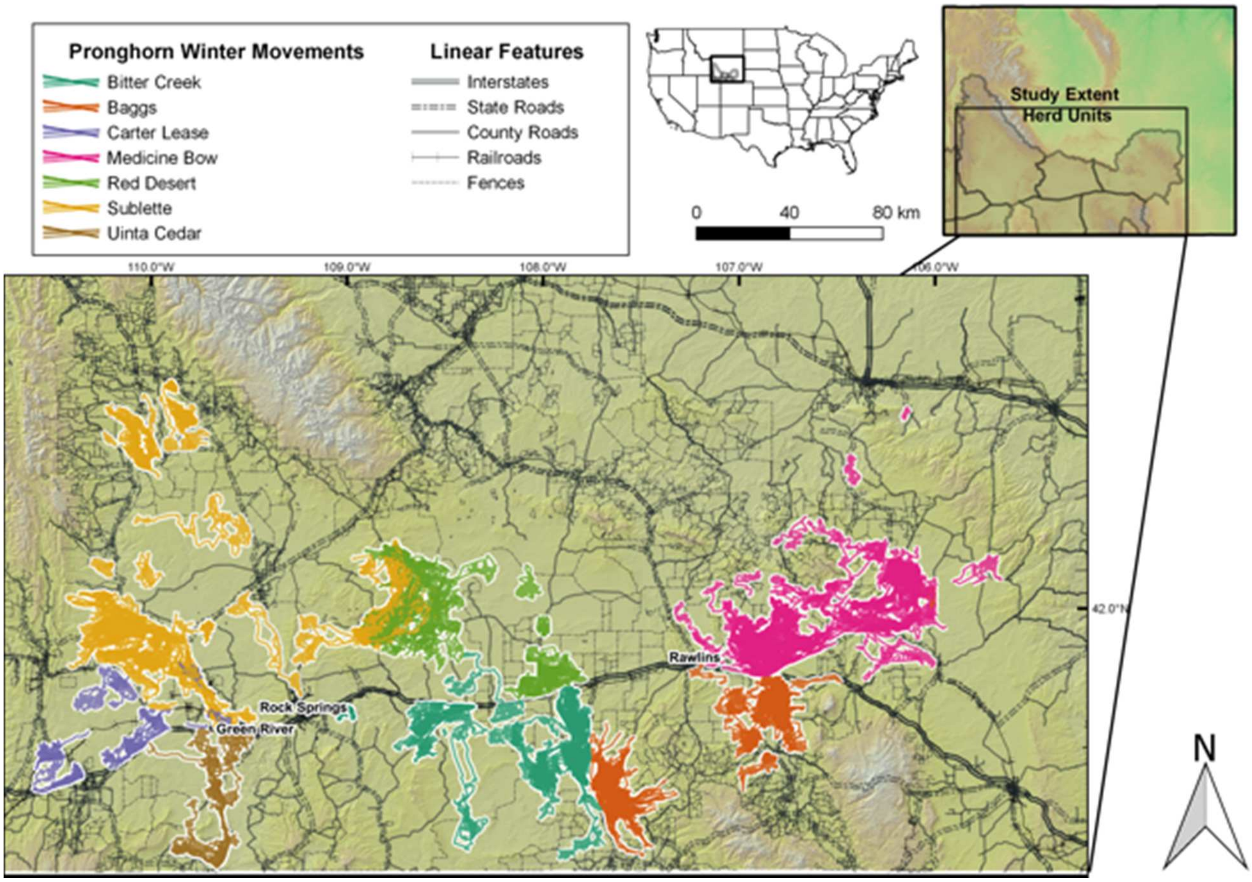


Figure 1.1. Study area map with pronghorn movements during the winter from the seven different populations used in this study.

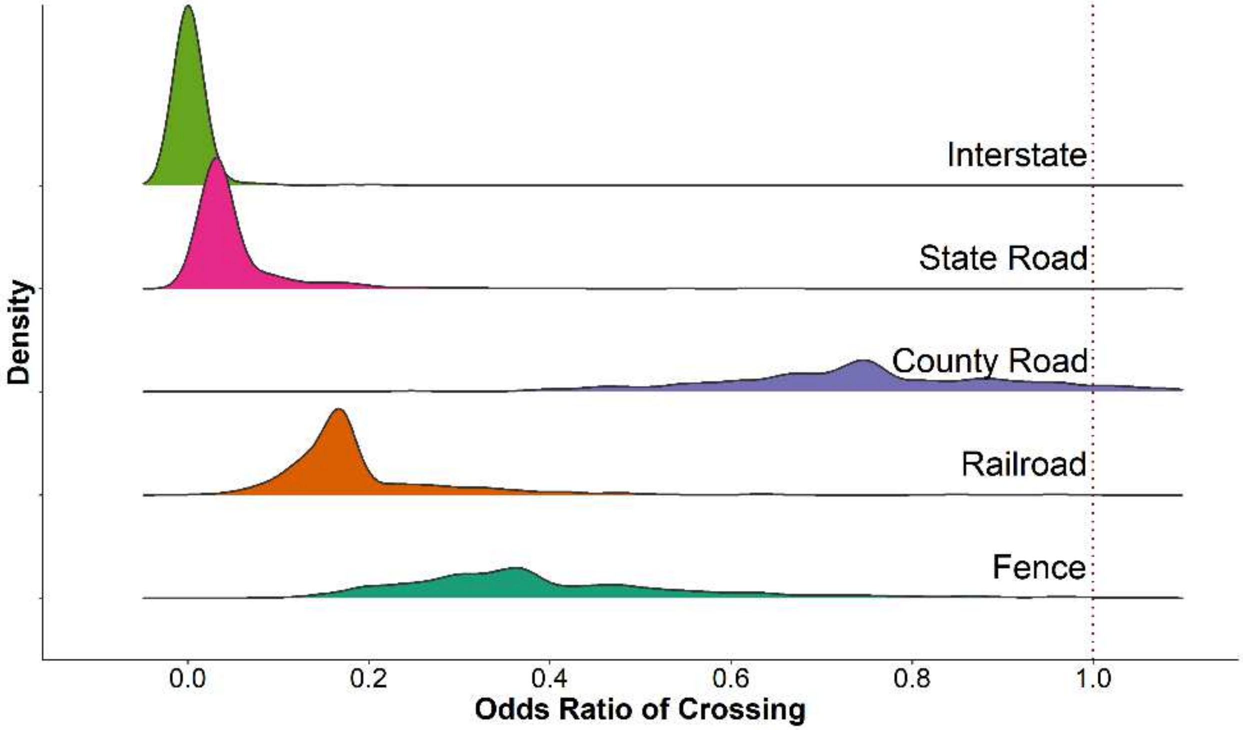


Figure 1.2. Odds ratios for individual animal years to crossing each anthropogenic linear feature, where the farther from 1 (no effect) suggests stronger avoidance to crossing the barrier type. We estimated the distribution of odds ratios by exponentiating the population coefficients for each barrier with the random slopes of the n = 1010 animal years.

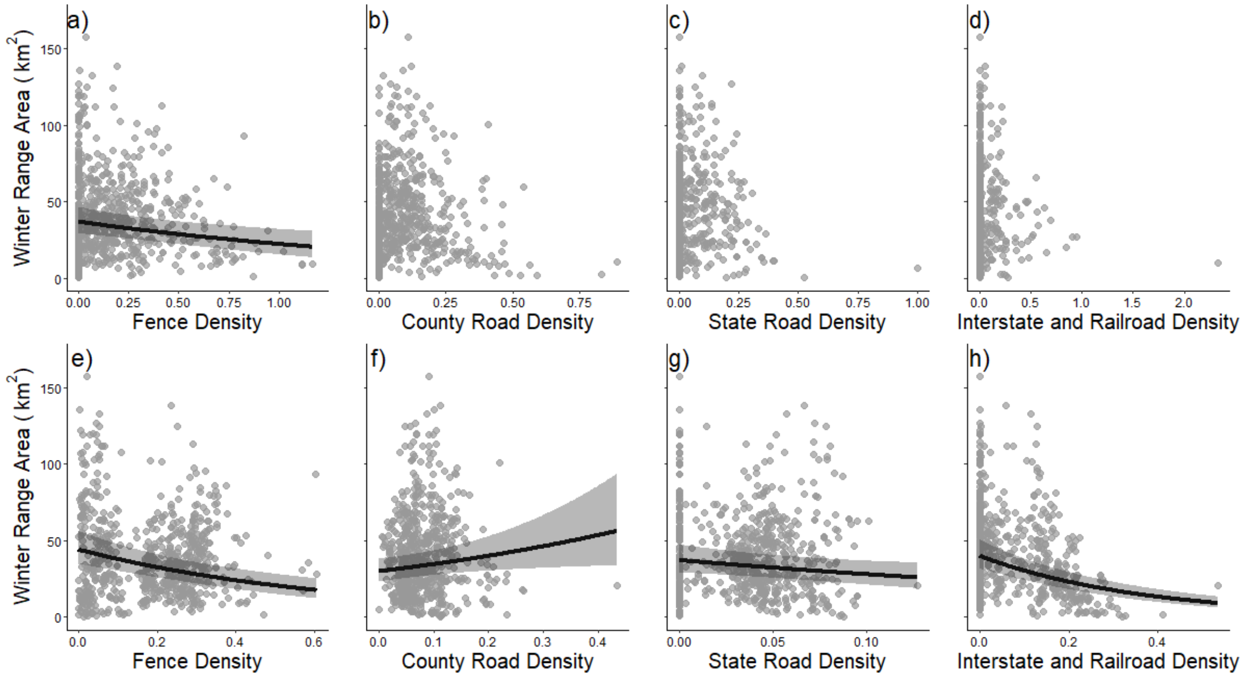
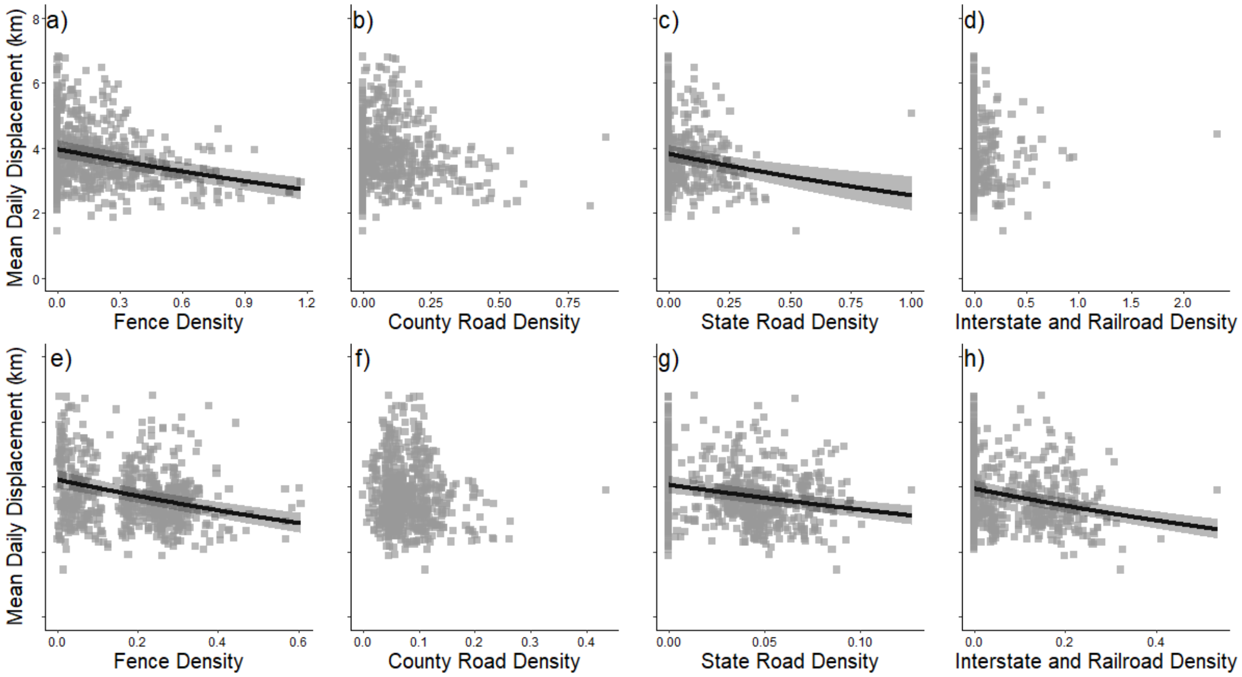


Figure 1.3. The effects of barriers on pronghorn winter range. Within core winter range, an increasing density of fences (a) decreased winter range area, but no effect was found for county roads (b), state roads (c), and interstate and railroads (d). Within exploratory winter range, increasing density of fences (e), state roads (g), and interstate and railroad (h) decreased pronghorn winter range area, but county roads (f) increased pronghorn winter range area, n = 682. Trend lines were only included for barriers with 95% confidence intervals that did not overlap with 0. Trend lines show the predicted effect of the given barrier with 95% confidence interval from a generalized linear mixed effect model, where all other variables were held at the mean for visualization. Density of barriers are in km/km^2.



a)
b)
c)
d)
e)
f)
g)
h)
Mean Daily Displacement (km)
0
2
4
6
8
Fence Density
0.0
0.3
0.6
0.9
1.2
County Road Density
0.00
0.25
0.50
0.75
State Road Density
0.00
0.25
0.50
0.75
1.00
Interstate and Railroad Density
0.0
0.5
1.0
1.5
2.0
Mean Daily Displacement (km)
Fence Density
0.0
0.2
0.4
0.6
County Road Density
0.0
0.1
0.2
0.3
0.4
State Road Density
0.00
0.05
0.10
Interstate and Railroad Density
0.0
0.2
0.4

Figure 1.4. The effects of barriers on pronghorn daily displacement while on winter range. Within core winter range, increasing density of fences (a), and state roads (c) lowered mean displacement, but the density of county roads (b) and interstate and railroads (d) did not have an effect on mean displacement. Within exploratory winter range, an increasing density of fences (e), state roads (g), and interstate and railroads (h) lowered mean displacement. Density of county roads (f) did not have an effect, n = 682. Trend lines were only included for barriers with 95% confidence intervals that did not overlap with 0. Trend line shows the predicted effect of the given barrier with 95% confidence interval from a generalized linear mixed effect model, where all other variables were held at the mean for visualization. Density of barriers are in km/km^2.

SUPPLEMENTARY MATERIALS

Table S1.1. Individual animal year random slopes relative to each movement barrier. The minimum and maximum odds ratios are the animal years with the lowest and highest random slopes across all pronghorn that encountered the given barrier (either a used or available step crossed the barrier).

Predictors	Minimum Odds Ratio	Maximum Odds Ratio	Number of Animal Years with Encounters
Fence	0.085	1.522	896
Railroad	0.014	0.958	358
County Road	0.207	2.016	911
State Road	0.004	1.073	629
Interstate	< 0.001	0.209	227

CHAPTER 2. Using Connectivity Models to Predict Historical Corridors Across a Nearly Impermeable Barrier

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ABSTRACT

Migrations can benefit wildlife populations by providing access to seasonal habitats, however the anthropogenic footprint is truncating wildlife movement. For species impacted by impermeable barriers, restoring lost movements can benefit wildlife populations. Wildlife crossing structures have been valuable to conserve wildlife movement, but rarely have they been implemented to restore movements lost to anthropogenic development. We studied pronghorn (*Antilocapra americana*) habitats and corridors in southern Wyoming, USA to predict the most likely locations of historical migration corridors prior to the development of Interstate 80 (I80), a nearly impermeable barrier to pronghorn movement. We used resource selection functions to assess components of pronghorn seasonal habitats (n = 704 animal years in summer and n = 679 in winter), first modeling winter and summer ranges for pronghorn unimpeded by I80 (summer n = 446 home range, n = 452 patch; winter n = 368 home range, n = 382 patch). Next, we applied a novel application of least-cost corridors to estimate pronghorn migrations (Sublette n = 29 autumn and n = 47 spring; Medicine Bow n = 57 autumn and n = 40 spring). We found that pronghorn impeded by I80 used lower quality habitat across the year than pronghorn unimpeded by I80. Our least-cost corridor models were more accurate than null models of connectivity, and were able to accurately predict held-out pronghorn corridors in the autumn. We simulated pronghorn corridors across I80 using 3000 pairings (between 30–300 km apart) of points sampled within high quality winter and summer range. Simulations of pronghorn historical corridors predicted the locations of pronghorn crossing locations from carcass data better than random, and were weakly correlated with locations of underpasses used by pronghorn. Our model predictions, along with empirical GPS data, all indicate that migration is a crucial behavior to survive on this landscape, yet I80 has severed movement and the ability of pronghorn to use high quality habitat. Our analysis provides an application of habitat use and connectivity modelling to retroactively assess where migrations could be restored with crossing structures.

INTRODUCTION

Animal movement is often tightly coupled to the dynamics of available resources (Mueller et al. 2011, Armstrong et al. 2016, Aikens et al. 2020b). Movement to access resources can promote large scale ecological processes such as migration that have cascading effects on ecosystems, including predator dynamics, nutrient input, and plant community composition (McNaughton 1976, Augustine and McNaughton 1998, Holdo et al. 2011). Migrating seasonally can benefit populations by minimizing exposure to costly conditions, such as excess snowfall (Cagnacci et al. 2011, Mysterud et al. 2011), while providing access to seasonal resources (Biebach et al. 1986, Sawyer and Kauffman 2011). Likewise, migration can lower competition with conspecifics on seasonal ranges (Grayson and Wilbur 2009, Chapman et al. 2011). In seasonal, predictable habitats, migration is often the optimal strategy to exploit dynamic resources

(Mueller et al. 2011), with migrants sometimes outnumbering resident counterparts by an order of magnitude (Fryxell et al. 1988).

Migration corridors enhance the connectivity in the surrounding landscape by linking seasonal habitats (Taylor et al. 1993), yet human development and resulting fragmentation are restricting animal movements by severing migration corridors (Schloss et al. 2012, Crooks et al. 2017). Migratory populations may be inhibited from optimally exploiting resources when these corridors are lost (Robinson et al. 2009, Tucker et al. 2018), which can lead to population crashes or growth of resident populations (Berger 2004, Harris et al. 2009). Moreover, the consequences of the loss of corridors has been exacerbated by the threat of climate change, which can inhibit animals from tracking key resources (Post and Forchhammer 2008, Aikens et al. 2020a). The conservation of animal movement has become a focus to sustain viable populations that must move through corridors to access seasonal habitats (Berger 2004, Noss and Daly 2006). The growing expansion of the anthropogenic footprint, coupled with climate change, have exacerbated the urgency of identifying where migration corridors remain and where they formerly occurred on the landscape.

By incorporating the restoration of movement into wildlife conservation, managers can improve access to seasonal ranges and enhance the long-term viability of populations (Baldwin et al. 2012). Empirical studies illustrate that given enough time lost migrations can be restored so long as corridors exist to facilitate movement. For example, between the Okavango Delta and Makgadikgadi grasslands in Botswana, plains zebra (*Equus burchelli a.*) reestablished migrations within four years of the removal of a veterinary cordon fence which had blocked the corridor for over three decades (Bartlam-Brooks et al. 2011, Bracis and Mueller 2017). Migratory behavior has also been restored in captive-bred whooping cranes (*Grus americana*), for which substantial learning (and active training) was required by released birds to restore migratory behavior and navigate their historical migration corridors (Mueller et al. 2013). Similarly, translocated bighorn sheep (*Ovis canadensis*) and moose (*Alces alces*) learned how to migrate after decades of occupying new landscapes, where potential corridors remained intact but the knowledge of how and where to migrate was lost due to translocation (Jesmer et al. 2018). Restoring migration is thus possible when corridors remain intact and animals have sufficient generational time to re-learn lost movements.

Wildlife crossing structures can restore movements through migration corridors severed by long-standing barriers (Clevenger and Waltho 2005, Sawyer et al. 2005). The implementation of crossing structures have mostly been to protect seasonal movements that intact populations still undergo, and such uses of crossing structures have been successful across a diversity of taxa ranging from brown bears (*Ursus arctos*) to squirrel gliders (*Petaurus norfolcensis*) (Clevenger and Waltho 2005, Berger et al. 2006, Soanes et al. 2018). Crossing structures have largely been motivated by the goal of minimizing road-related mortalities that pose a threat to the viability of mobile populations and their migrations. Nonetheless, the expansion of anthropogenic barriers (e.g., roads, railways, fences) have already severed the migration corridors of many taxa (Harris et al. 2009, Kauffman et al. 2018). Such crossing structures within historically lost corridors can provide population-level benefits by restoring currently inaccessible habitats. Crossing structures can not only protect existing movements but also restore movements lost from severe barriers.

When migrations are lost due to long-standing barriers, it is a distinct challenge to identify the best locations to restore movement because migration corridors and the location of crossing structures are best delineated using current GPS tracking data (Sawyer et al. 2009, Bastille-Rousseau et al. 2018). Additionally, for some species the location of suitable habitat (that animals will move through) can be more important to the use of crossing structure than their structural dimensions (Ng et al. 2004). It is thus critical that corridor restoration be informed by the distribution of suitable habitat, especially when such habitats may no longer be used due to severed movements. Moreover, the financial costs of designing and constructing crossing structures elevate the importance that managers locate crossing structures in the most optimal locations (Evink 2002). To restore seasonal migrations, the location of crossing structures will need to be grounded in an understanding of the landscape attributes that promote migration and the juxtaposition of seasonal ranges.

Given the mechanisms of how an animal moves through its surrounding landscape, connectivity can be quantified as the degree to which a landscape facilitates or impedes movement (i.e., functional connectivity; Taylor et al. 1993, Puth and Wilson 2001, Panzacchi et al. 2016). Because migration corridors are components of the landscape that facilitate movement (Noss 1991, Chetkiewicz et al. 2006), the location of corridors can be identified by the landscapes features that facilitate movement even when barriers sever migration. Thus, methods to quantify landscape connectivity hold potential to identify where historically important — but now lost — movements can be retroactively identified to guide restoration efforts.

Interstate 80 (I80), a transcontinental highway that runs east to west across the United States, was opened to traffic in Wyoming by 1970. In that time, the high traffic load, right-of-way fencing (usually 1.2 m in height; Goodwin and Ward 1976), and game-proof fencing (usually 2.4 m in height; Sawyer et al. 2012) have effectively severed long-distance movements of ungulates in southern Wyoming (Kauffman et al. 2018). Pronghorn (*Antilocapra americana*) rarely cross this nearly impermeable barrier (Chapter 1). Although enough pronghorn can cross to promote gene flow (Lacava et al. 2020), pronghorn as well as mule deer, moose, and elk have had their access to habitat severed due to this state-wide barrier (Kauffman et al. 2018). Along I80, one mule deer migration corridor is maintained only by a 61 m by 9 m by 4.5 m open span bridge underpass and associated game-proof fencing (Ward 1982, Plumb et al. 2003). Pronghorn, however, are averse to using underpasses (Plumb et al. 2003, Sawyer et al. 2016, Seidler et al. 2018), and the placement of existing underpasses largely fail to facilitate pronghorn movement across I80. During severe winters, when pronghorn make facultative movements to alternative ranges, I80 often inhibits access to critical habitat (Oakley and Riddle 1974, Deblinger and Alldredge 1984). The barrier effect of I80 could in part be mitigated through wildlife crossing structures such as wildlife overpasses (Clevenger and Waltho 2005). However, because pronghorn migrations are severed and individuals only rarely cross this barrier, predictive modelling is now needed to identify the optimal locations for crossing structures.

We sought to predict the most likely crossing locations for pronghorn across I80, given seasonal habitats and existing migratory patterns of pronghorn in southern Wyoming. We used a novel approach to develop connectivity models that assign the most likely estimates of movement costs as a function of landscape attributes to predict the probability of corridor use (Nuñez et al, *in prep*). By combining seasonal habitat predictions (at the home range and patch level of selection; Johnson 1980) with our connectivity models, we simulated the most probable locations of historical corridors used by pronghorn prior to the development of I80. We evaluated the accuracy of our predicted corridors using locations of pronghorn carcasses from attempted crossings as well as trail camera counts of pronghorn using underpasses. Our results provide a large-scale assessment of pronghorn seasonal habitat, connectivity, and the identification of crossing structures that may best restore migratory behavior across a nearly impermeable barrier.

METHODS

Study Area and GPS Data

We used a dataset of pronghorn GPS movements throughout southern Wyoming. We stratified our dataset by the population (n=7) in which each pronghorn (n=1028 animal years) spent the most time. The habitat characteristics of each population, as well as data cleaning of the subsampled GPS data, are described in Chapter 1. Our general approach was to model winter and summer range habitats, then to simulate migrations across the interstate with a rule-based connectivity model.

We visually identified migrations using net-squared displacement (NSD) plots for each animal year. To be classified as a migration, pronghorn NSD within a five-day window had to exceed 701 km^2, the squared diameter of the largest reported home range of a female pronghorn (O'Gara and Yoakum 2004). Because pronghorn can make non-migratory facultative movements (Jakes et al. 2018), we differentiated between seasonal migrations and facultative movements by the behavior of the pronghorn following the extended movement: instances where the movement was immediately followed by an asymptote within our NSD threshold were defined as a migration. Alternatively, if the extended movement did not asymptote within our threshold and continued progressing, or made a return trip, then such movements were considered facultative (Jakes et al. 2018). We only used migrations in our cost-distance analysis, because we sought to quantify the resistance to migratory corridors rather than facultative movements, which can be more analogous to dispersal (Poor et al. 2012, McClure et al. 2016). To avoid conflating stopover behavior with migration (Beier et al. 2008, Abrahms et al. 2017), we further filtered the migration GPS data by removing every subsequent GPS point within an individual migration that was within 1.5 km of the previous point. This threshold was visually verified. We removed seasonal migrations with less than 10 points, which resulted in losing n = 99 animal years. Due to low sample sizes, cost-distance analyses were only calculated on the Sublette (n = 29 animal year migrations in autumn, n = 47 animal year migrations in spring) and Medicine Bow populations (n = 57 animal year migrations in autumn, n = 40 animal year migrations in spring), and migrations from all other populations were used for cross-validation.

To calculate seasonal ranges, we removed all migrations and forays and defined summer as June through September, and winter as December through February. To estimate seasonal ranges, we used the 99% kernel density estimate of each pronghorn with a bivariate normal distribution. Individuals with a time gap in GPS fixes greater than 2 days within a season were estimated separately, before and after the gap, then combined. We only estimated seasonal ranges on pronghorn tracked for at least seven days in a given season. For resource selection analysis, GPS points were only used if they were within the respective animal year's seasonal range using the 99% contour. Additionally, to reduce pseudoreplication, GPS data were randomly sampled to one point per day for each animal year. This resulted in n = 704 animal years in the summer resource selection functions, and n = 679 animal years in the winter resource selection functions.

Resource Selection Functions

To estimate resource selection functions (RSFs), we used ten predictors known to influence pronghorn resource selection: slope, heat load, topographic position, density of rivers, sagebrush cover, herbaceous cover, annual cover, integrated Normalized Difference Vegetation Index (integrated NDVI), density of fences, and density of major highways. These predictors were used for both summer and winter RSFs with the exception of integrated NDVI, which was only used for the summer RSF. Slope, heat load index, and topographic position index were calculated from a digital elevation model, where topographic position index was classified using a 90 m moving window (Weiss 2001, McCune and Keon 2002). We retrieved shrubland fractional component data from the Multi-Resolution Land Characteristics Consortium database (Xian et al. 2015, Rigge et al. 2019, 2020). NDVI is an informative proxy of high quality forage and often underpins ungulate resource selection (Pettorelli et al. 2011). Integrated NDVI estimates the yearly sum of positive NDVI values within each pixel, which we averaged from 2002 to 2019 (Pettorelli et al. 2005). River data were available through the national hydrography dataset (USGS. 2015), filtered to all named rivers in Wyoming as well as the Blacks fork and the Hams fork rivers. Finally, we obtained fence data from the Wyoming Cooperative Fish and Wildlife Research Unit as well as the Wyoming Game and Fish Department and Bureau of Land Management, and highways were available through the Wyoming Department of Transportation. Any highway within 500 m of I80 was removed from the highways layer to avoid any habitat effect caused by I80. Prior to model fitting, we visually assessed whether any predictor was best explained by a quadratic effect. If a predictor appeared to have a quadratic effect, we compared model fit including a quadratic effect using AIC.

We sought to characterize the juxtaposition of winter and summer ranges across the I80 study area. Habitat selection is a spatially hierarchical process where different levels of selection can produce different definitions of habitat (Johnson 1980, Mayor et al. 2009). To account for the hierarchical process of habitat selection we estimated resource selection at the seasonal home range level and patch level, adapting methods used by Pitman et al (2017) and Zeller et al (2017), outlined below. For selection at the home range scale, we randomly sampled points within the 99% contour of each kernel density estimate as used points, and randomly sampled points within the population of that pronghorn as available (delineated by herd units created by the Wyoming Game and Fish Department). To avoid sample size bias between habitat levels, the number of used points for each animal year was equal to the number of GPS points used in the patch level resource selection analysis (see below). Available points were sampled within each population at a ratio of 1:1 to the number of used points within each population. Because wildlife often select for components of habitat at different scales (Wiens 1989, DeCesare et al. 2012), we buffered all points by eight radii (0.25 km, 0.50 km, 1.00 km, 3.00 km, 5.00 km, 7.50 km, 10.00 km, and 15.00 km) (Pitman et al. 2017). We extracted each predictor with each of the eight buffers, then fit a simple logistic regression to each predictor-buffer combination. We used corrected AIC (AICc) to select the optimal scale (buffer) of home range selection with a threshold of two AICc (Zeller et al. 2017). Multi-scale resource selection requires the assumption that there is an optimal scale of selection (DeCesare et al. 2012), so any predictor where the AICc values of each buffer were all within two, or where the lowest AICc was at the upper-bound buffer (15 km), was removed prior to model selection. Predictors for which there were multiple buffers within two AICc of one another (but not all eight) were assumed to both be optimal and their scale was averaged.

We likewise estimated resource selection at the patch level within home range. This level of selection was analogous to our methods to quantify home range selection, except at a finer extent and grain of analysis. We defined availability as the 99% contour of the kernel density estimate within each animal year. Within a use-available framework, we used GPS points within each seasonal range contour as the used points, and we sampled random points within each home range as available. We sampled available points at a ratio of 1:1 for the number of used points by each animal year. Points were buffered by eight radii (50 m, 100 m, 150 m, 200 m, 300 m, 500 m, 1000 m, and 1500 m). Any predictor where either every buffer was within 2 AICc of one another, or where the lowest AICc was the upper-bound cutoff (1500 m), was removed from further model fitting.

To estimate resource selection at both the home range and patch levels of selection, we used mixed effects conditional Poisson models with a large, fixed variance of 10^3 to avoid shrinkage of the intercepts towards the overall mean (Muff et al. 2020). We used a hierarchical random intercept structure with each animal year stratified by their respective population. We assigned a weight value of 1000 for available points and 1 for used points (Muff et al. 2020). To assess the predictive accuracy of each resource selection function, we used k-folds cross validation with three folds. We iterated 100 times a random sample where one-third of the animal years in the dataset were held out as testing data, then the rest of the dataset were used to refit the resource selection function (Boyce et al. 2002, Johnson et al. 2006). The refit resource selection function predicted habitat quality for the held-out pronghorn, where habitat quality was binned into 20 bins by percentile. We then compared the Spearman's rank correlations between predicted habitat quality (binned) and the number of GPS points within each habitat bin.

Effects of I80 on Pronghorn Resource Selection

To estimate whether I80 impedes pronghorn resource selection, we refit the resource selection functions at each level of selection, holding out pronghorn that moved within 15 km of I80. Thus, we estimated resource selection only for pronghorn unimpeded by the interstate highway at that level of selection (summer, n = 446 home range, n = 452 patch; winter, n = 368 home range, n = 382 patch). We assumed the optimal scale of selection (buffer size) for each predictor remained the same as from the full dataset analysis. We compared the three-fold cross-validations for each resource selection function of pronghorn unimpeded by the interstate to the held-out pronghorn. We used these resulting resource selection models of pronghorn unaffected by I80 to map pronghorn habitat in southern Wyoming. To estimate pronghorn seasonal range maps that combines home range level and patch level selection, we first used the optimal scale of selection from each model to resample each predictor. We then used the covariates from the resource selection function at each level to estimate home range and patch level habitat quality layers for summer and winter range. We normalized each prediction map so the values were between 0 and 1 by subtracting every value by the minimum predicted value, then dividing by the difference between the minimum and maximum predicted values. We multiplied the prediction maps between the home range and patch level maps for each season to emphasize the multi-level effect of habitat quality (DeCesare et al. 2012). We then renormalized the two resulting seasonal range prediction maps to be between 0 and 1. This gave us one overall habitat quality map for summer and one overall habitat quality map for winter range to characterize pronghorn habitat in the absence of I80.

To assess whether pronghorn near the interstate were using lower year-round habitat quality, we used prediction maps of habitat quality from pronghorn unimpeded by the interstate. We then converted the prediction map to 20 equal area bins using the quantiles of predicted habitat quality (Johnson et al. 2006). Because of differences in the number of pronghorn held-out at the home range and patch level, we only used pronghorn held-out at both levels of habitat selection for each season (n = 135). We extracted the mode of the seasonal habitat quality bin of each held-out pronghorn location for summer or winter range, depending on the date of the GPS location. We then associated whether or not the pronghorn interacted with the interstate by whether randomly sampled steps crossed I80. Random steps were sampled from a previous step-selection function, where 10 random steps were drawn for every used step with a maximum distance of 4741 m (Chapter 1). We considered any pronghorn with randomly sampled steps that crossed I80 as a pronghorn that was impeded by I80, and pronghorn within 15 km of I80 with no steps (used or sampled) that crossed I80 as not impeded by I80, thus the interaction with I80 was a binary covariate. Finally, to quantify whether pronghorn impeded by I80 are using lower quality habitat, we again estimated the Spearman's rank correlation between the number of GPS points within each habitat bin and the habitat bin, where a lower correlation indicates that pronghorn are using lower quality habitat than expected from the resource selection function.

Cost-Distance Models and Validations

To fit a cost-distance model to migration routes, we used six predictors we expected to be important to pronghorn migration corridors: slope, aspect, distance to roads, distance to rivers, sagebrush cover, and herbaceous cover. We used a decay function on the distance to roads and distance to rivers predictors ($1 - \exp^{-\alpha \times \text{distance}}$; Whittington et al. 2011). From preliminary cost-distance analysis from the Sublette population using five different values of alpha (–0.1, –0.01, –0.001, –0.0001, –0.0001), we selected based on AIC an alpha value of –0.001 as the decay transformation for both rivers and roads.

We fit cost-distance corridor models separately to the migration data for each of the two populations used to train the models (Sublette and Medicine Bow), for both spring and autumn migrations. We used maximum likelihood to estimate coefficients that translated environmental variables into cost-distance corridors, briefly outlined below (Nuñez et al, *in prep*). Conductance to migration was modeled as:

$$conductance = e^{\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n}$$

being the product of n environmental predictors $x_1 \dots x_n$ and conductance coefficients $\beta_1 \dots \beta_n$, where positive values of β imply that the predictor facilitates migratory movement and negative β values imply that the predictor inhibits migratory movement. Cost-distance is then calculated by dividing geographic distance by conductance to migration. For every migration track, we calculated a cost-distance corridor surface in two steps: first, we calculated two grids where every pixel is the minimum total cost-distance incurred to move there from the start point, and from the end point of a migration track. These two grids are averaged, then subtracted by the total cost-distance of the least-cost path (Dijkstra's algorithm, Dijkstra 1959) between the start and end points. This resulted in a grid of the normalized least-cost corridor D_t, where pixel values of D_t are the additional cost-distance incurred to move through that pixel relative to the least-cost path. We used the cost-distance values at each GPS point relative to the least cost path on the normalized least-cost corridor (D_t) to estimate an error distribution, analogous to residuals from the line of best fit in a regression.

$$D_{ti} = e^{\beta x} + \varepsilon, \quad \varepsilon \sim exponential(\lambda)$$

Where D_{ti} is the pixel-level additional cost distance relative to the least cost path for GPS point i for individual migration t, and λ is the rate parameter of an exponential distribution. With these parameters we could translate the cost-distance corridors into migration probability surfaces using an exponential distribution to estimate the pixel-level probability of observing a migratory GPS point. We estimated the likelihood of the migration data, given different candidate models of environmental predictors expected to influence pronghorn migration connectivity. Population-level coefficients for conductivity were estimated from a random slopes model. Starting with the full model of six predictors, we used backwards elimination by removing each predictor that had

95% confidence intervals overlapping zero in the full model and comparing the subsequent AIC. We selected the most parsimonious model as the lowest AIC with a threshold of two AIC. Additionally, we included a null model to compare, where the predictor was a raster of values randomly sampled from a normal distribution with mean of zero and a standard deviation of one.

To cross validate the accuracy of the cost-distance models, we used the best fitted models to predict migration probability surfaces from migrations excluded from modelling (pronghorn outside of the Sublette and Medicine Bow populations). We used two different cross-validations based off of McClure et al. (2016). First, we assessed whether the cost-distance model was more accurate than a null model with no environmental effects (i.e., a straight line), where the more accurate model should require less area to conserve movement. We predicted a migration probability surface for each individual migration and compared against a probability surface based on a straight line Euclidean model prediction, where the rate parameter was equal to the parameter from the compared model. We estimated area of each least-cost corridor that would encompass 95% of the GPS points by fitting splines to the percent of GPS points within each percentile of the predicted corridor. In our second cross-validation, we assessed whether the actual migration path was better predicted by our cost distance model than random paths, where if the cost distance model accurately predicts migrations then the accumulated cost of an actual migration track should be lower than the accumulated cost for a randomly sampled migration track. We randomly generated 99 paths for each migration by spinning the path around the centroid at a random angle (e.g., Cushman et al. 2010), we then jittered the x- and y-coordinates of each path by a random distance within 5 km. We then extracted the total cost given the cost surface predicted from our cost distance model across each migration track, buffered to 1 m. For each individual migration, we estimated the percentile of accumulated cost for the observed path compared to the distribution of accumulated cost for each available migration track.

Simulation across Interstate 80 and Validating Simulation Surface

We randomly sampled 3000 points within the upper 75th percentile of pronghorn winter range and summer range, given the seasonal range maps of pronghorn unimpeded by I80. We then randomly connected each winter range point with one summer range point on the other side of the interstate within a distance between 30 km and 300 km. These random pairings were the start and end points for the spring simulation; analogous autumn migration simulations were conducted with random pairings starting with summer range points and ending with winter range points. Upon running each of the 3000 least cost simulations, we took the sum across each corridor to get one connectivity layer. Because our simulation could have been biased towards points in the center of the study area, we divided the summed connectivity layer by a null connectivity layer, where each of the same 3000 individual start-end points were predicted against a flat cost-distance layer, then summed. Because there were likely more start-end pairs in the middle of our study area rather than on the periphery, dividing by a null model controlled for this spatial bias by normalizing the connectivity values to a null spatial prediction of expected connectivity just from arrangement of start-end points (McRae et al. 2016, Brennan et al. 2020, Jayadevan et al. 2020). Finally, we log transformed the resulting connectivity layer and converted the layer into 5 percentile bins so that the highest predicted connectivity were values between the 80th and 100th percentiles.

To cross validate our predicted surface of likely corridors across I80, we used pronghorn carcass data collected between 2009 and 2019 as well as camera trap data collected in 2018 and 2019. Carcass data were collected by the Wyoming Department of Transportation. We expected that if our simulated historical corridor surface accurately estimated pronghorn corridors, then the frequency of pronghorn attempted crossings (i.e., locations of carcasses) should be highest within our predicted corridors along I80. We removed all carcass points on the interstate east of Cheyenne, Wyoming because this was outside our study area, then we estimated attempted crossings as the daily presence of a pronghorn carcass at each mile post on I80. We then used a permutation test to assess whether the observed frequency of crossing locations within our connectivity model predictions was statistically significant. To do this, first we estimated the ratio of pronghorn crossing locations inside versus outside the highest connectivity bin (80th to 100th percentile) for autumn and spring maps. We then randomly sampled 3000 times an equal number of points along the interstate and compared the ratio of randomly distributed points inside versus outside the highest connectivity bin. We used the percentage of random iterations with a ratio greater than or equal to the observed ratio as an empirical estimate for a p-value (Collingridge 2013). Additionally, we assessed counts of pronghorn using underpasses along the interstate between October and December 2018 (autumn, n = 20) and March and June of 2019 (spring, n = 21). These underpasses were selected because they were span bridges with an opening to the sky in the middle; none were tunnels, had paved roads, or cattle guards at the entrance. For each season, we counted total pronghorn using these underpasses in either direction, where we used a time threshold of three minutes between pictures to identify unique crossing events. Within each crossing event, we counted the maximum number of individual pronghorn within a given picture. We then took the sum of the maximum number of individuals during a crossing event by camera for each season. We estimated whether there was a correlation between the total pronghorn counts for each season compared to the predicted connectivity bin using Spearman's rank correlation.

We did all analysis in program R (version 3.5.1 for estimating cost distance models, version 3.6.2 for all other analysis; R Core Team 2016). We calculated kernel density estimates from the package ‘adehabitatHR’ (Calenge 2006), Poisson conditional mixed effects models from the package ‘glmmTMB’ (Brooks et al. 2017), and cost distance calculations from the package ‘gdistance’ (van Etten 2018).

RESULTS

Overall, pronghorn habitat at the home range level was characterized by fewer covariates compared to the patch level. At both levels of resource selection, pronghorn avoided steep slopes across seasons, but pronghorn selected for ridges only in the summer (Table 2.1). Pronghorn selected for warmer locations at the home range level in both summer and winter and at the patch level in the winter, but selected for cooler locations at the patch level in the summer. Pronghorn habitat selection had a quadratic effect to integrated NDVI at the home range level in the summer as well as sagebrush cover at the home range level in the winter. Pronghorn only responded to the density of rivers in the winter, which was selected for at the home range level but avoided at the patch level of selection. In the summer, pronghorn selected for higher sagebrush cover at the home range level but avoided higher sagebrush cover at the patch level. Pronghorn selected for both higher herbaceous cover and annual vegetation cover at the patch level in the summer. In the winter, pronghorn avoided herbaceous cover and selected for annual cover at both levels. Pronghorn avoided the density of fences at the patch level in both summer and winter. Finally, pronghorn selected for a higher density of highways at the home range level in the summer, but avoided density of highways at the patch level in the winter (Table 2.1).

Using k-fold cross-validation to assess the accuracy of the full resource selection function models, holding out one-third of the animal years, Spearman's rank correlation for home range level habitat was 0.993 and 0.987 in the winter and summer, respectively. At the patch level, k-folds correlations were 0.945 and 0.822 for winter and summer, respectively. Upon refitting the resource selection functions only using pronghorn farther than 15 km from the interstate (Fig. 2.1), pronghorn near the interstate used high quality habitat across seasons at the home range level (Spearman's rank correlation of 0.982 for winter and 0.861 for summer home range habitat). Likewise, in the winter pronghorn near the interstate used high quality habitat at the patch level (Spearman's rank correlation of 0.940). However, in the summer pronghorn near the interstate used low quality habitat at the patch level (Spearman's rank correlation of -0.017). Further comparing the habitat use of pronghorn that ever came within the vicinity of the interstate, pronghorn impeded by the interstate (i.e., had a random step cross the interstate) used lower quality habitat across seasons compared to pronghorn also within 15 km of the interstate that were not impeded by the interstate (Welch's two-sample t-test with equal variances p-value = 0.0005 for winter habitat and 0.002 for summer habitat; Fig. 2.2). In an ad hoc test to evaluate if this trend was caused by poor quality habitat within the vicinity of I80 rather than the barrier effect itself, we randomly sampled 10000 points within 15 km and within 200 km of I80 and compared the quality of winter and summer habitat. We observed marginally higher quality habitat available near I80 compared to the larger landscape (Welch's two-sample t-test with unequal variances p-values < 0.0001for summer habitat and for winter habitat; Fig. S2.1), indicating that the lower quality habitat used by pronghorn impeded by I80 is more likely driven by the barrier effect on pronghorn movements rather than a confounding effect of the surrounding landscape.

Pronghorn migrations in Sublette and Medicine Bow were best explained by the full connectivity model with six predictors (Fig. 2.3, Fig. 2.4), as the AICs of the full model were lower than the next-lowest AIC models with a ΔAIC ranging from 6 (Medicine Bow in the spring) to 124 (Sublette in the spring). Likewise, the full models had substantially lower AIC compared to the null connectivity models with ΔAIC ranging from 717 (Sublette in the autumn) to 1375 (Sublette in the spring) (Table S2.1). Across seasons and populations, migrating pronghorn were inhibited both by higher slope and areas closer to rivers (Table S2.2). Pronghorn migrations in the Sublette population in autumn were facilitated in habitats closer to roads, but pronghorn in the Medicine Bow population were inhibited closer to roads in both the autumn and spring. Pronghorn autumn migrations were not affected by vegetation, but in the spring pronghorn were facilitated by sagebrush cover and inhibited by herbaceous cover. Cross-validating the connectivity models using held-out pronghorn migrations from other populations, pronghorn autumn migrations were significantly better predicted by each of the two connectivity models than by a null (straight line) model (paired t-test, p-value = 0.0006 using the Sublette model, and p-value = 0.0001 using the Medicine Bow model; Table 2.2). Autumn migration corridors from the least cost corridor models were between 133.310 km^2 and 343.970 km^2 more efficient at containing 95% of GPS points as the null corridors predicted from the null model, indicating that the least cost model is more predictive than a straight line null. In contrast, pronghorn spring migrations were not significantly better predicted compared to the null model (paired two sample t-test, p-value = 0.615 using the Sublette model, and p-value = 0.328 using the Medicine Bow model; Table 2.2). Pronghorn spring migrations used to cross validate were on average 20 km shorter than autumn migrations. In our second cross-validation, we compared the sum cost of the used migration track to 99 randomly sampled migration tracks. In the autumn, the percentiles for the cost of pronghorn migration tracks relative to the available costs were 0.031 (Sublette model) and 0.022 (Medicine Bow model). In the spring, the percentiles for the cost of pronghorn migration tracks relative to the available costs were 0.052 (Sublette model) and 0.073 (Medicine Bow model).

Using total pronghorn counts from camera traps set up in 20 underpasses in autumn (October to December, 2018) and 21 underpasses in spring (March to June, 2019), there were 5 underpasses within the highest predicted connectivity in the autumn and 5 underpasses within the highest predicted connectivity in the spring (Fig. 2.5). There was only a weak correlation between counts of pronghorn using underpasses and the predicted connectivity (Spearman's rank correlation = 0.087 in the autumn and 0.463 in the spring). Of pronghorn crossing locations between 2009 and 2019, for the autumn and spring connectivity layers there were significantly more pronghorn crossings within the highest predicted connectivity bin than expected by chance (Fig. 2.6, Fig. 2.7). No random iteration in the autumn, and only 1 iteration in the spring had a ratio greater than or equal to the observed ratio of crossing locations within versus outside our predicted connectivity surfaces (autumn p-value < 0.001, spring p-value < 0.001; Fig. 2.7).

DISCUSSION

The expansion of anthropogenic barriers are threatening migration corridors that remain intact, while the restoration of corridors can improve access to habitats by re-establishing migratory behavior. We used predictions from seasonal resource selection functions as well as cost-distance models to estimate the most likely locations of historical migration corridors in southern Wyoming prior to the development of Interstate 80. We found that winter ranges were confined to flat areas with intermediate sagebrush cover and warmer facing slopes and a higher density of rivers. Summer habitats were less flat, had higher herbaceous cover, and were in cooler areas. From our predicted map of habitat quality for pronghorn farther than 15 km from I80, summer ranges tended to be closer to the foothills of mountain ranges compared to winter ranges, which were closer to the center of our study area, characterized by lower elevation basins with nearby topographic features providing insulation. Intersecting our cost-distance model predictions with I80 indicated three overall corridor networks linking pronghorn seasonal ranges: i) east of Lyman, ii) north and south of Wamsutter, and iii) west of Laramie, Wyoming. Though few pronghorn used underpasses along I80, we observed a correlation (albeit weak) between predicted connectivity and underpass use in the spring. We also observed more pronghorn attempted crossings within our predicted connectivity corridors than expected by chance, indicating that pronghorn have been attempting to cross I80 at the locations identified by our corridor models. Our modeling approach thus accurately predicts the present-day movements of pronghorn across I80, which adds to our confidence that corridors delineated from this analysis can be used to inform locations for potential crossing structures to reconnect this core swath of pronghorn's current range.

Pronghorn selected seasonal ranges consistent with findings of previous studies, in particular, flat habitats with nearby topographic features offering some warmth and with intermediate levels of sagebrush cover. It has been well documented that pronghorn habitat is composed of flat mixed-grassland and shrubland habitat, with summer ranges often on plateaus or foothills along mountain ranges and winter ranges on lower elevation basins (Sundstrom 1969, Oakley and Riddle 1974, Deblinger and Alldredge 1984). In the winter, topographic features such as ridgelines can provide important cover from snow and wind (Guenzel 1988). That pronghorn in our study only selected ridgelines in the summer may have been because summer range in our study was more topographically variable compared to flatter winter ranges.

Pronghorn in our study selected for habitats with intermediate sagebrush cover, and selected summer ranges with higher herbaceous and annual cover than winter range habitats. We expected this seasonal variation in vegetation, because pronghorn switch from foraging on sagebrush in the winter to forbs in the summer (O'Gara and Yoakum 2004). Particularly in the winter, pronghorn habitat is characterized by sagebrush, because it offers forage above the snow level (Sundstrom 1969, Reinking et al. 2019). But pronghorn habitat also requires access to forbs and grasses, especially in the spring and summer when forbs become more abundant (Boccadori et al. 2008, Cain et al. 2017). That pronghorn avoided sagebrush at the summer patch level and selected annual and herbaceous cover indicates the dietary shift towards more available forbs in the summer.

We found evidence that pronghorn constrained by I80 used lower quality habitat compared to pronghorn unimpeded by I80 despite relatively higher quality available habitat along I80 compared to the larger landscape. This effect occurred for both pronghorn winter and summer habitats. There are three ways barriers can relegate wildlife to lower quality habitat: avoidance effects, semi-permeability effects, and density effects (Beyer et al. 2016). By reducing available area (avoidance) and increasing transit time between patches (semi-permeability), barriers can cause wildlife to use lower quality habitat than is otherwise available (Dyer et al. 2002, Beyer et al. 2016). Pronghorn did not seem to avoid I80, so the low permeability of I80 is more likely driving lower quality habitat use. Low permeability barriers inhibit crossing, thus effectively isolating habitats by increasing the time necessary to move between patches. Increasing the travel time to move between habitat patches (i.e., across I80) should cause pronghorn to spend more time at one patch along I80 than would otherwise be optimal (Charnov 1976). This effect has been observed of pronghorn on stopover habitat during migration, where pronghorn aggregate disproportionally on one side of roads within stopover because the barrier effect increases transit time to the other side (Seidler et al. 2014). In the third habitat effect, barriers can redistribute wildlife so that there is an increased density of wildlife at intermediate distances to barriers (Fortin et al. 2013). Higher densities of conspecifics can cause wildlife to select for lower quality habitat than would otherwise be ideal (Fretwell and Lucas 1970, Kie and Bowyer 1999, Mobæk et al. 2009). A higher density of pronghorn caused by I80 could alter habitat selection and force some pronghorn into lower quality habitat, as we observed in our study.

Our least cost path modeling indicated that pronghorn movements were facilitated by some habitat features and deterred by others — i.e., pronghorn corridors were neither straight lines nor random. Pronghorn corridors had low slope, were farther from rivers, and in the spring had high sagebrush cover and low herbaceous cover. That pronghorn corridors in our study were inhibited by herbaceous cover was likely a result of stopover behavior, which is partially driven by early spring phenology (Seidler et al. 2014, Jakes et al. 2018). Our results indicate that pronghorn corridors are mostly characterized by the features of the landscape that inhibit movement. In Alberta, Canada, pronghorn migration corridors follow V-shaped valleys, where rivers act as semi-permeable barriers that inhibit crossing (Gates et al. 2012). The one pronghorn migration corridor between the upper Green River basin and Grand Teton National Park, Wyoming, that has not been cut off by roads is delineated by mountain passes and two rivers (Berger et al. 2006). In Greater Yellowstone, pronghorn migrate through grassland-sagebrush corridors less than 300 m wide due to topography and high conifer forest cover constraining access to suitable habitat for movement (White et al. 2007). Thus, features of the landscape that inhibit pronghorn movement likely channel movement into corridors. The availability of pronghorn migration corridors likely results from whether intact habitats still exists when landscape elements such as barriers or topography inhibit or constrain movement.

That our spring connectivity model was less accurate than the autumn connectivity model was likely because the cross-validation spring migrations were shorter than the autumn migrations, and so potentially more analogous to a null straight line. Nonetheless pronghorn were likely responding to components of the landscape that we did not model. We did not include snow distribution or accumulation as a covariate of connectivity because it likely would have been a stochastic process more important to interannual variability in connectivity rather than long-term trends (i.e., snow would have been a nuisance variable). How far pronghorn migrate in the autumn and their winter distributions are often tightly coupled to winter severity (Bruns 1977, Hoskinson and Tester 1980, Barrett 1982, Deblinger and Alldredge 1984). For example, pronghorn in southeast Oregon, USA migrated farther and more directionally during a winter with higher snowfall (Collins 2016). Snow is energetically costly for pronghorn to move through (Telfer and Kelsall 1984), and the distribution of snow most likely can shape the migratory movements of pronghorn. Because we were interested in structural components of connectivity that do not vary between years, we did not include snow variables in our cost distance model. However, snowpack may have been correlated with proximity to roads, the only predictor in our cost distance model with different effects on pronghorn migration depending on population. Roads can create snow-free refuges on the leeward side and snowbanks on the windward side, both of which can influence habitat use by ungulates (Rost and Bailey 1979, Gates et al. 2012). Although we did not include any snow features to our model, the different effects of major highways on pronghorn migrations could have been a result of finer-scale effects of roads on snow. Likewise, the placement of roads can also covary with other features of the landscape, which could have contributed to connectivity.

Although few pronghorn use underpasses (Plumb et al. 2003, Sawyer et al. 2016, Seidler et al. 2018) , in our study they mostly did so in areas predicted by our model to have higher connectivity. Of the underpasses within the highest percentile of connectivity (five in autumn and five in spring), three had either completely or partially fenced entrances, which likely construed our crossing results. Heavily used wildlife crossing structures have been located within corridors predicted from cost distance models (Cushman et al. 2013). Even underpasses not designed, or located, for wildlife use can still be utilized by ungulates (Clevenger et al. 2001, Bhardwaj et al. 2020). Poorly located crossing structures can enhance energetic costs to migratory wildlife such as Tibetan antelope (*Pantholops hodgsonii*), which have to extend migrations by 86 km to access one railway underpass (Xu et al. 2019). Although the purpose of monitoring underpass use was to cross validate our connectivity model, pronghorn use of underpasses may be profitably combined with our model predictions to enhance movement across I80 (Plumb et al. 2003, Sawyer et al. 2016, Seidler et al. 2018). Viable pronghorn populations need to have access to movement between habitats (Barrett 1982). It would likely be a valuable management strategy to mitigate these fenced underpasses located within areas of high connectivity by raising the bottom-wire to permit pronghorn passage (Jones et al. 2018). Locations of carcasses and underpass crossings indicate that pronghorn are still attempting to access habitat on the other side of I80, but the barrier effect constrains the number of pronghorn and their success rate.

Pronghorn have used migration bottlenecks such as Trappers Point in western Wyoming for over 6000 years (Miller and Sanders 2000), and archeological evidence of pronghorn bonebeds and hunting traps in southwestern Wyoming (Fenner 2009, Kornfeld et al. 2010) further characterize the historical distribution of seasonal ranges and potential migration corridors. The seasonal ranges and historical corridors from our models, along with extant pronghorn migrations shown by our GPS data, indicate that migration was a common movement strategy across southern Wyoming prior to the construction of I80. This landscape inherently requires pronghorn to migrate, yet I80 is a nearly complete barrier to pronghorn movement. In Norway, migration corridors and winter ranges of reindeer (*Rangifer tarandus*) have been fragmented by anthropogenic barriers and development, causing the complete loss of some migrations (Skogland 1986, Vistnes et al. 2004, Panzacchi et al. 2013b). Archeological hunting sites have helped characterize historical migration corridors (Panzacchi et al. 2013a), and efforts to minimize anthropogenic disturbances have returned wild reindeer to historical distributions (Nellemann et al. 2010). Worldwide, wildlife are being truncated by anthropogenic disturbance (Tucker et al. 2018), which limits access to habitat and threatens the viability of populations (Van Moorter et al. 2020). Although conserving present-day migration corridors can deaccelerate this loss of movement, the global reduction in wildlife movement can be reversed by restoring migration corridors and redesigning anthropogenic landscapes to promote connectivity (Rosenzweig 2003, Baldwin et al. 2012).

Our analyses provides a promising application of connectivity and habitat selection to locate where crossing structures may facilitate the restoration of lost seasonal migrations. Restoration of lost migrations will benefit the productivity of ungulate herds, but any restoration of migratory behavior would likely take several generations to establish. For ungulates, knowledge of the landscape and its seasonal habitats underpins migratory behavior (Bracis and Mueller 2017, Jesmer et al. 2018, Merkle et al. 2019). Crossing structures can remove barriers and restore connectivity, but knowledge of those movement will likely have been lost in the memory of living animals. Any management actions to restore migration will thus need to leverage efforts to facilitate the learning of lost behavior (Mueller et al. 2013). Nonetheless, the restoration of migratory behavior can be a valuable management strategy to buffer wildlife populations from the consequences of climate change and anthropogenic fragmentation.

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CHAPTER 2 TABLES

Table 2.1. Resource selection function coefficients at the home range and patch level. Bolded coefficients were significant at the 95% confidence interval, squared coefficients had quadratic effects. In the winter models, n = 679 animal years. In the summer models, n = 704 animal years. Predictors with an optimal scale of 15,000 m at the home range level, or 1,500 m at the patch level, or where all scales were within two AICc, were excluded from model fitting at that level of selection.

	Home Range Selection			Patch Selection		
	Scale (m)	β	95% Confidence Interval	Scale (m)	β	95% Confidence Interval
Summer						
Slope	3000	**-1.244**	**(-1.268, -1.221)**	175	**-0.121**	**(-0.136, -0.106)**
Heat Load Index	10000	**31.266**	**(29.550, 32.982)**	1000	**-3.732**	**(-4.603, -2.861)**
TPI Valley	10000	**-0.330**	**(-0.368, -0.291)**	300	0.001	(-0.034, 0.037)
TPI Lower Slope	10000	-	-	300	-0.050	(-0.178, 0.078)
TPI Middle Slope	10000	-	-	300	0.195	(-0.098, 0.488)
TPI Upper Slope	10000	-	-	300	**0.278**	**(0.106, 0.449)**
TPI Ridge	10000	**1.462**	**(1.419, 1.506)**	300	**0.133**	**(0.097, 0.169)**
integrated NDVI	3000	**-0.152**^{2}	**(-0.162, -0.141)**	475	-	-
Density of Rivers	15000	-	-	125	-	-
Sagebrush Cover	250	**0.220**	**(0.210, 0.231)**	50	**-0.149**	**(-0.161, -0.137)**
Herbaceous Cover	250	-	-	50	**0.115**	**(0.099, 0.131)**
Annual Cover	250	-	-	50	**0.066**	**(0.053, 0.078)**
Density of Fences	15000	-	-	100	**-1.516**	**(-1.676, -1.357)**
Density of State Roads	10000	**3.620**	**(3.344, 3.895)**	75	-	-
Winter						
Slope	7500	**-1.279**	**(-1.304, -1.255)**	100	**-0.231**	**(-0.245, -0.217)**
Heat Load Index	10000	**40.781**	**(38.723, 42.840)**	825	**2.073**	**(1.276, 2.870)**
TPI Valley	-	-	-	500	**-0.159**	**(-0.196, -0.122)**
TPI Lower Slope	-	-	-	500	-0.090	(-0.415, 0.235)
TPI Middle Slope	-	-	-	500	0.176	(-0.631, 0.982)
TPI Upper Slope	-	-	-	500	-0.349	(-1.487, 0.790)
TPI Ridge	-	-	-	500	-0.018	(-0.057, 0.021)
Density of Rivers	10000	**4.052**	**(3.822, 4.283)**	300	**-0.402**	**(-0.481, -0.324)**
Sagebrush Cover	250	**-0.168**^{2}	**(-0.177, -0.158)**	50	**0.176**	**(0.165, 0.188)**
Herbaceous Cover	250	**-0.569**	**(-0.586, -0.552)**	50	**-0.086**	**(-0.100, -0.071)**
Annual Cover	250	**0.369**	**(0.360, 0.378)**	50	**0.118**	**(0.105, 0.130)**
Density of Fences	15000	-	-	1000	**-5.412**	**(-5.885, -4.939)**
Density of State Roads	15000	-	-	500	**-0.544**	**(-0.607, -0.481)**

Table 2.2. Cross-validation of the connectivity model using held-out pronghorn migrations. The average predicted area of competing connectivity models that would contain 95% of the GPS points of the pronghorn migration track were compared as validation. Null models had no landscape elements to predict connectivity, so were straight lines from the first and last point of a migration track. The least-cost surface was the full cost-distance model with six predictors.

Season	Model Training Herd	Surface Type	Average Area (km^2) of Corridor	n	p-value
Autumn					
	Sublette	Null	1450.287	30	< 0.001
		Least Cost Surface	1106.317		
	Medicine Bow	Null	1450.287	30	< 0.001
		Least Cost Surface	1316.977		
Spring					
	Sublette	Null	388.412	50	0.615
		Least Cost Surface	395.028		
	Medicine Bow	Null	388.501	50	0.328
		Least Cost Surface	377.885		

CHAPTER 2 FIGURES

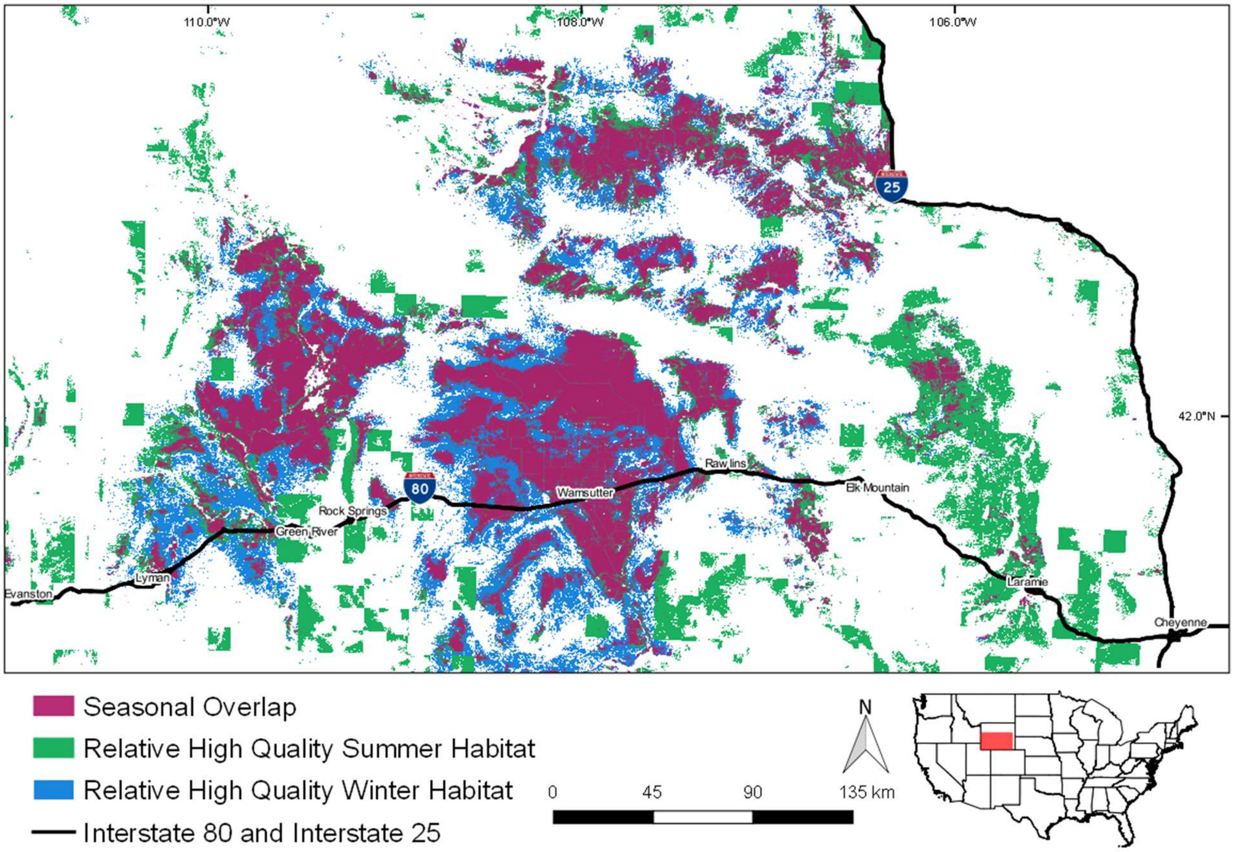

Figure 2.1. Modeled seasonal habitat of pronghorn in southern Wyoming, USA, north and south of Interstate 80. Predicted relative habitat quality greater than the 75th percentile from seasonal RSFs are shown for winter in blue and for summer in green, with overlap areas shown in magenta.

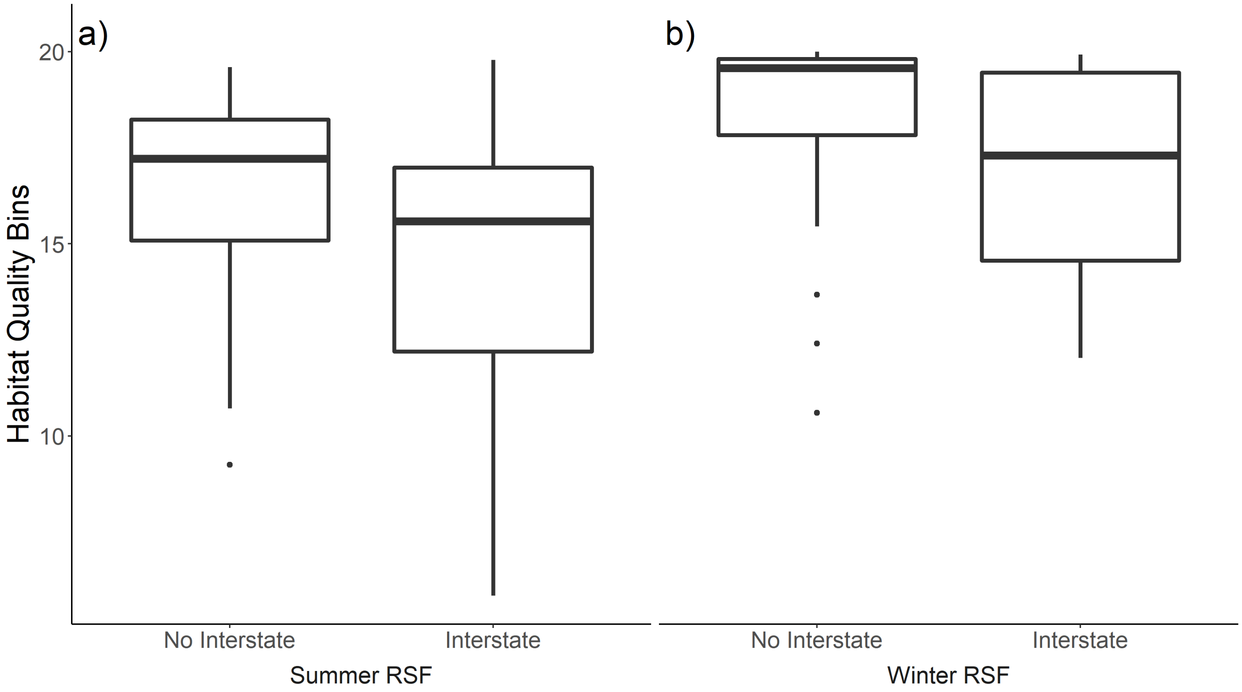

Figure 2.2. Pronghorn that interact with the I80 barrier experience lower habitat quality (converted to 20 equal area bins, 20 being highest quality) compared to animals that do not experience the barrier. Habitat quality for both summer (a) and winter (b) ranges were derived from a resource selection function that did not include animals potentially impeded by the I80. Interaction with I80 was determined by step lengths identified in Chapter 1, where the results of a step-selection function were used so that any randomly sampled step that crossed the interstate was considered as interacting with the interstate. Of pronghorn within 15 km of the interstate, n = 44 were not affected by the interstate, while n = 91 had a used or randomly sampled step that crossed the interstate.

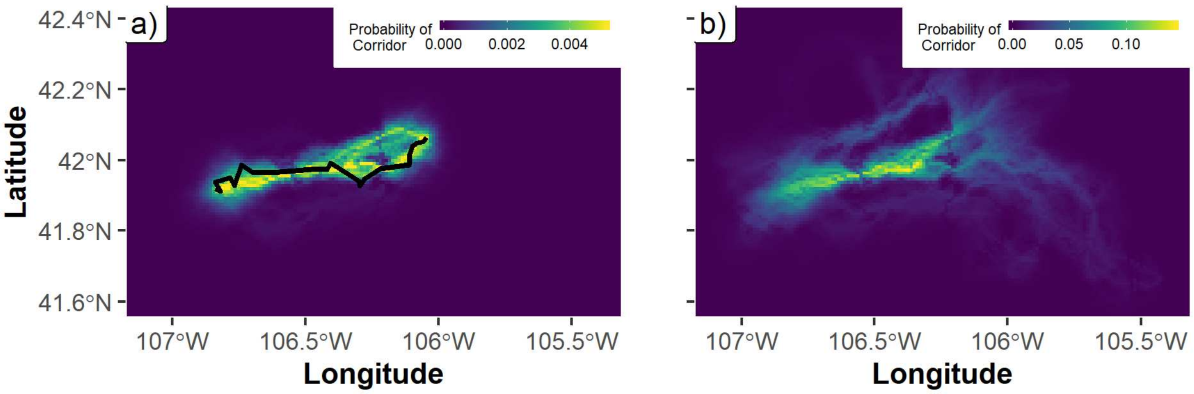

Figure 2.3. Predicted cost distance surface for one individual migration along with the empirical track (a, black line) and the sum predicted corridor for the Medicine Bow population (b) in the spring. This model was trained from n =40 spring migrations.

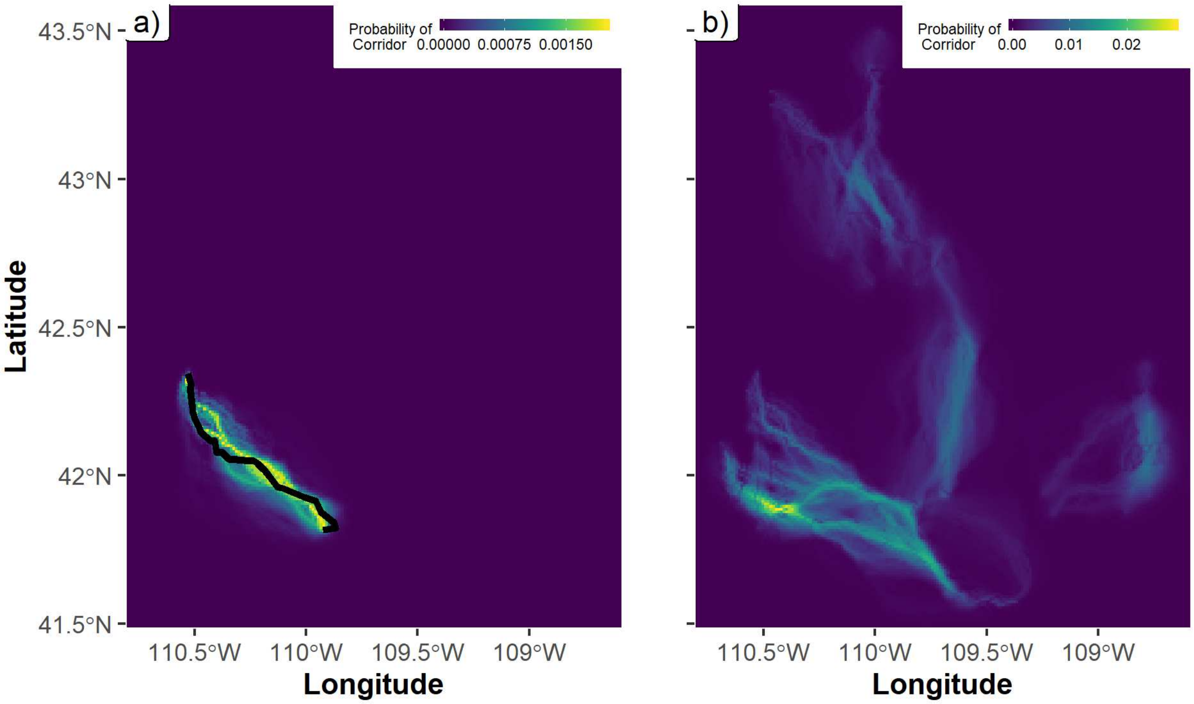

Figure 2.4. Predicted cost distance surface for one individual migration along with the empirical track (a, black line) and the sum predicted corridor for the Sublette population (b) in the spring. This model was trained from n = 47 spring migrations.

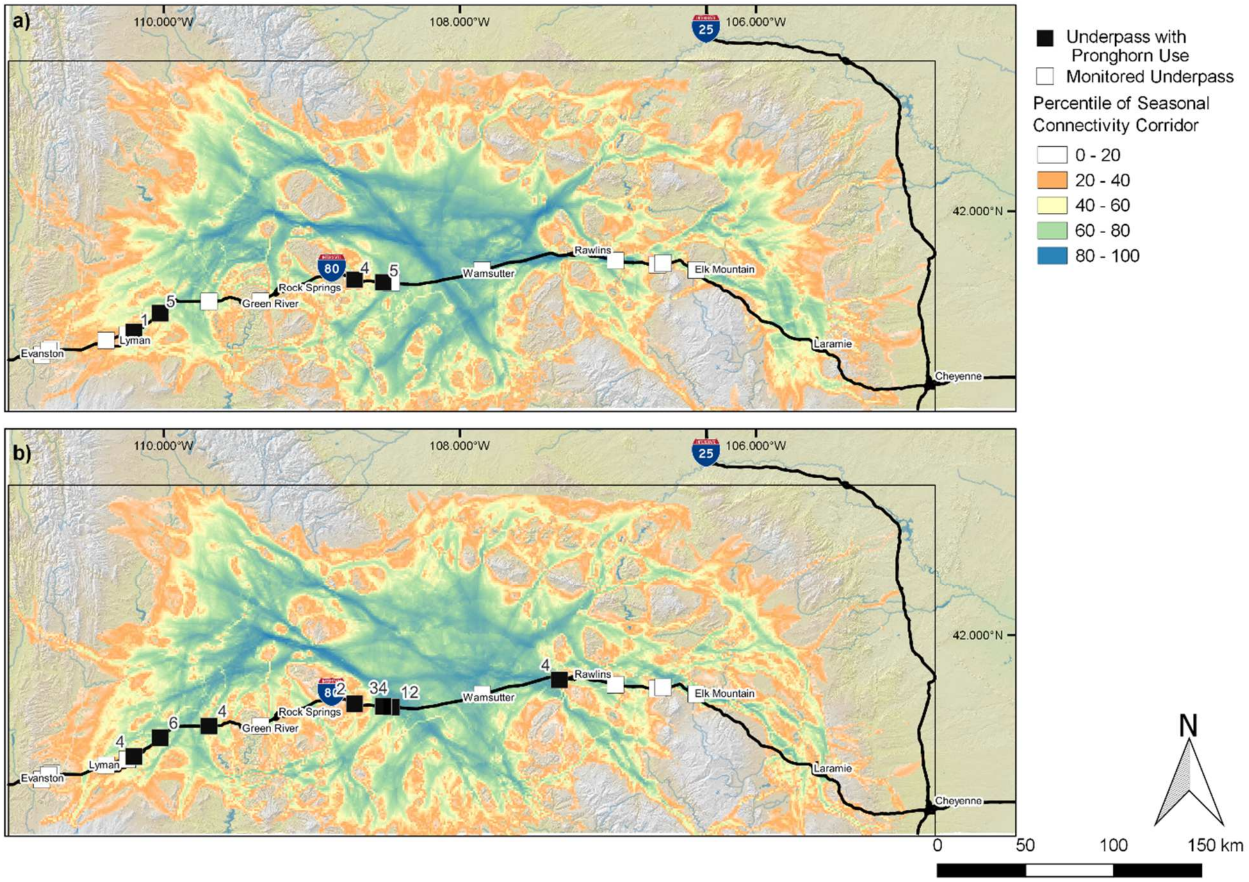

Figure 2.5. Predicted cost-distance corridors for pronghorn connecting seasonal ranges across Interstate 80 for autumn (a) and spring (b) migrations. Predicted connectivity values were converted to 5 bins by percentile, where the highest predicted connectivity is in dark blue. Black squares indicate locations of underpasses with pronghorn use, with the associated label indicating the total number of pronghorn crossings for that season (autumn 2018, spring 2019). White squares show locations of monitored underpasses with no use by pronghorn.

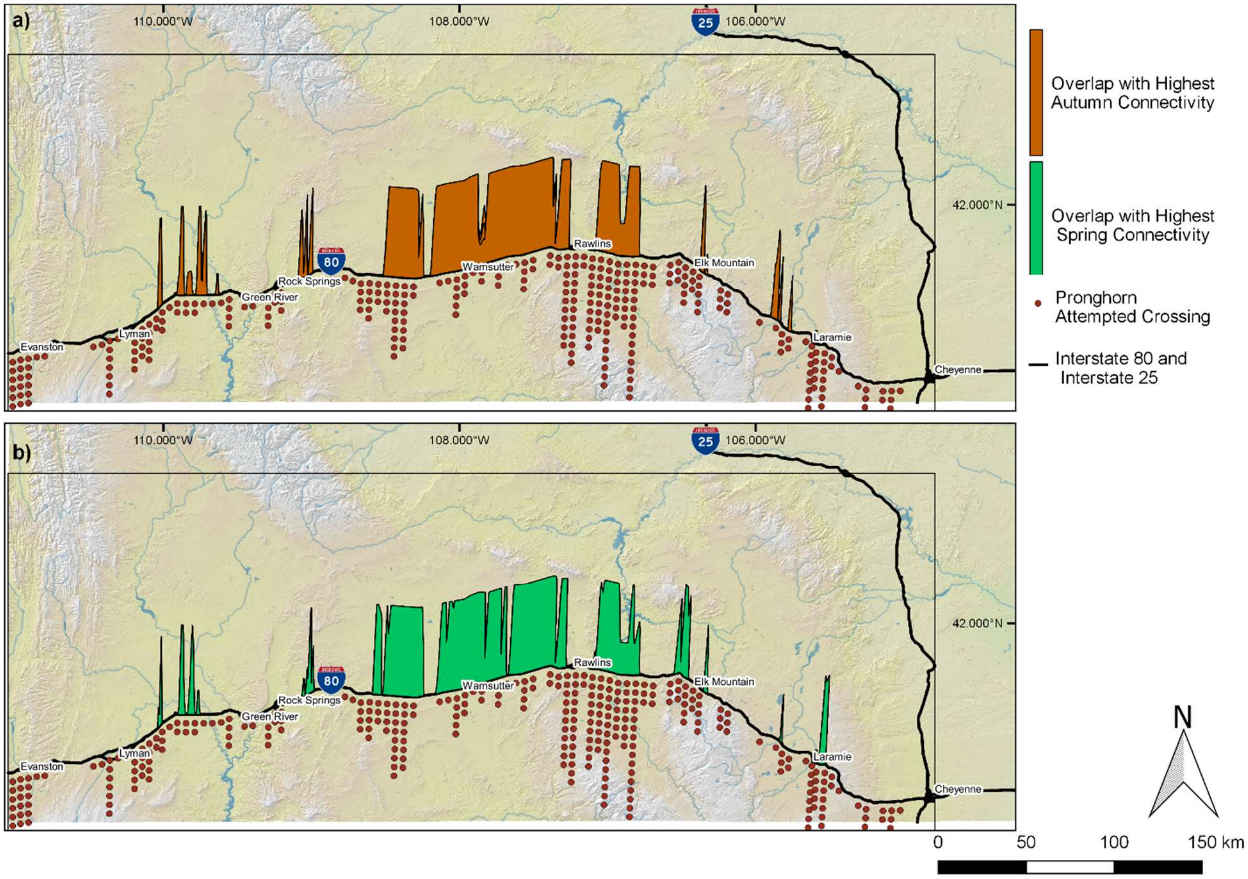

Figure 2.6. Sections along Interstate 80 that overlap with the highest predicted connectivity (80th to 100th percentile) from autumn (a, orange polygons) and spring (b, green polygons) models of cost-distance corridors. The height of the polygon is relative to amount of overlap with the connectivity surface (complete overlap has a height of 50 km from I80). Stacked red points indicate the frequency of pronghorn attempted crossings, measured from carcass data between 2009 and 2019 within a 5 km area.

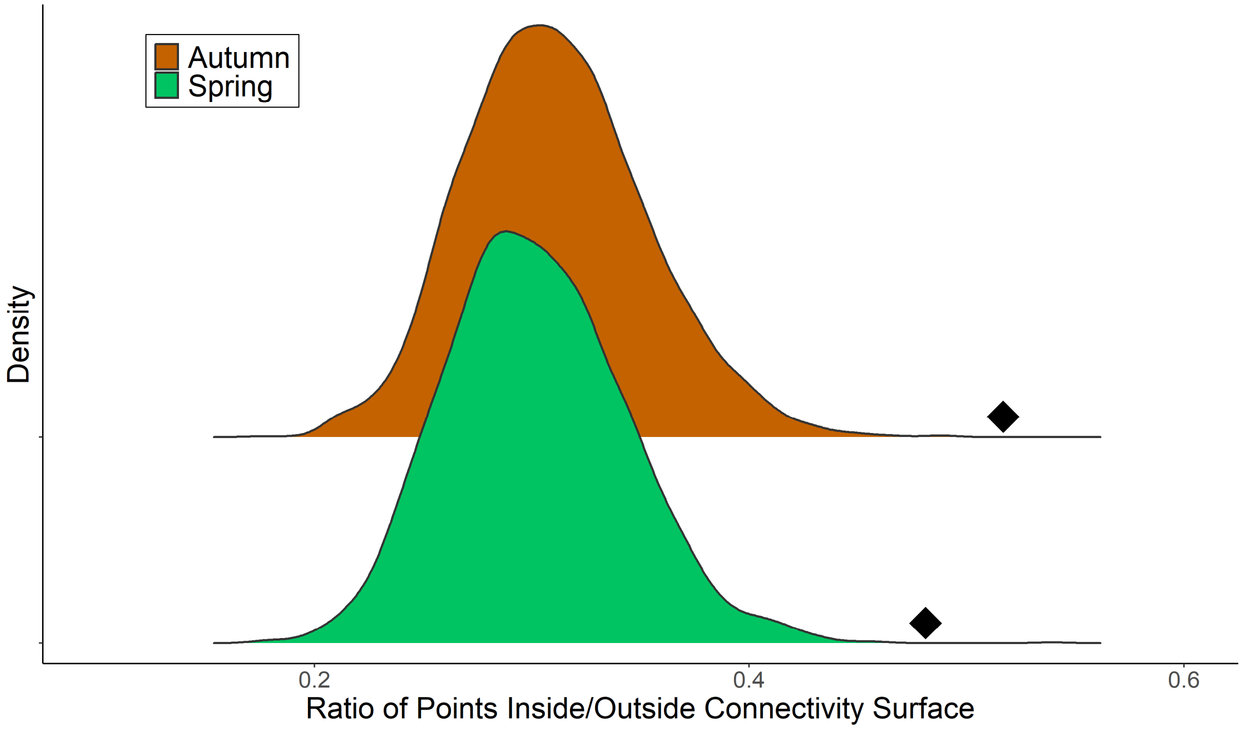

Figure 2.7. Distribution of randomly sampled ratios of pronghorn crossings observed inside versus outside predicted 80th to 100th percentile of connectivity surfaces. Diamonds indicate the observed ratio of pronghorn attempted crossings inside versus outside of each season connectivity surface. Each random sample had an equal number of points as the observed carcass points and were iterated 3000 times. Of the random distribution of crossings along I80, relative to the connectivity surface, 0/3000 and 1/3000 runs had a ratio greater than or equal to the observed ratio of crossings within the highest connectivity for autumn and spring respectively.

SUPPLEMENTARY MATERIALS

Table S2.1. AIC table of connectivity models compared with the 2nd lowest AIC model (drop one model selection), and the AIC of the null connectivity model with an uninformative predictor randomly sampled with a normal distribution. The value of ΔAIC is relative to the lowest AIC model for each season and population.

Population	Full Model	ΔAIC	2nd Model	ΔAIC	Null ΔAIC
Autumn					
Sublette	slope + aspect + distrivers + distroads + sage + herb	0	slope + aspect + distrivers + distroads + herb	53.737	717.816
Medicine Bow	slope + aspect + distrivers + distroads + sage + herb	0	slope + aspect + distrivers + distroads + herb	118.106	1121.581
Spring					
Sublette	slope + aspect + distrivers + distroads + sage + herb	0	slope + distrivers + distroads + sage + herb	124.463	1375.989
Medicine Bow	slope + aspect + distrivers + distroads + sage + herb	0	slope + distrivers + distroads + sage + herb	6.331	1195.489

Table S2.2. Beta coefficients of conductivity for the connectivity models of pronghorn migrations in the spring and autumn in Sublette and Medicine Bow herds. Bold coefficients were significant at the 95% confidence interval. Positive coefficients indicate facilitation of migratory connectivity, while negative coefficients indicate inhibition of migratory connectivity.

Season	Parameters	Sublette Coefficient	Confidence Interval	Medicine Bow Coefficient	Confidence Interval
Autumn					
	Slope	**-1.204**	**(-1.730, -0.678)**	**-0.618**	**(-0.770, -0.467)**
	Aspect	-0.019	(-0.146, 0.108)	0.043	(-0.029, 0.115)
	Distance to Rivers	**0.822**	**(0.507, 1.136)**	**0.601**	**(0.264, 0.938)**
	Distance to Roads	**-0.404**	**(-0.709, -0.099)**	**1.288**	**(1.041, 1.536)**
	Sagebrush Cover	0.075	(-0.171, 0.322)	-0.067	(-0.499, 0.364)
	Herbaceous Cover	-0.215	(-0.635, 0.204)	-0.231	(-0.521, 0.058)
Spring					
	Slope	**-0.820**	**(-1.124, -0.516)**	**-1.102**	**(-1.323, -0.882)**
	Aspect	-0.056	(-0.169, 0.057)	0.060	(-0.026, 0.145)
	Distance to Rivers	**0.814**	**(0.451, 1.176)**	**0.884**	**(0.570, 1.197)**
	Distance to Roads	-0.127	(-0.406, 0.151)	**1.603**	**(1.219, 1.986)**
	Sagebrush Cover	**0.371**	**(0.194, 0.548)**	**0.306**	**(0.057, 0.555)**
	Herbaceous Cover	**-0.455**	**(-0.796, -0.114)**	**-0.955**	**(-1.233, -0.678)**

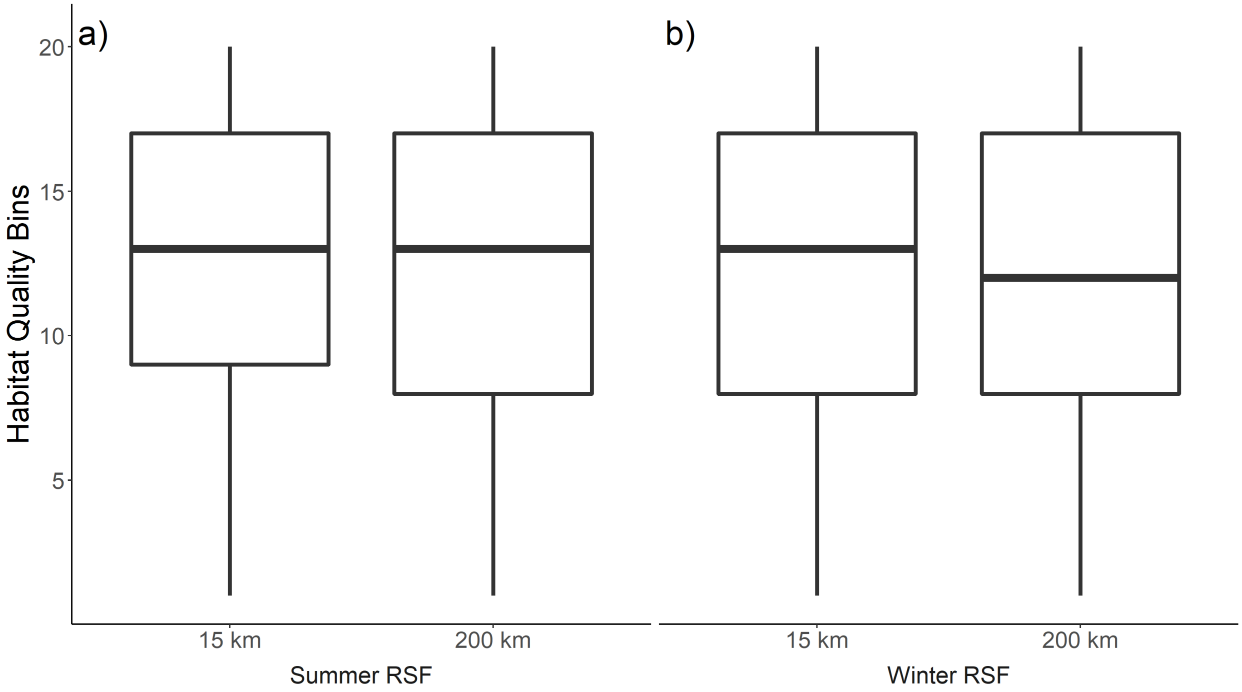
a)
b)
Habitat Quality Bins
20
15
10
5
15 km
200 km
Summer RSF
15 km
200 km
Winter RSF

Figure S2.1. Comparing the availability of habitat quality near the interstate (within 15 km) and the larger landscape (200 km from I80) by randomly sampling 10000 points, there is marginally higher quality summer (a) and winter (b) habitat near the interstate compared to the larger landscape. The y-axis are the equal area bins (20 being the highest quality habitat) from the multilevel resource selection function maps for summer and winter habitats.

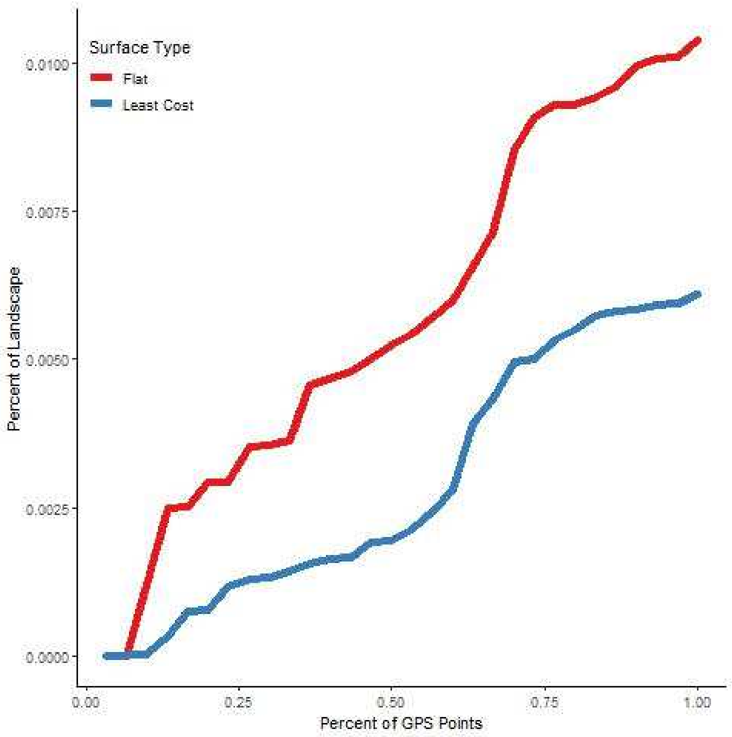

Figure S2.2. Cross-validation for one migration track between a cost distance model (blue line) against a null (straight line) model (red line). The lines indicate the percentage of actual GPS points of the given track relative to the predicted area of the landscape. For each migration track cross validation, we estimated the area of the landscape necessary to contain 95% of the GPS points by fitting a spline.

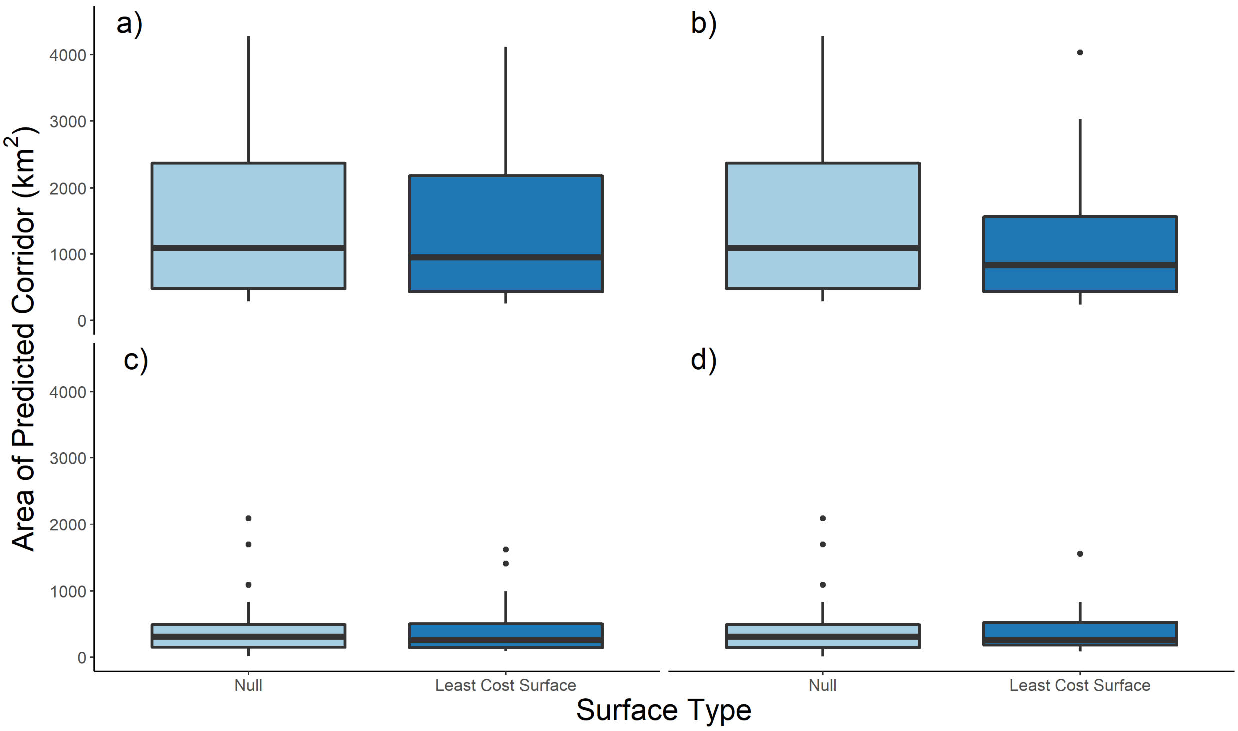

Figure S2.3. Comparison of area of predicted corridors that encompass 95% of cross-validation GPS points between a null (straight line) connectivity model and the cost distance models. Of autumn migrations, the least cost corridors from the Medicine Bow (a) and Sublette (b) models were more efficient at containing GPS points than the null models. Of spring migrations, the Medicine Bow (c) and Sublette (d) models were no more efficient at containing GPS points than the null models. In this cross-validation, n = 29 autumn migration tracks (a and b) and n = 43 spring migration tracks (c and d).

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